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The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses

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The relative importance of bay habitats, consisting of mangrove creeks and channel, seagrass beds, and mud and sand flats, as feeding grounds for a number of fish species was studied in Chwaka Bay, Zanzibar, Tanzania, using gut content analysis and stable isotope analysis of carbon and nitrogen. Gut content analysis revealed that within fish species almost the same food items were consumed regardless of the different habitats in which they were caught. Crustaceans (mainly copepods, crabs and shrimps) were the preferred food for most zoobenthivores and omnivores, while fishes and algae were the preferred food for piscivores and herbivores, respectively. The mean $\delta^{13}C$ values of fishes and food items from the mangrove habitats were significantly depleted to those from the seagrass habitats by 6·9 and 9·7‰ for fishes and food items, respectively, and to those from the mud and sand flats by 3·5 and 5·8‰, respectively. Fishes and food items from the mud and sand flats were significantly depleted as compared to those of the seagrass habitats by 3·4 and 3·9‰, for fishes and food, respectively. Similar to other studies done in different geographical locations, the importance of mangrove and seagrass themselves as a primary source of carbon to higher trophic levels is limited. The different bay habitats were all used as feeding grounds by different fish species. Individuals of the species *Gerres filamentosus*, *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma*, *Pelates quadrilineatus* and *Siganus sutor* appeared to show a connectivity with respect to feeding between different habitats by having $\delta^{13}C$ values which were in-between those of food items from two neighbouring habitats. This connectivity could be a result of either daily tidal migrations or recent ontogenetic migration.

Key words: feeding areas; habitat connectivity; juvenile fishes; mangroves; stable isotopes; seagrass beds.

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INTRODUCTION

Mangrove and seagrass habitats are often characterized by high densities of juvenile fishes and are therefore often referred to as nursery habitats (Robertson & Duke, 1987; Little *et al.*, 1988; Parrish, 1989), although little evidence has yet been provided for this (Beck *et al.*, 2001; Chittaro *et al.*, 2004). Protection against predation, a high food abundance and easy interception of planktonic fish larvae due to the large areas of the habitats are among the assumptions used in explaining the high abundances of juvenile reef fish species in these habitats (Parrish, 1989; Robertson & Blaber, 1992). Few studies have, however, tested these hypotheses (Laegdsgaard & Johnson, 2001; Cocheret de la Morinière *et al.*, 2004; Verweij *et al.*, 2006) in contrast to numerous studies that describe the fish assemblages of such habitats. The contradicting information about the functioning of these habitats (Chong *et al.*, 1990) creates a need to investigate several regions independently. As pointed out by Hartill *et al.* (2003), a better understanding is required of the resources used by different fish species and life stages, and of how important different habitats are in maintaining fish populations before management plans can be improved.

Mangrove and seagrass habitats are often interlinked through diurnal and tidal fish migrations (Rooker & Dennis, 1991; Vance *et al.*, 1996; Nagelkerken *et al.*, 2000; Dorenbosch *et al.*, 2004). Little is known, however, of the degree to which these habitats are used as feeding habitats (Nagelkerken & van der Velde, 2004). Conventional techniques such as gut content analysis may provide unreliable results with respect to the diet composition and the source of the food due to the following reasons: 1) differences in digestion rates of ingested material, 2) contents can be hard to identify, 3) not all contents are digested, 4) it provides just a snapshot of the true diet and 5) it does not show from where the food originates (MacDonald *et al.*, 1982; Gearing, 1991; Polis & Strong, 1996). Nonetheless, it proves to be the only means of establishing details of the types and amounts of prey taken (Sydeman *et al.*, 1997). Analysis of the stable isotopes of carbon and nitrogen can provide a clearer understanding of diets because they reflect the actual assimilation of organic matter into consumer tissue rather than merely its consumption, and provide an average of the diet over periods of weeks to months (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 (Bouillon *et al.*, 2002*a*). The stable isotopic composition of an animal reflects that of its diet with up to 1·0‰ enrichment in ^{13}C and an average of 3·5‰ enrichment in ^{15}N between a consumer and its food source (DeNiro & Epstein, 1978; Fry & Sherr, 1984; Minagawa & Wada, 1984) due to the discrimination against lighter isotopes during assimilatory and excretory functions within consumers (Minagawa & Wada, 1984). The actual degree of fractionation, however, varies as a function of taxonomy, food quality and environmental factors (Vanderklift & Ponsard, 2003).

The aim of the present study was to establish the relative importance of different bay habitats, namely, mangroves, seagrass beds, and mud and sand flats, as feeding areas for juveniles of a number of commercially important fish

species in Chwaka Bay, Zanzibar. The combination of gut analysis and stable isotope analysis was expected to provide information on both the type and relative amount of prey ingested and to reflect the sources of the food assimilated by different fish species over periods of weeks up to months. This study endeavoured to answer the following questions: 1) Is there a significant difference in stable isotopic signature (C and N) of fishes and food items in different bay habitats? 2) In which habitats do fishes eat and what do they consume? 3) To what degree does connectivity between habitats due to feeding by fishes exist?

MATERIALS AND METHODS

STUDY AREA

The study was carried out in Chwaka Bay, a shallow bay located on the east coast of Unguja Island, Zanzibar, Tanzania (Fig. 1). Chwaka Bay consists of a large intertidal flat partly covered with mixed assemblages of algae and seagrass beds with an average depth of 3·2 m, an estimated area of 50 km^2 at high spring tide and 20 km^2 at low spring tide, and a mean tidal range of 3·2 m (Cederlöf *et al.*, 1995; Mahongo, 1997). Chwaka Bay is protected from the high-energy ocean on the east coast by a reef system running along the coastline, as well as the Michamvi Peninsula (Fig. 1). On the landward side, the bay is fringed by a dense mangrove forest of *c.* 3000 ha (Mohammed *et al.*, 2001). The mangrove forest has a number of tidal creeks fringed by prop roots of the mangrove *Rhizophora mucronata* (Lamarck), with Mapopwe Creek (*c.* 2 m deep) being the largest and the main water exchange route between the forest and the bay. The mangrove creeks and the channel are intertidal in nature and none have any significant freshwater input other than rain. The sampled habitats were: mangrove creeks, mangrove channel, mud and sand flats, Chwaka seagrass beds (seagrass beds close to the mangroves) and Marumbi seagrass beds (seagrass beds far from mangroves) (Fig. 1). The sampled seagrass beds consisted of vast fields of *Enhalus acoroides* (L.)

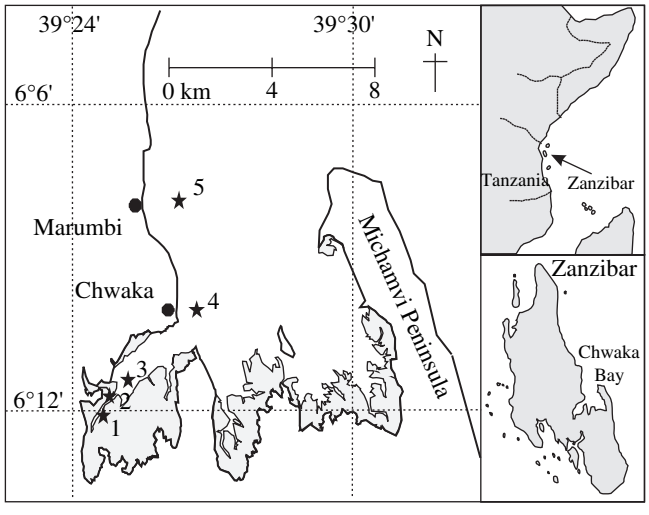

FIG. 1. Map of Unguja Island (Zanzibar) showing the location of Chwaka Bay and the sampled habitats (1, mangrove creeks; 2, mangrove channel; 3, mud and sand flats; 4, Chwaka seagrass beds; 5, Marumbi seagrass beds). Grey areas in Chwaka Bay indicate mangrove forests.

Royle interrupted by small patches of *Thalassodendron ciliatum* (Forsskål) den Hartog and the calcareous algae *Halimeda* spp.

SAMPLING DESIGN

Sample collections were carried out between November 2001 and October 2002. Fish samples were collected using a seine, while macrofauna and macroflora samples were collected by hand. Zooplankton samples were collected using a plankton net (80 μm mesh). In the field, samples were put in a cool box and later frozen at −20° C pending analysis. Fish species were selected in such a way that they represented commercially important fish species found abundantly (see Table I) in more than one bay habitat, and they included five feeding guilds: herbivores [*Siganus sutor* (Valenciennes)], insectivores [*Zenarchopterus dispar* (Valenciennes)], omnivores [*Monodactylus argenteus* (L.)], piscivores [*Sphyraena barracuda* (Walbaum)] and zoobenthivores [*Gerres filamentosus* Cuvier, *Gerres oyena* (Forsskål), *Lethrinus lentjan* (Lacepède), *Lutjanus fulviflamma* (Forsskål) and *Pelates quadrilineatus* (Bloch)]. Fish guild membership was assigned using Smith & Heemstra (1991), Khalaf & Kochzius (2002) and Froese & Pauly (2004), which were also used as a guide for the sampling of potential food items for each fish species. Detailed information on the environmental variables and the fish community structure (and their temporal variation) of Chwaka Bay can be found in other studies (Lugendo *et al.*, 2005, in press; B. R. Lugendo, I. Nagelkerken, N. S. Jiddawi, G. van der Velde and Y. D. Mgaya, unpubl. data).

