Utilisation by fishes of shallow-water habitats including mangroves and seagrass beds along the Tanzanian coast

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“*Anyone can give up; it's the easiest thing in the world to do.*
But to hold it together when everyone else would understand
if you fell apart, that's true strength.”
-Unknown

To my husband John, and my daughters Gladys and Vicky

Contents

Chapter 1

General introduction and outline of the thesis

INTRODUCTION

Mangroves and seagrass beds form characteristic habitats along most tropical and subtropical coasts. The importance of coastal habitats harbouring mangroves and seagrass beds as habitats for fishes is well documented (Blaber 1980; Bell *et al*. 1984; Robertson & Duke 1987; Thayer *et al*. 1987; Little *et al*. 1988; Morton 1990; van der Velde *et al*. 1995a,b; Kimani *et al*. 1996; Pinto & Punchihewa 1996; Wakwabi 1999; Nagelkerken *et al*. 2000a,b,c,2001,2002; Cocheret de la Morinière *et al*. 2002; Dorenbosch *et al*. 2004, 2005; Nakamura & Sano 2004a,b; Verweij *et al*. 2006). Since most of the fishes found in these habitats are juveniles, they are frequently referred to as nursery habitats (e.g. Robertson & Duke 1987; Little *et al*. 1988; Parrish 1989; Nagelkerken *et al*. 2001; Cocheret de la Morinière *et al*. 2002; Dorenbosch *et al*. 2004; Mumby 2006); however, real evidence to support the nursery role of these habitats is still lacking (Beck *et al*. 2001; Heck *et al*. 2003; Chittaro *et al*. 2004).

Mangroves and seagrass beds as juvenile habitats for fishes

Several assumptions have been made to explain the high abundance of juvenile fishes in these habitats. These assumptions are based on avoidance of predators (Blaber & Blaber 1980; Shulman 1985; Parrish 1989; Robertson & Blaber 1992; Nakamura & Sano 2004), higher abundance of food (Ogden & Zieman 1977; Orth *et al*. 1984; Nagelkerken *et al*. 2000a) and interception of fish larvae since these habitats cover extensive areas (Parrish 1989). Few studies, however, have tested these hypotheses experimentally (e.g. 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. And yet, this hypothesized nursery importance of these habitats is commonly used as the main argument for their protection and proper management to stop their degradation and rapid loss and for stimulating their regeneration (Beck *et al*. 2001).

Inconsistent information in the Indo-Pacific region

The importance of both mangroves and seagrass beds as a juvenile habitat for coral reef fishes has been well demonstrated in the Caribbean region (Nagelkerken *et al*. 2000c; Cocheret de la Morinière *et al*. 2002; Nagelkerken *et al*. 2002; Mumby *et al*. 2004). The general situation in the Indo-Pacific region may differ considerably from the Caribbean in particular, since bays and estuaries along the continental coastline in the former area are often characterised by turbid waters, a larger tidal range and a muddy substratum (Blaber 2000). In addition, the existing literature shows that the functioning of these shallow water habitats and particularly the mangroves within the Indo-Pacific region is contradictory. While in some regions these habitats are considered important for fishes and other macrozoobenthos (Blaber 1980, Bell *et al*. 1984; Little *et al*. 1988, Tzeng & Wang 1992; Marguillier *et al*. 1997; Sheaves & Molony 2000; Chong *et al*. 2001; Guest & Connolly 2004), this importance is refuted in other regions (Quinn & Kojis 1985; Thollot & Kulbicki 1988; Blaber & Milton 1990; Chong *et al.* 1990; Thollot 1992; Bouillon *et al.* 2002a,b). This inconsistency calls for the need to investigate each area separately in order to establish the possible functioning of these habitats. As pointed out by Hartill *et al.* (2003), a better understanding is required of the resources used by different fish species and/or life stages, and of how important different habitats are in maintaining fish populations before management plans can be improved.