STABLE ISOTOPE ANALYSIS

Muscle tissues were removed from the fishes, while molluscs (gastropods and bivalves) and crustaceans (crabs and shrimps) were dissected from their exoskeleton or shells prior to drying. The zooplankton samples were cleaned from detritus, sediments and other materials, under a dissecting microscope. Samples were dried at 70° C for 48 h and ground to powder (homogeneous mixture). For samples rich in carbonates such as detritus and whole individuals of small hermit crabs, sub-samples were acid-washed and oven-dried. These sub-samples were used for stable carbon isotope analysis only, while the remaining untreated sub-samples were used for stable nitrogen isotope analysis since acid-washing interferes with stable nitrogen isotopes (Pinnegar & Polunin, 1999). Samples were placed in ultra-pure tin capsules and combusted in a Carlo Erba® NA 1500 elemental analyser coupled on-line *via* a Finnigan Conflo III interface with a ThermoFinnigan DeltaPlus mass spectrometer. Carbon and nitrogen isotope ratios are expressed in the delta notation ($\delta^{13}C$ and $\delta^{15}N$) relative to Vienna PDB and atmospheric nitrogen. The potential food items and possible feeding habitat for fishes were determined in view of the enrichment in isotope signatures of 1 and 3·5‰, for carbon and nitrogen, respectively, between fishes and their potential food items (DeNiro & Epstein, 1978; Minagawa & Wada, 1984). The term 'macroinvertebrate' is used in the figures to denote zoobenthos and insects together, while the term 'zoobenthos' whenever used in the figures excludes the insects.

GUT CONTENT ANALYSIS

For fishes, fork length (L_F) was measured to the nearest 0·1 cm, and the entire gut extracted and frozen pending analysis. The gut was then split, the gut contents placed in a Petri dish under a dissecting microscope and food items were identified to the lowest taxa possible. The percentage of the total stomach volume that each food category comprised was determined using the point method (Hyslop, 1980) in which the food items in each fish gut was allotted a number of points depending on its abundance and size of an organism (*i.e.* one large organism counted as much as a large number of small ones). The points and the percentages they represented were 5 (75–100%), 4 (50–75%), 3 (25–50%), 2 (5–25%) and 1 (up to 5%). All the points gained by each

TABLE I. Stable carbon and nitrogen isotope signatures (mean ± S.E.) of different fork length (L_F) classes of fish species in different bay habitats. The overall mean $\delta^{13}C$ is also shown where more than one size class of fish species was present in a habitat. Relative abundance and relative biomass for each species in each bay habitat are also given. Numbers in bold print show relative proportions of each species for the whole bay. Different superscript lowercase letters and numbers represent statistical *post hoc* results and denote significantly different ($P < 0{\cdot}05$) stable carbon isotope values of a fish species for similar L_F classes and for overall $\delta^{13}C$ among different bay habitats

Species	L_F class (cm)	N	$\delta^{13}C$	$\delta^{15}N$	Species	Overall mean $\delta^{13}C$	Relative abundance (%)	Relative biomass (%)
Gerres filamentosus					*Gerres filamentosus*		**7·5**	**3·6**
Mangrove creeks	0–5	2	−21·3 ± 0·3	8·3 ± 0·1	Mangrove creeks	$-21{\cdot}2 \pm 0{\cdot}4^{a}$	9·6	5·8
Mangrove creeks	5–10	3	$-21{\cdot}1 \pm 0{\cdot}5^{a}$	8·0 ± 0·1	Mangrove channel	$-21{\cdot}6 \pm 0{\cdot}5^{a}$	24·3	17·0
Mangrove channel	5–10	5	$-21{\cdot}6 \pm 0{\cdot}5^{a}$	8·4 ± 0·1	Mud and sand flats	$-19{\cdot}2 \pm 1{\cdot}0^{a}$	0·8	1·1
Mud and sand flats	5–10	4	$-19{\cdot}2 \pm 1{\cdot}0^{a}$	8·0 ± 0·2				
Gerres oyena					*Gerres oyena*		**22·6**	**21·2**
Mangrove creeks	5–10	10	$-19{\cdot}4 \pm 0{\cdot}3^{a}$	7·5 ± 0·2	Mangrove creeks		7·1	7·1
Mangrove channel	5–10	10	$-17{\cdot}0 \pm 0{\cdot}7^{b}$	7·4 ± 0·1	Mangrove channel		25·6	35·0
Mud and sand flats	5–10	10	$-13{\cdot}8 \pm 0{\cdot}3^{c}$	6·6 ± 0·2	Mud and sand flats		62·6	56·2
Chwaka seagrass beds	5–10	10	$-12{\cdot}8 \pm 0{\cdot}7^{c}$	7·5 ± 0·1	Chwaka seagrass beds		37·6	38·8
Lethrinus lentjan					*Lethrinus lentjan*		**2·7**	**1·6**
Mangrove channel	5–10	10	$-21{\cdot}8 \pm 0{\cdot}3^{a}$	8·0 ± 0·1	Mangrove channel	$-21{\cdot}8 \pm 0{\cdot}3^{a}$	2·4	1·2
Mud and sand flats	5–10	9	$-19{\cdot}3 \pm 0{\cdot}7^{b}$	6·8 ± 0·2	Mud and sand flats	$-19{\cdot}3 \pm 0{\cdot}7^{b}$	6·8	3·4
Chwaka seagrass beds	5–10	10	$-12{\cdot}3 \pm 0{\cdot}2^{c}$	8·0 ± 0·1	Chwaka seagrass beds	$-12{\cdot}3 \pm 0{\cdot}2^{c}$	3·9	3·0
Marumbi seagrass beds	5–10	4	$-12{\cdot}4 \pm 0{\cdot}6^{c}$	8·3 ± 0·2	Marumbi seagrass beds	$-12{\cdot}0 \pm 0{\cdot}4^{c}$	1·7	1·1
Marumbi seagrass beds	10–15	2	−11·6 ± 0·1	8·3 ± 0·0				
Lutjanus fulviflamma					*Lutjanus fulviflamma*		**2·0**	**3·3**
Mangrove channel	5–10	4	$-21{\cdot}0 \pm 0{\cdot}2^{1}$	8·5 ± 0·1	Mangrove creeks	$-20{\cdot}1 \pm 0{\cdot}9^{a}$	0·8	2·0
Chwaka seagrass beds	5–10	4	$-15{\cdot}2 \pm 0{\cdot}7^{2}$	8·0 ± 0·2	Mangrove channel	$-21{\cdot}8 \pm 0{\cdot}1^{a}$	1·4	2·1
Mangrove creeks	10–15	3	$-20{\cdot}1 \pm 0{\cdot}9^{ab}$	8·6 ± 0·4	Mud and sand flats	$-15{\cdot}2 \pm 0{\cdot}5^{b}$	3·8	5·6
Mangrove channel	10–15	2	$-22{\cdot}6 \pm 0{\cdot}0^{a}$	9·2 ± 0·0				
Mud and sand flats	10–15	5	$-15{\cdot}2 \pm 0{\cdot}5^{c}$	7·6 ± 0·2				