Scarcity of knowledge in East Africa

The present knowledge on the functioning of mangrove and seagrass ecosystems as habitats for fishes is mostly based upon research conducted in North America (Thayer *et al.* 1987; Sogard *et al.* 1989; Kieckbusch *et al.* 2004), Tropical South America (Barletta *et al.* 2000,2003,2005; Barletta-Bergan et al. 2002a,b), Australia (Blaber *et al.* 1985; Robertson & Duke 1987; Morton 1990; Robertson & Duke 1990; Laedgsgaard & Johnson 1995; Laedgsgaard & Johnson 2001; Kwak & Klump 2004) and the Caribbean (Parish 1989; Nagelkerken *et al.* 2000a,b,c; 2001; Nagelkerken & van der Velde 2002, 2004; Cocheret de la Morinière *et al.* 2002; Dorenbosch *et al.* 2004, Verweij *et al.* 2006). The few studies on the structure of fish assemblages utilizing mangroves and seagrass beds along the east African coast are based on studies done in Kenyan estuaries (Little *et al.* 1988; van der Velde *et al.* 1995a; De Troch *et al.* 1996; Kimani *et al.* 1996; Wakwabi 1999; Marguillier *et al.* 1997; Huxham *et al.* 2004). Hence it is not clear how non-estuarine embayments in this region are utilised by juvenile fishes. This situation could accelerate degradation and/or loss of these habitats by ignorance of these values (Morton 1990; Nagelkerken *et al.* 2002). Given the worldwide rate of decline of shallow water habitats such as coral reefs, seagrass beds and mangroves (Shepherd *et al.* 1989; Spalding 1998; Pockley 2000; Valiela *et al.* 2001), knowledge on habitat utilisation by fishes of these habitats is fundamental so as to establish effective conservation strategies as well as development of sustainable fisheries.

According to the 1989 inventory, the mangroves of mainland Tanzania cover a total area of about 115,500 hectares (Semesi 1991). However, knowledge on their utilisation by fishes, or estimates of the fish densities in microhabitats within mangrove forests or adjacent habitats such as seagrass beds is limited to a few studies in the country (Dorenbosch *et al.* 2004, 2005).

Inadequacy and confounded sampling

In recent years, there has been a worldwide increase in recognition of the general importance of the mangrove and seagrass ecosystems as important nursery habitats for juvenile fishes. However, the utilisation by fishes and/or specific roles of these habitats remains largely unclear. Several attempts have been done to describe the fish abundances and densities in these habitats. Most of these studies have mostly focused on a single habitat type, either mangroves (Bell *et al.* 1984; Blaber *et al.* 1985; Little *et al.* 1988; Morton 1990; Robertson & Duke 1990; Rooker & Dennis 1991; Tzeng & Wang

1992; Laroche *et al*. 1997; Ley *et al*. 1999; Lin & Shao 1999; Ikejima *et al*. 2003) or seagrass beds (Livingston 1982; Beckley 1983; Stoner 1983; Bell & Westoby 1986; Nakamura & Sano 2004; Kwak & Klumpp 2004). In cases where more than one habitat is studied usually different sampling procedures are involved (see for example, Weinstein & Heck 1979; Blaber *et al*. 1985; Thayer *et al*. 1987; Thollot & Kulbicki 1988; Morton 1990; Robertson & Duke 1990; Acosta 1997; Nagelkerken *et al*. 2001). Few studies, however, have used balanced sampling strategies that provide comparable data on fish densities between these habitats and other adjacent habitats (Nagelkerken *et al*. 2000a; Chittaro *et al*. 2005; Nakamura & Sano 2005). Furthermore, most studies describing the importance of mangrove and seagrass ecosystems as fish habitats made no distinction between abundance of juvenile and adult fishes, and did not give size-frequency distribution in these habitats. This resulted into difficulties in comparison between studies, locations or different habitats hence difficulties in establishing the relative importance of these habitats as well as any interrelations between these habitats. Balanced sampling procedures among different shallow water habitats and involvement of new technique such as stable isotope analysis coupled with proper data presentation may offer more possibilities of getting insight into the use of these habitats by fishes.

Shallow-water habitats as feeding areas for fishes

Shallow-water habitats harbouring mangroves, seagrass beds and unvegetated habitats such as mud/sand flats are often interlinked through diurnal, tidal as well as ontogenetic fish migrations (Rooker & Dennis 1991; Vance *et al*. 1996; Nagelkerken *et al*. 2000a,c; Cocheret de la Morinière *et al*. 2002; Dorenbosch *et al*. 2004). However, little is known of the degree to which these habitats are used as feeding areas for fishes (Nagelkerken & van der Velde 2004) as well as their interconnection through feeding migration. Studies demonstrating which habitat constitutes the ultimate source of nutrition for shallow water fish communities can provide additional data for an objective determination of the relative value of different habitats (Melville & Connolly 2003). The relative conservation value of habitats has been determined largely by estimating the diversity and abundance of species present (Beck *et al*. 2001). Levin & Hay (2003) point out that the knowledge on why fish use specific habitats is also important in habitat conservation. As pointed out by Polis *et al*. (1997), the source of an animal's food is a central organizing theme in ecology. Understanding the role of shallow-water habitats as feeding grounds for fish and sources of food has important implications for management and conservation such as setting management priorities in situations of limited funding and man-power as has been always the case in many tropical developing countries.