TABLE I. Continued

Species	L_F class (cm)	N	$\delta^{13}C$	$\delta^{15}N$	Species	Overall mean $\delta^{13}C$	Relative abundance (%)	Relative biomass (%)
Chwaka seagrass beds	10–15	2	$-14{\cdot}2 \pm 0{\cdot}0^{bc}$	$9{\cdot}0 \pm 0{\cdot}2$	Chwaka seagrass beds	$-14{\cdot}5 \pm 0{\cdot}4^{b}$	5·2	8·2
Marumbi seagrass beds	10–15	4	$-11{\cdot}2 \pm 0{\cdot}4^{d}$	$9{\cdot}0 \pm 0{\cdot}1$	Marumbi seagrass beds	$-11{\cdot}2 \pm 0{\cdot}4^{c}$	0·3	0·4
Monodactylus argenteus					*Monodactylus argenteus*		**3·1**	**1·2**
Mangrove creeks	0–5	11	$-22{\cdot}1 \pm 0{\cdot}2^{a}$	$8{\cdot}0 \pm 0{\cdot}1$	Mangrove creeks		5·5	2·8
Mangrove channel	5–10	3	$-24{\cdot}0 \pm 0{\cdot}6^{b}$	$8{\cdot}4 \pm 0{\cdot}4$	Mangrove channel		5·5	3·8
Pelates quadrilineatus					*Pelates quadrilineatus*		**2·5**	**2·4**
Mud and sand flats	5–10	9	$-17{\cdot}1 \pm 0{\cdot}1^{a}$	$7{\cdot}2 \pm 0{\cdot}1$	Mud and sand flats		2·9	1·9
Chwaka seagrass beds	5–10	10	$-16{\cdot}2 \pm 0{\cdot}4^{b}$	$7{\cdot}8 \pm 0{\cdot}2$	Chwaka seagrass beds		12·3	10·8
Siganus sutor					*Siganus sutor*		**1·6**	**3·6**
Mud and sand flats	5–10	7	$-22{\cdot}8 \pm 0{\cdot}5^{a}$	$5{\cdot}6 \pm 0{\cdot}3$	Mud and sand flats	$-22{\cdot}8 \pm 0{\cdot}5^{a}$	1·3	1·2
Chwaka seagrass beds	5–10	4	$-20{\cdot}7 \pm 0{\cdot}8^{a}$	$7{\cdot}0 \pm 0{\cdot}2$	Chwaka seagrass beds	$-19{\cdot}5 \pm 0{\cdot}7^{b}$	2·8	2·0
Marumbi seagrass beds	5–10	4	$-15{\cdot}5 \pm 0{\cdot}7^{b}$	$6{\cdot}7 \pm 0{\cdot}3$	Marumbi seagrass beds	$-16{\cdot}1 \pm 0{\cdot}5^{c}$	7·4	11·4
Chwaka seagrass beds	10–15	1	$-15{\cdot}4$	6·1				
Marumbi seagrass beds	10–15	11	$-16{\cdot}2 \pm 0{\cdot}6$	$6{\cdot}5 \pm 0{\cdot}1$				
Marumbi seagrass beds	15–20	11	$-16{\cdot}5 \pm 0{\cdot}2$	$6{\cdot}3 \pm 0{\cdot}1$				
Sphyraena barracuda					*Sphyraena barracuda*		**0·9**	**3·8**
Mangrove creeks	10–15	2	$-20{\cdot}6 \pm 1{\cdot}0^{1}$	$9{\cdot}2 \pm 0{\cdot}0$	Mangrove creeks	$-20{\cdot}6 \pm 1{\cdot}0^{a}$	0·9	3·1
Mangrove channel	10–15	5	$-19{\cdot}9 \pm 0{\cdot}5^{1}$	$9{\cdot}8 \pm 0{\cdot}1$	Mangrove channel	$-19{\cdot}9 \pm 0{\cdot}5^{a}$	1·1	4·5
Mud and sand flats	15–20	5	$-15{\cdot}7 \pm 0{\cdot}2$	$8{\cdot}5 \pm 0{\cdot}2$	Mud and flats	$-15{\cdot}9 \pm 0{\cdot}4^{b}$	1·5	7·2
Mud and sand flats	20–25	2	$-16{\cdot}1 \pm 0{\cdot}5^{a}$	$8{\cdot}2 \pm 0{\cdot}4$	Chwaka seagrass beds	$-14{\cdot}6 \pm 1{\cdot}8^{b}$	0·7	5·9
Chwaka seagrass beds	20–25	2	$-14{\cdot}6 \pm 1{\cdot}8^{a}$	$9{\cdot}1 \pm 0{\cdot}6$				
Zenarchopterus dispar					*Zenarchopterus dispar*		**3·9**	**4·8**
Mangrove creeks	10–15	9	$-22{\cdot}8 \pm 0{\cdot}1^{a}$	$8{\cdot}1 \pm 0{\cdot}1$	Mangrove creeks		8·2	14·6
Mangrove channel	10–15	9	$-22{\cdot}7 \pm 0{\cdot}1^{a}$	$8{\cdot}2 \pm 0{\cdot}1$	Mangrove channel		2·9	4·9

N, sample size.

food item were scaled down to percentages, to give percentage composition of each food item in a diet of individual fish species examined.

STATISTICAL ANALYSIS

Each bay habitat was treated as a sample unit. First, data were pooled for each habitat for fishes and for food items, respectively, in order to test for the overall differences among habitats. Subsequently, each fish species was treated separately. The numbers of individual fishes analysed for each particular species (*i.e.* sample size) equalled the number of replicates (N; Table I). Data were checked for homogeneity of variances using a Levene's test (Field, 2000). In case variances were homogeneous, a one-way ANOVA or t-test was employed to test for differences in stable isotope signatures of carbon for fishes and food items among different habitats. Since fish sample sizes were very different (see Table I), a Hochberg's GT2 was used as a *post hoc* test due to its greater statistical power in such kinds of data compared to other tests (Field, 2000). All data that did not show homogeneous variances were $\log_{10}$-transformed, and a Levene's test was performed once again. Either Kruskal–Wallis test or Mann–Whitney U-test (depending on the number of sample units involved) on the non-transformed data was used as a non-parametric test equivalent when variances were not homogeneous, even after $\log_{10}$-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 $P < 0{\cdot}05$ was used in all tests. All analyses were performed using the programme SPSS 11.5 for Windows (Field, 2000).

RESULTS

GUT CONTENT ANALYSIS

Gut analysis indicated a food preference by different fish species, despite the fact that they ingested a variety of food items (Table II). While some fish species maintained a quite similar diet type regardless of the different habitats from which they were caught (*G. filamentosus*: copepods; *S. sutor*: macroalgae; *S. barracuda*: fishes; *Z. dispar*: insects), the diet of the other species (*G. oyena*, *L. lentjan*, *L. fulviflamma* and *M. argenteus*) differed within species in different habitats. The main food of *G. oyena* from the mangrove channel and from Chwaka seagrass beds consisted mainly of copepods while fishes from mud and sand flats fed mainly on detritus (Table II). *Lethrinus lentjan* fed mainly on ostracods in the mangrove channel, on copepods on the mud and sand flats and on crustaceans and insects in the Chwaka seagrass beds. The diet of *L. fulviflamma* consisted mainly of crustaceans in the mangroves, of copepods on the mud and sand flats, of crabs and shrimps in Chwaka seagrass beds, and of crabs and fishes in Marumbi seagrass beds. *Monodactylus argenteus* from the mangrove creeks fed mainly on copepods while those from mangrove channel fed mainly on algae (Table II).

MEAN δ^{13}C SIGNATURES FOR FISHES AND FOOD ITEMS

A clear gradient in δ^{13}C could be discerned for fishes as well as food items from the mangrove habitats located deep into the bay to the seagrass beds at the mouth of the bay (Fig. 2). Fishes and food items from the mangrove habitats were significantly depleted (Hochberg's GT2, $P < 0{\cdot}001$) to those from the

TABLE II. Mean percentage composition of diet for different fish species and fork length (L_F) classes in different bay habitats. Grey boxes highlight all food items with a relative abundance of >19%.

Species/site	L_F class (cm)	*N*	Copepod	Crab	Shrimp	Ostracod	Crustacean Parts	Fishes	Detritus	Gastropod	Nematode	Insect	Algae	Seagrass	Sediment	Unidentified animal material	Unidentified plant material	Other
Gerres filamentosus (ZB)																		
Mangrove creeks	0–5, 5–10	3	95·8			1·0												3·2
Mangrove channel	0–5, 5–10	45	71·2		1·9	0·3			11·4			0·1			2·3	9·9		2·8
Gerres oyena (ZB)																		
Mangrove channel	5–10	15	42·9			2·0			15·2	7·1	0·2				9·8	12·5	6·2	4·2
Mud and sand flats	0–5, 5–10, 10–15	16	21·2			2·1			53·3		8·4	0·2	1·9		8·7			4·2
Chwaka seagrass beds	10–15	11	39·2			2·7			26·1	3·4	4·8					11·2		12·6
Lethrinus lentjan (ZB)																		
Mangrove channel	5–10	7	12·9			53·6	14·3		2·1							17·1		
Mud and sand flats	5–10	12	70·8				3·1	8·3	0·3				0·3			17·0		0·3
Chwaka seagrass beds	5–10, 10–15	3					33·3					33·3				33·3		
Lutjanus fulviflamma (ZB)																		
Mangrove channel	5–10	6		19·2	19·2		27·1	16·7								16·7		1·2
Mud and sand flats	5–10, 10–15	12	39·6		8·3		20·8		0·3						8·3	8·3		14·3
Chwaka seagrass beds	5–10, 10–15	30		40·4	22·7			10·4	0·1						4·2	20·1		2·1
Marumbi seagrass beds	10–15	3		45·8	20·8			33·3										
Monodactylus argenteus (O)																		
Mangrove creeks	0–5, 5–10	18	46·0		50*				0·8							3·0		0·2

TABLE II. Continued

Species/site	L_F class (cm)	*N*	Copepod	Crab	Shrimp	Ostracod	Crustacean Parts	Fishes	Detritus	Gastropod	Nematode	Insect	Algae	Seagrass	Sediment	Unidentified animal material	Unidentified plant material	Other
Mangrove channel	5–10	10	6·3						17·8			10·0	65·0			0·9		
Pelates quadrilineatus (ZB)																		
Mud and sand flats	5–10, 10–15	5	32·5						27·5						20·0	20·0		
Zenarchopterus dispar (ZB)																		
Mangrove creeks	10–15, 15–20	9						0·3	11·4	9·7		69·4	4·2				4·2	0·7
Mangrove channel	15–20	5					20·0				20·0	40·0				20·0		
Siganus sutor (H)																		
Mangrove channel	5–10	5											92·5				7·5	
Mud and sand flats	5–10, 10–15	5							4·4				72·5	7·5		15·6		
Marumbi seagrass beds	5–10, 10–15, 15–20	23							7·1				79·4	2·3			11·2	
Sphyraena barracuda (P)																		
Mangrove channel	10–15	5						100·0										
Mud and sand flats	10–15, 15–20, 20–25	7	16·7					62·5	1·0							18·8		1·0
Chwaka seagrass beds	10–20, 20–30	4	21·9			1·0		71·9	1·0							1·5		2·7

H, herbivore; O, omnivore; P, piscivore; ZB, zoobenthivore; *N*, number of fish analysed; *, shrimp larvae.

seagrass habitats by on average 6·9 and 9·7‰ for fishes and food items, respectively, and from the mud and sand flats by on average 3·5 and 5·8‰, respectively. Food items from the mud and sand flats were significantly depleted (Hochberg's GT2, $P < 0{\cdot}01$) as compared to those of the seagrass habitats by on average 3·9‰. Fishes from the mud and sand flats were depleted by an average of 3·4‰, but this difference was not significant (Hochberg's GT2, $P > 0{\cdot}05$). There were no significant differences (Hochberg's GT2, $P > 0{\cdot}05$) in $\delta^{13}C$ between the two mangrove habitats (average difference of 0·2 and 1·5‰, for fishes and food, respectively), and between the two seagrass habitats (average difference of 1·9 and 0·2‰, for fishes and food, respectively).

TROPHIC LEVELS OF FISHES AND FOOD ITEMS

The food web in the bay showed various trophic levels. Detritus and plant material were generally more depleted in $\delta^{15}N$ as compared to zooplankton and macroinvertebrates (zoobenthos + insects) found within the same habitat, while fishes were the most enriched in $\delta^{15}N$ (Fig. 3). Also, clear gradients in both $\delta^{13}C$ and $\delta^{15}N$ could be observed for different feeding guilds of fishes and for different habitats [Fig. 3(b)]. Three trophic levels could be discerned for the fishes, with increasing values of $\delta^{15}N$ from herbivores to omnivores and zoobenthivores to piscivores. For each feeding guild, $\delta^{13}C$ increased along the spatial gradient from mangroves in the bay to seagrass beds at the mouth of the bay [Fig. 3(b)].

STABLE ISOTOPIC SIGNATURES OF FISH SPECIES

Individual fish species from the mangrove habitats were generally more depleted in $\delta^{13}C$ compared to those of the same species from either mud and

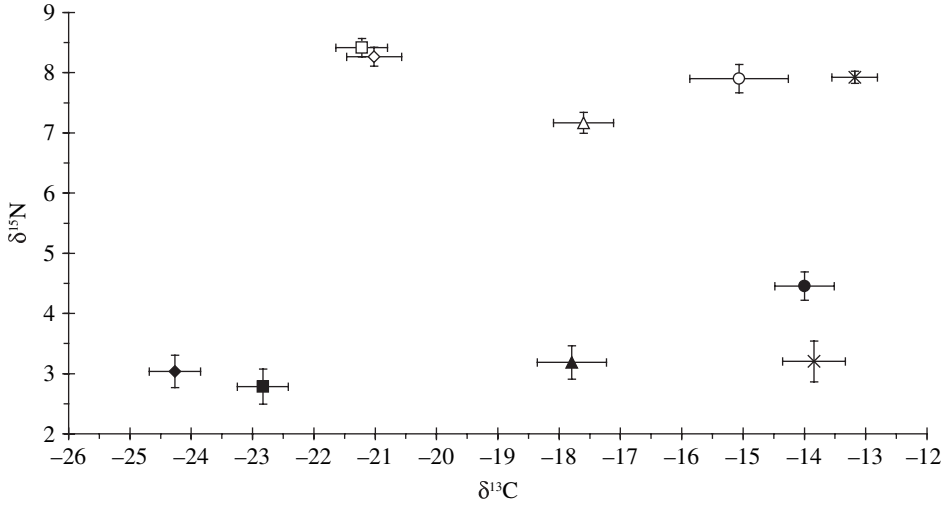

FIG. 2. Pooled mean ± S.E. stable carbon and nitrogen isotope values of fishes (◇, □, △, ○, *) and food items (◆, ■, ▲, ●, ×) in different bay habitats. (◇, ◆, mangrove creeks; □, ■, mangrove channel; △, ▲, mud and sand flats; ○, ●, Chwaka seagrass beds; *, ×, Marumbi seagrass beds).

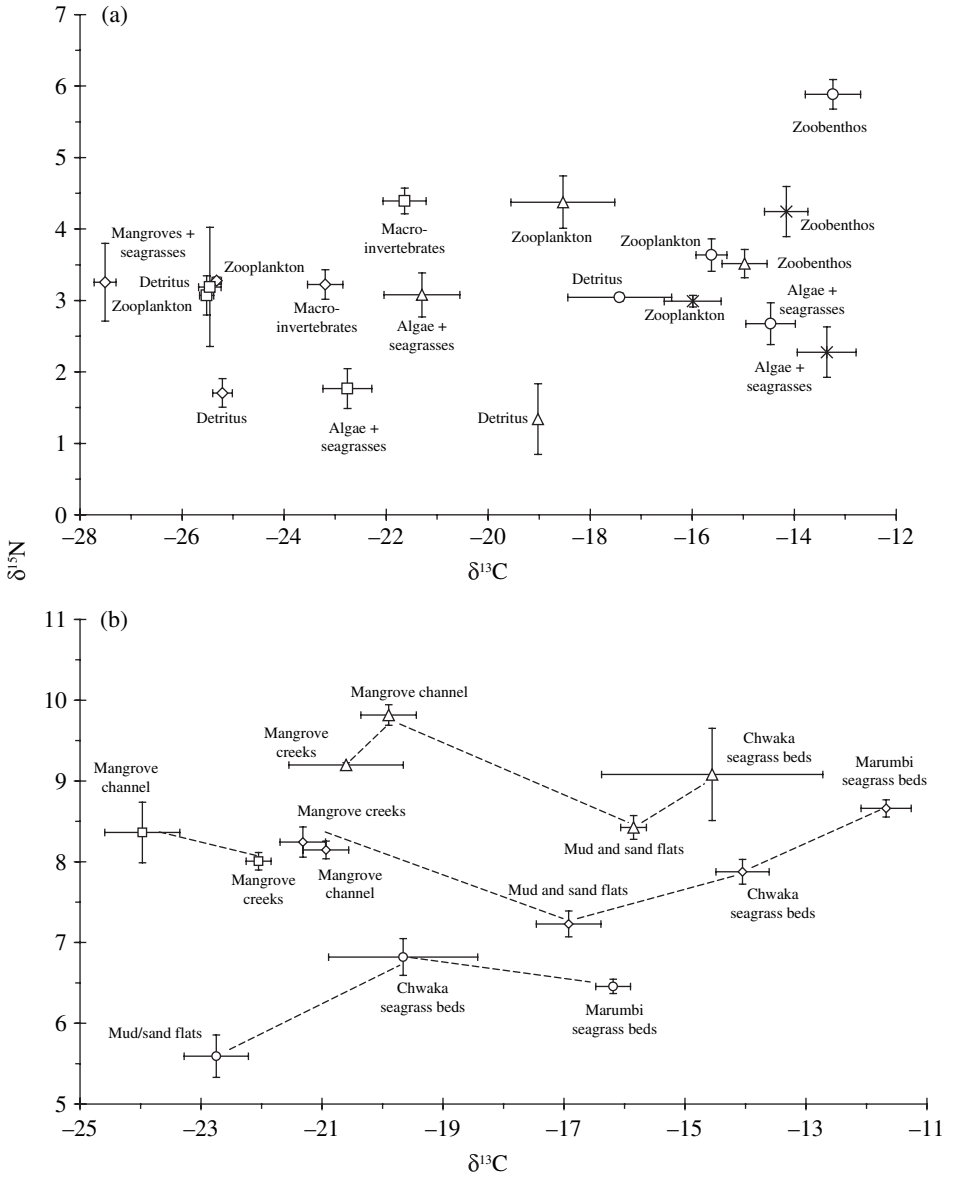

FIG. 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values of different (a) trophic groups of food items in different bay habitats. ($\diamond$, mangrove creeks; $\square$, mangrove channel; $\triangle$, mud and sand flats; $\bigcirc$, Chwaka seagrass beds; *, Marumbi seagrass beds), and (b) feeding guilds of fish in different bay habitats ($\triangle$, piscivores; $\square$, omnivores; $\diamond$, zoobenthivores; $\bigcirc$, herbivores).

sand flats or the seagrass habitats (Table I). The $\delta^{13}C$ depletion of individual species was generally in the order: mangrove habitats < mud and sand flats < seagrass habitats. The highest enrichment in $\delta^{13}C$ between two neighbouring habitats was observed for individuals of the same L_F class (10–15 cm) of *L. fulviflamma* (mangrove channel and mud and sand flats: 7·4‰). With regard

to $\delta^{15}N$, the herbivore *S. sutor* was the most depleted and the piscivore *S. barracuda* the most enriched fish species, with a range of 2·6–2·8‰ (considering the overall mean for L_F classes) between the two species when occurring in the same habitat. Considering individuals of the same species and similar size classes in different bay habitats, $\delta^{13}C$ of five species, namely, *G. oyena* (5–10 cm), *L. lentjan* (5–10 cm), *L. fulviflamma* (10–15 cm), *P. quadrilineatus* (5–10 cm) and *S. sutor* (5–10 cm), differed significantly between habitats (one-way ANOVA, d.f. = 3,36, $P < 0{\cdot}001$ for *G. oyena*, Kruskal–Wallis, d.f. = 3, $P < 0{\cdot}001$ for *L. lentjan*, Kruskal–Wallis, d.f. = 4, $P < 0{\cdot}01$ for *L. fulviflamma*, *t*-test, d.f. = 1, $P < 0{\cdot}05$ for *P. quadrilineatus* and one-way ANOVA, d.f. = 2,12, $P < 0{\cdot}001$ for *S. sutor*), while those of *G. filamentosus* (5–10 cm) and *Z. dispar* (10–15 cm) did not differ significantly between different bay habitats (Kruskal–Wallis, d.f. = 2, $P > 0{\cdot}05$ for *G. filamentosus*, Mann–Whitney *U*-test, d.f. = 1, $P > 0{\cdot}05$ for *Z. dispar*). Similar results were obtained when different L_F classes of individual species were pooled within each habitat in which case also *M. argenteus* differed significantly between the two mangrove habitats (*t*-test, d.f. = 1, $P < 0{\cdot}01$). The *post hoc* results are presented in Table I.