Early food-web studies attempted to use conventional techniques such as gut content analysis of organisms at higher trophic levels to clarify trophic dynamics. This method has difficulties and if used alone 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 snap-shot 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). One method that allows measurement of assimilated and therefore nutritionally important materials is stable isotope analysis. 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).

Mangroves as feeding habitats for fishes

The importance of mangroves as feeding grounds for fishes and other macrozoobenthos of commercial importance has become the subject of considerable research and debate. While some mangroves are reported to form a significant feeding habitat for fishes and macrozoobenthos in some parts of the Indo-Pacific (e.g. Rodelli *et al*. 1984; Marguillier *et al*. 1997; Sheaves & Molony 2000; Chong *et al*. 2001; Guest & 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 & van der Velde 2004a). The topography and tidal characteristics of a mangrove ecosystem are mentioned as important factors that could determine the degree of ‘outwelling’ of mangrove carbon to adjacent aquatic environments (Boto & Wellington 1988; Lee 1995, 1999; Dittmar & Lara 2001). However, it is not clear if these factors could as well influence the importance of mangroves as feeding grounds for fishes from both within the mangrove ecosystems and adjacent habitats. Studies that compare the importance of mangroves as feeding grounds for fishes in mangrove ecosystems that differ in tidal ranges and/or topography are scarce. This calls for further research on mangrove ecosystems that differ in their topography in order to establish which factor is influential in the functioning of mangroves as important feeding habitats for fishes.

This thesis

The main aim of this thesis is to provide an insight into the functioning of tropical East African (Tanzanian) coastal habitats, such as mangroves and seagrass beds, as juvenile habitats. The key question is: ‘***Do the mangroves and seagrass beds along the Tanzanian coast serve as important habitats for juvenile fishes***?’

This key question was addressed in this thesis through a series of sub-questions:

1. What fish assemblages are found in different bay habitats?
2. To what degree do the fish species use the bay habitats as juvenile habitats?
3. Are there spatial and temporal variations in fish community structure (density, biomass, size-related distribution patterns, and species richness) and in physico-chemical variables within different bay habitats?

4. Is the distribution of fishes related to environmental variables?
5. Do fish species and/or specific size classes of fish exhibit habitat preferences within the bay?
6. How does the fish assemblage of Chwaka Bay compare to those of estuaries and non-estuarine habitats within the Indo-Pacific region and elsewhere?
7. What is the importance of different bay habitats as feeding areas for fishes?
8. To what degree does connectivity between bay habitats due to feeding by fishes exist?
9. Is the importance of mangroves as feeding habitats for fishes similar in mangrove ecosystems with different landscape configuration?

This thesis is subdivided into two main parts: (1) a part with field observations, in which information on the fish community structure and spatial-temporal variations in fish assemblages of different bay habitats of a marine embayment (Chwaka Bay, Zanzibar) is provided, and (2) a part in which stable isotope analysis is used to support the interpretation of the field observations and to provide further insights into the functioning of these shallow-water habitats (see Fig. 1).

Chapter 2 forms the backbone of this thesis. It addresses key questions 1 and 2 of this thesis. It provides a general overview of the fish community composition of different bay habitats in Chwaka Bay. It gives an insight into the fish assemblage found in each bay habitat and the importance of each bay habitat (mangroves, mud/sand flats and seagrass beds) and Chwaka Bay as a whole as a juvenile and as a potential nursery habitat for fishes of commercial fishery importance.

Chapter 3 addresses key questions 3 and 4 of this thesis. It describes the seasonal variation in fish community structure in relation to environmental variables in different bay habitats in Chwaka Bay.

Chapter 4 addresses key questions 4, 5 and 6. It describes the size-related distribution patterns of fishes of selected commercially important fish species in different bay habitats. It gives an insight into how individuals of the same species are distributed within the bay in terms of size-related distribution patterns and abundance, and discusses the implications of this size-related distribution patterns.

Chapter 5 dwells on the possible reasons for the observed size-related distribution patterns within different bay habitats in Chwaka Bay as reported in Chapter 4. It addresses key questions 7 and 8 of this thesis. By using combined methods of gut content analysis and stable carbon and nitrogen isotope analysis of food items and fish, the types of food items consumed, their sources and the possible connectivity between habitats is established. Chapter 5 further demonstrates the relative importance of different bay habitats (mangroves, seagrass beds and mud/sand flats) as feeding areas for juveniles of a number of fish species.