ANALYSIS OF POTENTIAL FOOD AND FEEDING HABITATS OF DIFFERENT FISH SPECIES

The herbivore *S. sutor* ingested mainly macroalgae (Table II). The $\delta^{13}C$ and $\delta^{15}N$ values of the average diet of this species were generally quite similar to those of macroalgae, but very distinct from those of seagrasses or mangrove leaves [Fig. 4(a)]. *Siganus sutor* from the mud and sand flats showed stable isotope signatures indicating various types of macroalgae from the mangrove channel as a potential food source, while fish from Chwaka seagrass beds showed values indicating green and brown algae from mud and sand flats and the calcareous green algae (*Halimeda* sp.) from Chwaka seagrass beds as a potential food source. *Siganus sutor* from Marumbi seagrass beds showed an intermediate value for its average diet that lay in-between those of green algae from the mud and sand flats, *Halimeda* sp. from Chwaka seagrass beds, and calcareous green algae (*Udotea* sp.) and red algae from Marumbi seagrass beds.

The gut content of the insectivore *Z. dispar* showed that insects formed a major part of its diet (Table II), while the stable isotope values from both mangrove habitats suggested a mixed diet of crabs (*Sesarma* sp. and Portunidae), shrimps and insects from the mangroves [Fig. 4(b)].

FIG. 4. Mean ± S.E. $\delta^{13}C$ and $\delta^{15}N$ values of fish species (a) *Siganus sutor*, (b) *Zenarchopterus dispar*, (c) *Monodactylus argenteus*, (d) *Sphyraena barracuda*, (e) *Gerres filamentosus*, (f) *Gerres oyena*, (g) *Lethrinus lentjan*, (h) *Lutjanus fulviflamma* and (i) *Pelates quadrilineatus* (large symbols) and potential food items (small symbols) in different bay habitats. (◇, mangrove creeks; □, mangrove channel; △, mud and sand flats; ○, Chwaka seagrass beds; *, Marumbi seagrass beds). The arrow heads indicate the predicted average $\delta^{13}C$ and $\delta^{15}N$ values (based on the 1 and 3·5‰ enrichment, respectively, in $\delta^{13}C$ and $\delta^{15}N$ between an animal and its food source) of the diet of fishes. The dashed lines combine potential food sources within a habitat. Prey species are depicted on lowest taxonomic level for each habitat in which the fish species was found; for the remainder of the habitats the prey species are pooled to higher taxonomic levels (*e.g.* macroinvertebrates, zoobenthos and seagrasses).

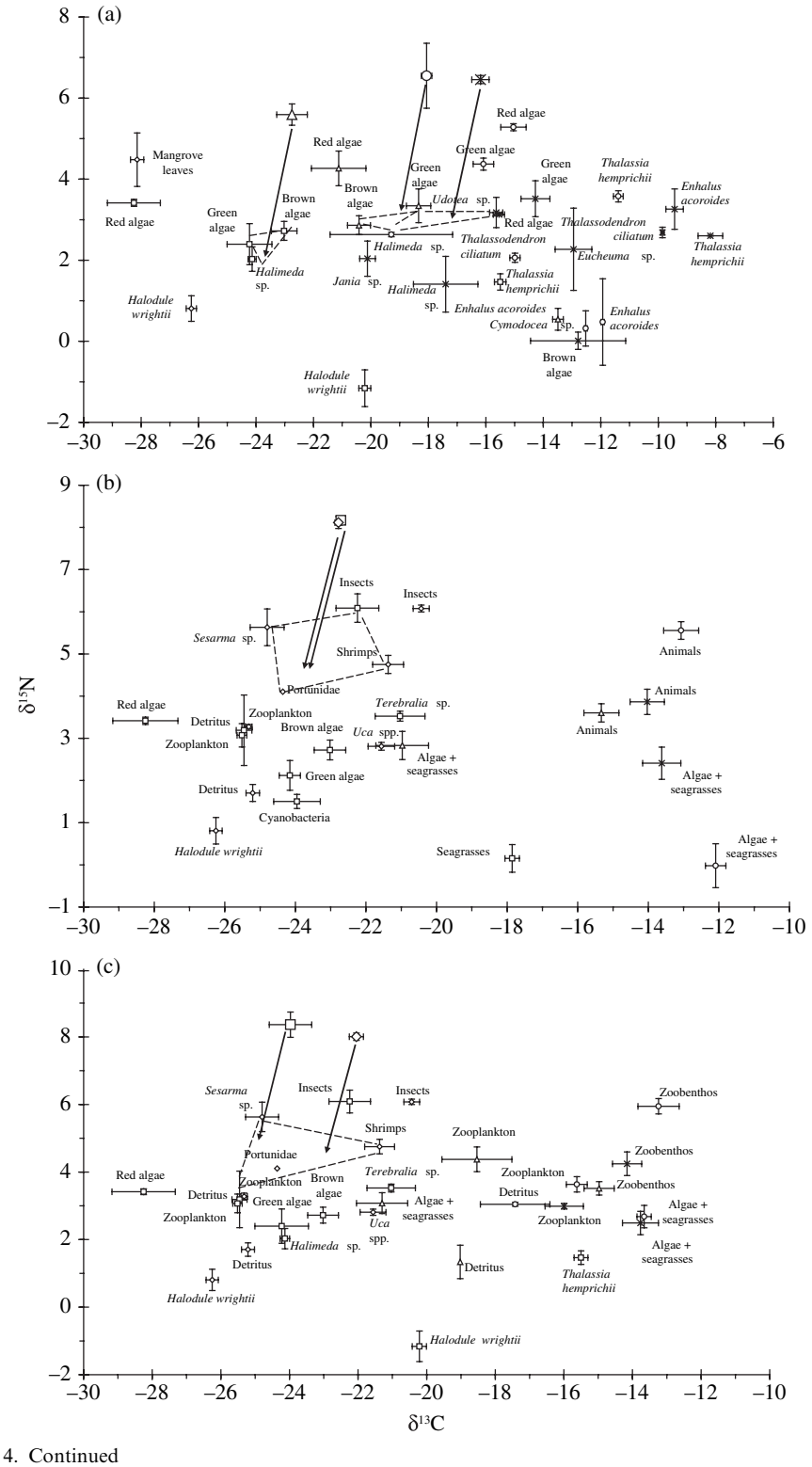

FIG. 4. Continued

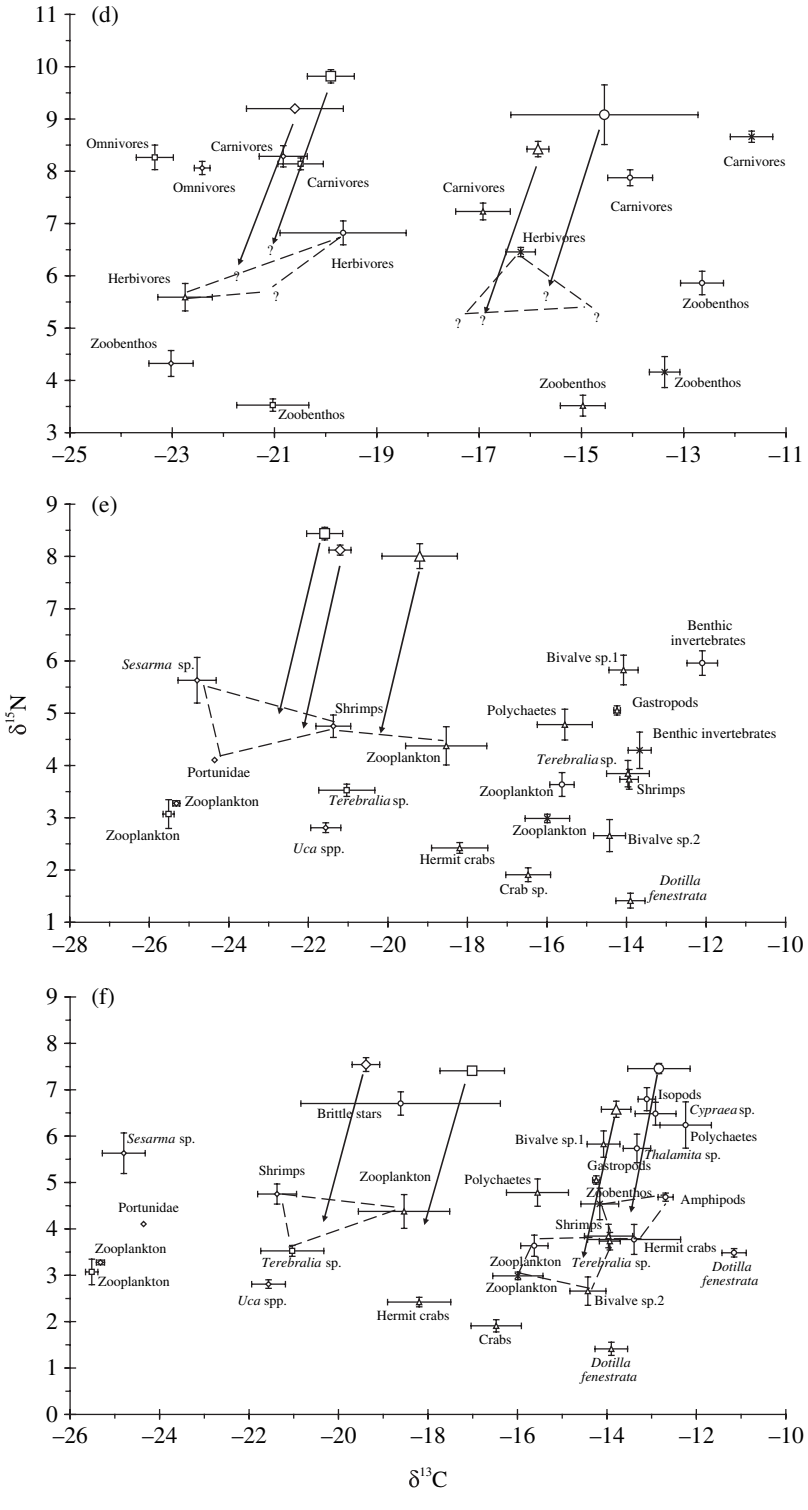

FIG. 4. Continued

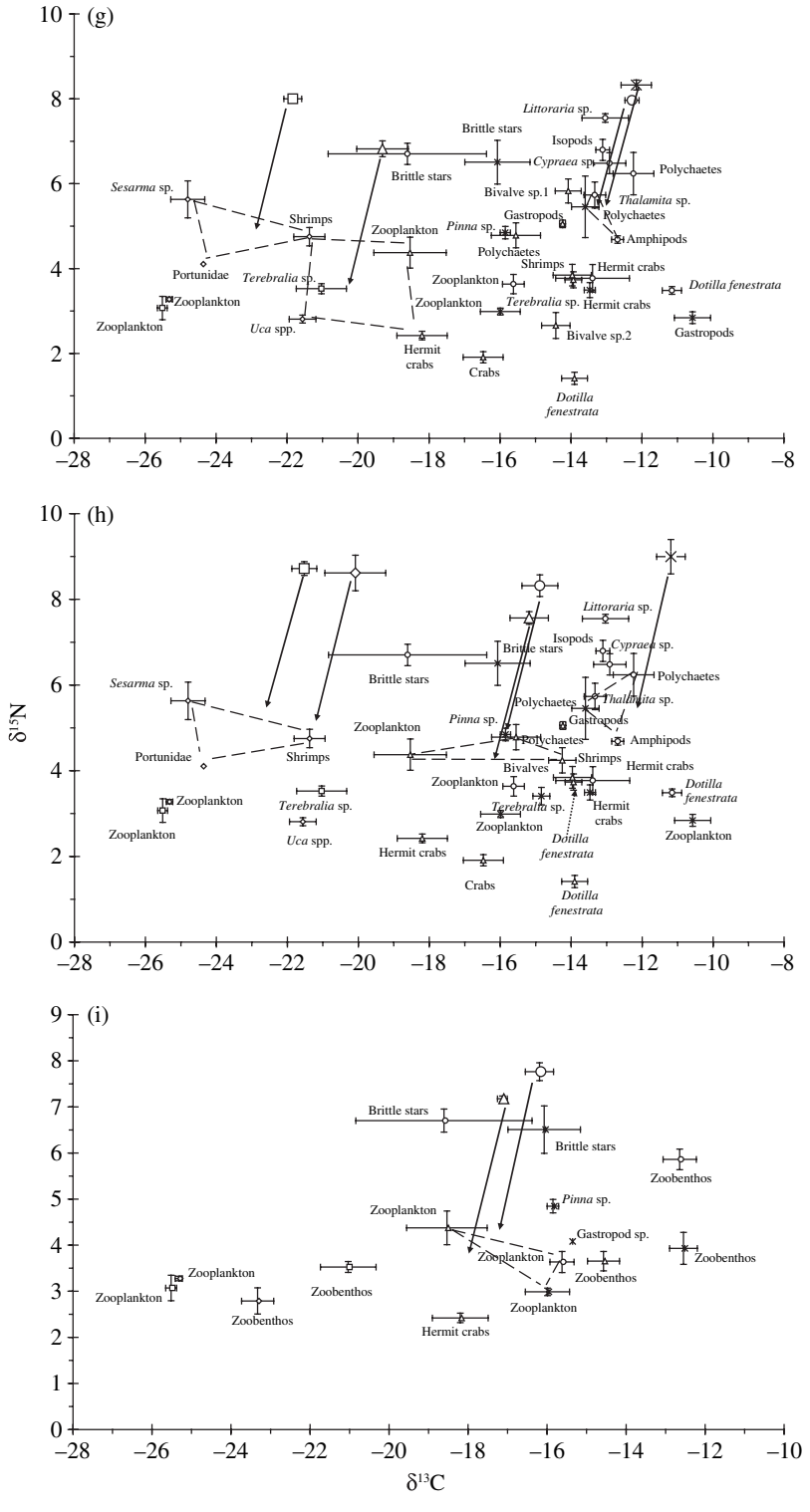

FIG. 4. Continued

The omnivore *M. argenteus* ingested zooplankton, algae and some detritus (Table II). The ingestion of zooplankton and detritus is supported by the $\delta^{13}C$ for fish from the mangrove channel, although the enrichment in $\delta^{15}N$ was larger than the usual 3·5‰ [Fig. 4(c)]. For fish from the mangrove creeks, the $\delta^{13}C$ signature suggests the diet to consist of a mixture of decapods (*Sesarma* sp., Portunidae and shrimps) from the mangrove creeks and zooplankton and detritus from the mangrove channel, but without an indication of dependence on algae as a food source [Fig. 4(c)].

Although the gut content analysis shows that fishes formed major part of the diet of the piscivore *S. barracuda*, the stable isotope signatures of the average diet of *S. barracuda* was not close enough to those of the selected fish species of this study to depend solely on these species as a food source. *Sphyraena barracuda* from the mangrove habitats had an isotope signature of its average diet that was closest to that of herbivorous fishes from the mud and sand flats and Chwaka seagrass beds, while for *S. barracuda* from the mud and sand flats and Chwaka seagrass beds this was the case for herbivorous fish from the Marumbi seagrass beds, with a possibility of feeding partly on macrofauna too [Fig. 4(d)].

In conformity with the gut content analysis where crustaceans (mainly copepods, crabs and shrimps) formed a major part of the diet of most zoobenthivores (Table II), *G. filamentosus* from the mangrove habitats had stable isotope signatures for its average diet which lay in-between those of crustaceans (*Sesarma* sp., Portunidae and shrimps) from the mangrove creeks, while fish from mud and sand flats had isotope signatures for their average diet which lay in-between values for shrimps from the mangrove creeks and zooplankton from mud and sand flats [Fig. 4(e)]. *Gerres oyena* from the mangrove creeks showed an isotope signature of its average diet close to the signatures of shrimps from the mangrove creeks, gastropods (*Terebralia* sp.) from the mangrove channel and zooplankton from the mud and sand flats, while *G. oyena* from mangrove channel had signatures closest to zooplankton from the mud and sand flats [Fig. 4(f)]. *Gerres oyena* from the mud and sand flats showed an average diet signature close to that of bivalves, gastropod (*Terebralia* sp.) and shrimps from mud and sand flats and zooplankton from the seagrass beds. *Gerres oyena* from Chwaka seagrass beds showed a signature of its average diet close to that of shrimps and gastropods (*Terebralia* sp.) from the mud and sand flats, hermit crabs and amphipods from the Chwaka seagrass beds, and zoobenthos from the Marumbi seagrass beds [Fig. 4(f)]. *Lethrinus lentjan* from the mangrove channel showed an isotope signature of its average diet that was intermediate between crabs and shrimps of the mangrove creeks, while for the mud and sand flats the signatures suggested a possible mix of shrimps, crabs (*Uca* spp.) and gastropod (*Terebralia* sp.) from the mangroves and hermit crabs and zooplankton from the mud and sand flats as a food source [Fig. 4(g)]. *Lethrinus lentjan* from the seagrass habitats showed an average stable isotope signature for its diet that was close to that of the zoobenthos from the seagrass habitats. The isotope signature of the average diet of *L. fulviflamma* from the mangrove habitats showed proximity to isotope signatures of crabs and shrimps from the mangrove habitats, while that of fish from the mud and sand flats and Chwaka seagrass beds suggested an intermediate isotope

signature of polychaetes, shrimps and zooplankton from the mud and sand flats [Fig. 4(h)]. *Lutjanus fulviflamma* from the Marumbi seagrass bed showed a stable isotope signature of its diet in close proximity to zoobenthos from the seagrass beds. *Pelates quadrilineatus* from both the mud and sand flats and Chwaka seagrass beds showed isotope signatures for their average diet close to zooplankton from mud and sand flats and the two seagrass beds [Fig. 4(i)].

CONNECTIVITY BETWEEN HABITATS

The isotopic signatures of the fish species in relation to that of the possible food items suggest four possibilities of feeding connectivity between adjacent bay habitats (Fig. 4): 1) connectivity between the two mangrove habitats for *G. filamentosus*, *L. lentjan*, *L. fulviflamma*, *M. argenteus* and *Z. dispar*, 2) connectivity between mangrove habitats and mud and sand flats for *G. filamentosus*, *L. lentjan* and *S. sutor*, 3) connectivity between mud and sand flats and seagrass habitats for *G. oyena*, *L. fulviflamma*, *P. quadrilineatus* and *S. sutor*, and 4) connectivity between the two seagrass habitats for *L. fulviflamma* and *L. lentjan*.

DISCUSSION

Both gut content and stable carbon isotope analyses showed evidence that the studied fish species generally relied as a food source on algae (herbivores) and macroinvertebrates (omnivores and zoobenthivores), with crustaceans (crabs, shrimps and copepods) playing a major role. The different $\delta^{13}C$ or $\delta^{15}N$ values of the piscivore *S. barracuda* from those of herbivorous fishes indicate a possible dependence for juveniles (10–25 cm) of this species on other animals than fishes alone. Copepods were found to some degree in the guts of the juveniles. In a study in Gazi Bay (Kenya), de Troch *et al.* (1998) identified other animals like gammaridean amphipods, mysids, crabs and shrimps in the stomachs of piscivorous fishes (including *S. barracuda*), an observation that indicates that at juvenile stages *S. barracuda* is not solely piscivorous.

Although the stable isotope signatures showed evidence for food dependence of the studied fish species on mangrove and seagrass habitats, the direct consumption of either mangrove or seagrass leaves seemed to be absent or very low. The mean $\delta^{13}C$ of mangrove leaves of $-28{\cdot}1‰$ is similar to the overall values for mangrove leaves recorded in the Caribbean, India, Malaysia and in Kenya (Rao *et al.*, 1994; Chong *et al.*, 2001; Bouillon *et al.*, 2002*a*; Cocheret de la Morinière *et al.*, 2003). Similar to what was observed by Sheaves & Molony (2000), Bouillon *et al.* (2002*b*) and Kieckbusch *et al.* (2004), however, this value is much more depleted as compared to either fish species (Sheaves & Molony, 2000; Kieckbusch *et al.*, 2004; this study) or to most of the macroinvertebrates (Hsieh *et al.*, 2002; Bouillon *et al.*, 2002*b*; Guest & Connolly, 2004; Kieckbusch *et al.*, 2004; Abed-Navandi & Dworschak, 2005) so as to function as a (direct and significant) source of carbon for these fauna. The most depleted fish species in this study was *M. argenteus* with a mean $\delta^{13}C$ of $-24{\cdot}0‰$, which is far more enriched as compared to mangrove leaves. Similarly, Guest & Connolly (2004) in Moreton Bay (Australia), Macia (2004) in

Inhaca Island (Mozambique) and Abed-Navandi & Dworschak (2005) on the Belize Barrier Reef (Caribbean Sea) observed that the $\delta^{13}C$ of most crabs and shrimps from the mangrove habitats was close to that of microphytobenthos and distinct from that of mangrove leaves.

Seagrasses (with exception of *Halodule wrightii* in the mangrove creeks and channel with a mean $\delta^{13}C$ of $-26{\cdot}3$ and $-20{\cdot}2$‰, respectively) were too far enriched in $\delta^{13}C$ ($-15{\cdot}5$ to $-8{\cdot}2$‰) as compared to the herbivore *S. sutor*. This suggests that seagrasses did not contribute to the diet of this herbivorous fish species. The low contribution of seagrasses and the high contribution of algae to the food web that was observed by Moncreiff & Sullivan (2001) in the Gulf of Mexico and by Kieckbusch *et al.* (2004) in Biscayne Bay is another example that seagrass plays a minor role in the food web and that algae are the primary source of organic matter for higher trophic levels. Mangroves and seagrasses do not appear to be direct sources of carbon in the diets of the fish species studied; they probably serve as refugia as well as a substratum for a variety of primary producers and consumers that are important in the food webs of these habitats (Kieckbusch *et al.*, 2004). Presence of food in addition to structural complexity has been reported to account for the strong association of large numbers of juvenile fishes within mangrove forests (Laegdsgaard & Johnson, 2001). In addition, seagrass beds have also been reported to harbour a high abundance of small invertebrates that are an important food of many juvenile fish species (Nakamura & Sano, 2005).

Using stable carbon isotope analysis different habitats were distinguished, which functioned as a source of carbon. Fish species from the mangroves were more depleted in $\delta^{13}C$ as compared to individuals of the same species caught from either the mud and sand flats or seagrass habitats. Similarly, fish species from the mud and sand flats were more depleted relative to individuals of the same species occurring in seagrass beds. The $\delta^{13}C$ of food also showed this trend. This is in agreement with other studies showing that the importance of mangrove-derived carbon (if any) is limited to the surroundings of the mangrove habitats, and decreases when moving away from the mangroves (Rodelli *et al.*, 1984; Newell *et al.*, 1995; Dehairs *et al.*, 2000; Chong *et al.*, 2001; Guest & Connolly, 2004). In agreement with Dehairs *et al.* (2000), this observation calls for critical evaluation on the assumption that mangrove ecosystem represent a source of organic nutrients for the coastal ecosystems. Like in other studies from around the world, the present study shows significant feeding of fishes (and macrobenthos) in the mangroves (Rodelli *et al.*, 1984; Marguillier *et al.*, 1997; Sheaves & Molony, 2000; Chong *et al.*, 2001; Cocheret de la Morinière *et al.*, 2003; Guest & Connolly, 2004; Nagelkerken & van der Velde, 2004; Abed-Navandi & Dworschak, 2005).

The overlap in stable carbon isotopes of some fish species in different bay habitats suggests connectivity between these habitats, with the possibility that fishes used more than one habitat as a feeding ground. Some fish species (*G. filamentosus*, *L. lentjan* and *S. sutor*) from the mud and sand flats showed a possible connection to the mangrove habitats as feeding habitats. Likewise, some fish species (*G. oyena*, *L. fulviflamma*, *P. quadrilineatus* and *S. sutor*) from Chwaka seagrass beds showed some evidence of using mud and sand flats as feeding habitats. An explanation for this observation could firstly be recent ontogenetic

migration (Cocheret de la Morinière *et al.*, 2003). The fishes could have migrated from one habitat to another habitat recently, as a result of which they still show part of the signature of their previously used habitat. It could take several weeks to months to acquire the signature of the food from the new habitat (Gearing, 1991; Hobson, 1999; Nagelkerken & van der Velde, 2004).

Since the fish samples were collected during low tide, a second possibility is that fishes migrated with the tides (with a spring tidal difference of 2 m) from the mangroves to the mud and sand flats and from the mud and sand flats to Chwaka seagrass beds. Migration in relation to feeding (Reis & Dean, 1981), preference of particular salinities (Quinn & Kojis, 1987) and avoidance of being stranded during low tide in areas that fall dry (van der Veer & Bergman, 1986) has been suggested to be among the reasons that can trigger tidal migrations. Since the $\delta^{13}C$ signature showed intermediate values between habitats, this could suggest that they fed at low tide as well as high tide, in two different habitats. Tidal migration between bay habitats in Chwaka Bay by Lutjanidae has been shown by Dorenbosch *et al.* (2004), and other species possibly follow the same pattern of behaviour.

Distance to be covered during (tidal) migration, however, seems important in terms of energy budget especially when juvenile fishes (<20 cm length) are considered, in which case long-distance migration costs may exceed energy intake (Nøttestad *et al.*, 1999). This may also be the case in the present study (in which the majority of the fishes were 5–10 cm L_F) where there appears to be substantial connectivity for fish species between neighbouring habitats, but not between habitats that were located far away from one another, such as Marumbi seagrass beds located 8 and 6 km away from the mangrove and mud and sand flat habitats, respectively.

The significant difference observed for some species in stable carbon isotopes in individuals of the same species and similar size classes between bay habitats suggests two situations: 1) the individuals of each habitat belong to different assemblages, each depending completely (in terms of nutrition) on different bay habitats, and 2) the different bay habitats all have the potential of providing sufficient food sources to the fish assemblage found therein. The differences in fish densities of particular species and size class in different bay habitats as observed by Lugendo *et al.* (2005), however, suggests that other factors than food alone control the distribution of juvenile fishes. As observed from other studies, structural complexity and shade in relation to predation risk are among the important factors in determining distribution of juvenile fishes (Laegdsgaard & Johnson, 2001; Cocheret de la Morinière *et al.*, 2004; Verweij *et al.*, 2006).

In conclusion, this study revealed that significant differences in stable isotope signatures (C and N) exist in food and fishes from different bay habitats in Chwaka Bay, which could be used to delineate feeding habitats of fishes. Fishes appear to forage in all studied bay habitats. Seagrasses and mangroves do not appear to be direct sources of carbon in the diets of studied fish species; rather, they probably serve as refuge as well as a substratum for a variety of primary producers and consumers that are important in the food webs of these habitats. Some fish species of similar feeding guilds showed some degree of segregation by feeding on different food resources. Zoobenthivores, however, showed an

overlap in diet and mainly fed on copepods, shrimps and crabs. There appears to exist a connectivity for some fish species between different bay habitats with respect to feeding (between the mud and sand flats and the mangroves, and between the seagrass beds and the mud and sand flats), which could be a result of either ontogenetic or tidal migration.

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References

Abed-Navandi, D. & Dworschak, P. C. (2005). Food sources of tropical thalassidean shrimps: a stable-isotope study. *Marine Ecology Progress Series* **291,** 159–168.

Beck, M. W., Heck, K. L. Jr, Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F. & Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51,** 633–641.

Bouillon, S., Koedam, N. & Dehairs, F. (2002*a*). Primary producers sustaining macroinvertebrate communities in intertidal mangrove forests. *Oecologia* **130,** 441–448.

Bouillon, S., Raman, A. V., Dauby, P. & Dehairs, F. (2002*b*). Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). *Estuarine Coastal and Shelf Science* **54,** 901–913.

Cederlöf, U., Rydberg, L., Mgendi, M. & Mwaipopo, O. (1995). Tidal exchange in a warm tropical lagoon: Chwaka Bay, Zanzibar. *Ambio* **24,** 458–464.

Chittaro, P. M., Fryer, B. J. & Sale, R. (2004). Discrimination of French grunts (*Haemulon flavolineatum* Desmarest, 1823) from mangrove and coral reef habitats using otolith microchemistry. *Journal of Experimental Marine Biology and Ecology* **308,** 168–183.

Chong, V. C., Sasekumar, A., Leh, M. U. C. & Cruz, R. D. (1990). The fish and prawn communities of a Malaysian coastal mangrove ecosystem, with comparisons to adjacent mud/sand flats and inshore waters. *Estuarine Coastal and Shelf Science* **31,** 703–722.

Chong, V. C., Low, C. B. & Ichikawa, T. (2001). Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Marine Biology* **138,** 77–86.

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., Hemminga, M. A., Huiskes, A. H. L. & van der Velde, G. (2003). Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotope and gut-content analysis. *Marine Ecology Progress Series* **246,** 279–289.

Cocheret de la Morinière, E., Nagelkerken, I., van der Meij, H. & van der Velde, G. (2004). What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Marine Biology* **144,** 139–145.

Dehairs, F., Rao, R. G., Chandra Mohan, P., Raman, A. V., Marguillier, S. & Hellings, L. (2000). Tracing mangrove carbon in suspended matter and aquatic fauna of the Gautami–Godavari Delta, Bay of Bengal (India). *Hydrobiologia* **431,** 225–241.

DeNiro, M. J. & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **45,** 341–351.

Dorenbosch, M., Verweij, M. C., Nagelkerken, I., Jiddawi, N. & van der Velde, G. (2004). Homing and daytime tidal movements of juvenile snappers (Lutjanidae)

between shallow-water nursery habitats in Zanzibar, western Indian Ocean. *Environmental Biology of Fishes* **70,** 203–209.
Field, A. (2000). *Discovering Statistics Using SPSS for Windows*. London: Sage Publications.
Fry, B. & Sherr, E. B. (1984). $\delta^{13}C$ measurements as indicators of carbon flow on marine and freshwater ecosystems. *Contributions in Marine Science* **27,** 13–47.
Gearing, J. N. (1991). The study of diet and trophic relationships through natural abundance ^{13}C. In *Carbon Isotope Techniques* (Coleman, D. C. & Fry, B., eds), pp. 201–218. San Diego, CA: Academic Press.
Guest, M. A. & Connolly, R. M. (2004). Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitats by resident animals. *Aquatic Ecology* **38,** 599–609.
Hartill, B. W., Morrison, M. A., Smith, M. D., Boubée, J. & Parsons, D. M. (2003). Diurnal and tidal movements of snapper (*Pagrus auratus*, Sparidae) in an estuarine environment. *Marine & Freshwater Research* **54,** 931–940.
Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120,** 314–326.
Hsieh, H., Chen, C., Chen, Y. & Yang, H. (2002). Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary: $\delta^{13}C$ and $\delta^{34}S$ signals. *Marine Ecology Progress Series* **227,** 145–155.
Hyslop, E. J. (1980). Stomach content analysis – a review of methods and their application. *Journal of Fish Biology* **17,** 411–429.
Khalaf, M. A. & Kochzius, M. (2002). Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* **239,** 287–299.
Kieckbusch, D. K., Koch, M. S., Serafy, J. E. & Anderson, W. T. (2004). Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. *Bulletin of Marine Science* **74,** 271–285.
Laegdsgaard, P. & Johnson, C. R. (2001). Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* **257,** 229–253.
Little, M. C., Reay, P. J. & Grove, S. J. (1988). The fish community of an East African mangrove creek. *Journal of Fish Biology* **32,** 729–747.
Lugendo, B. R., Pronker, A., Cornelissen, I., de Groene, A., Nagelkerken, I., Dorenbosch, M., van der Velde, G. & Mgaya, Y. D. (2005). Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. *Aquatic Living Resources* **18,** 149–158.
Lugendo, B. R., de Groene, A., Cornelissen, I., Pronker, A., Nagelkerken, I., van der Velde, G. & Mgaya, Y. D. (in press). Spatial and temporal variation in fish community structure of a marine embayment in Zanzibar, Tanzania. *Hydrobiologia*.
MacDonald, J. S., Waiwood, K. G. & Green, R. H. (1982). Rates of different digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 651–659.
Macia, A. (2004). Primary carbon sources for juvenile penaeid shrimps in a mangrove-fringed bay of Inhaca Island, Mozambique: a dual carbon and nitrogen isotope analysis. *Western Indian Ocean Journal of Marine Science* **3,** 151–161.
Mahongo, S. B. (1997). Surface heat exchange and bottom reflection in a tidal, shallow tropical lagoon: Chwaka Bay, Zanzibar. MSc Thesis, Gothenburg University, Sweden.
Marguillier, S., van der Velde, G., Dehairs, F., Hemminga, M. A. & Rajagopal, S. (1997). Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}C$ an $\delta^{15}N$. *Marine Ecology Progress Series* **151,** 115–121.
Minagawa, W. & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta* **48,** 1135 –1140.

Mohammed, S. M., Johnstone, R. W., Widen, B. & Jordelius, E. (2001). The role of mangroves in the nutrient cycling and productivity of adjacent seagrass communities, Chwaka Bay, Zanzibar. In *Marine Science Development in Tanzania and Eastern Africa. Proceedings of the 20th Anniversary Conference on Advances in Marine Science in Tanzania, 1999* (Richmond, M. & Francis, J., eds), pp. 205–226. Zanzibar: IMS/WIOMSA.

Moncreiff, C. A. & Sullivan, M. J. (2001). Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* **215,** 93–106.

Nagelkerken, I. & van der Velde, G. (2004). Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Marine Ecology Progress Series* **274,** 153–159.

Nagelkerken, I., Dorenbosch, M., Verberk, W. C. E. P., Cocheret de la Morinière, E. & van der Velde, G. (2000). Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series* **194,** 55–64.

Nakamura, Y. & Sano, M. (2005). Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. *Fisheries Science* **71,** 573–550.

Newell, R. I. E., Marshall, N., Sasekumar, A. & Chong, V. C. (1995). Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. *Marine Biology* **123,** 595–606.

Nøttestad, L., Giske, J., Chr. Holst, J. & Huse, G. (1999). A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 26–34.

Parrish, J. D. (1989). Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series* **58,** 143–160.

Pinnegar, J. K. & Polunin, N. V. C. (1999). Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implication for the study of trophic interactions. *Functional Ecology* **13,** 225–231.

Polis, G. & Strong, D. R. (1996). Food web complexity and community dynamics. *American Naturalist* **147,** 813–846.

Quinn, N. J. & Kojis, B. L. (1987). The influence of diel cycle, tidal direction and trawl alignment on beam trawl catches in an equatorial estuary. *Environmental Biology of Fishes* **19,** 297–308.

Rao, R. G., Woitchik, A. F., Goeyens, L., van Riet, A., Kazungu, J. & Dehairs, F. (1994). Carbon, nitrogen contents and stable isotope abundance in mangrove leaves from an east African coastal lagoon (Kenya). *Aquatic Botany* **47,** 175–183.

Reis, R. R. & Dean, J. M. (1981). Temporal variations in the utilization of an intertidal creek by the Bay Anchovy (*Anchoa mitchilli*). *Estuaries* **4,** 16–23.

Robertson, A. I. & Blaber, S. J. M. (1992). Plankton, epibenthos and fish communities. In *Tropical Mangrove Ecosystems* (Robertson, A. I. & Alongi, D. M., eds), pp. 173–224. Washington, DC: American Geographical Union.

Robertson, A. I. & Duke, N. C. (1987). Mangrove as nursery sites: comparison of the abundance and species composition of fish and crustaceans in mangroves and other near shore habitats in tropical Australia. *Marine Biology* **96,** 193–205.

Rodelli, M. R., Gearing, J. N., Gearing, P. J., Marshall, N. & Sasekumar, A. (1984). Stable isotope ratios as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* **61,** 326–333.

Rooker, J. R. & Dennis, G. D. (1991). Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science* **49,** 684–698.

Sheaves, M. & Molony, B. (2000). Short-circuit in the mangrove food chain. *Marine Ecology Progress Series* **199,** 97–109.

Smith, M. M. & Heemstra, P. C. (Eds) (1991). *Smith's Sea Fishes*, 1st edn. Johannesburg: Southern Book Publishers.

Sydeman, W. J., Hobson, K. A., Pyle, P. & McLaren, E. B. (1997). Trophic relationships among seabirds in Central California. *The Condor* **99,** 327–336.
de Troch, M., Mees, J. & Wakwabi, E. (1998). Diets of abundant fishes from beach seine catches in seagrass beds of a tropical bay (Gazi Bay, Kenya). *Belgian Journal of Zoology* **128,** 135–154.
Vance, D. J., Haywood, M. D. E., Heales, D. S., Kenyon, R. A., Loneragan, N. R. & Pendrey, R. C. (1996). How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns, *Penaeus merguiensis*, and fish in a tropical mangrove forest in northern Australia. *Marine Ecology Progress Series* **131,** 115–124.
Vanderklift, M. A. & Ponsard, S. (2003). Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. *Oecologia* **136,** 169–182.
van der Veer, H. M. & Bergman, M. N. J. (1986). Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) populations in the western Wadden Sea. *Marine Ecology Progress Series* **31,** 121–129.
Verweij, M. C., Nagelkerken, I., de Graaff, D., Peeters, M., Bakker, E. J. & van der Velde, G. (2006). Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. *Marine Ecology Progress Series* **306,** 257–268.

Electronic Reference

Froese, R. & Pauly, D. (Eds) (2004). *FishBase*. Available at www.fishbase.org (version 08/2004).