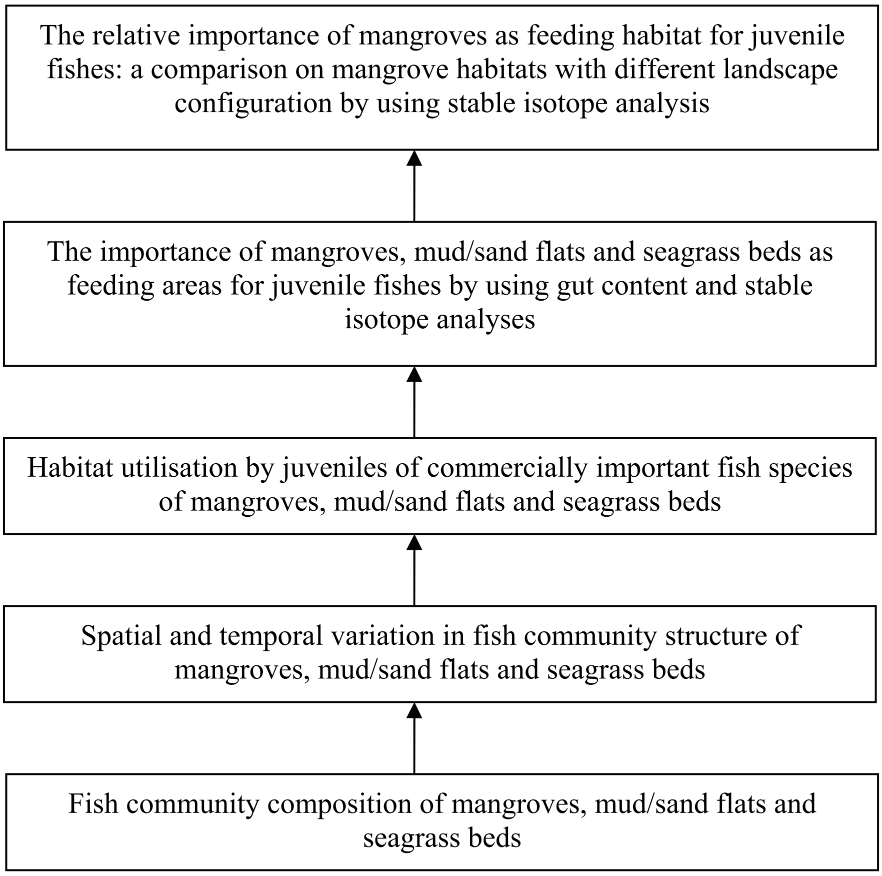

Fig. 1 Scheme of the study showing the different levels at which the fish community was studied (bottom = lowest level; top = highest level)

In Chapter 6, a more in-depth analysis is provided of the relative importance of mangroves with different landscape configuration patterns as feeding areas for juveniles of a number of fish species. It addresses the key question 9 of this thesis. Chwaka Bay, a non-estuarine (marine) embayment, is compared with a mangrove channel, and intertidal (coastal) and estuarine mangrove fringes.

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Chapter 2

Fish community composition of a tropical non-estuarine embayment in Zanzibar, Tanzania

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Abstract: Mangroves and seagrasses are important juvenile habitats for commercially valuable fish species. Along the east African coast, knowledge of fish assemblages utilizing these habitats is limited to studies done in estuaries, and hence this knowledge is scarce for non-estuarine embayments. In this study seine samples were taken from the non-estuarine Chwaka Bay (Zanzibar, Tanzania) along a gradient of the following habitats: mangroves, mud/sand flats and seagrass beds (Chwaka: in the bay, Marumbi: near the coral reef). Sampling was done bimonthly at each spring tide between November 2001 and October 2002. A total of 150 fish species belonging to 55 families were identified. Diversity (H') ranged from 1.9 in mud/ sand flats to 3.4 within Chwaka seagrass beds. The low species diversity at mud/sand flats was due to the numerical dominance of one species, viz. *Gerres oyena*, in this habitat. Overall, mean density of fishes was significantly higher in the mangrove creeks than in any other habitat (mean = 238.7 ind. 1000 m^{-2}). Highest, but non-significantly different, mean biomasses were recorded in the mangrove creeks (1.7 kg 1000 m^{-2}) and in Marumbi seagrass beds (1.6 kg 1000 m^{-2}) with the mangrove channel having the lowest biomass (0.6 kg 1000 m^{-2}). A high overlap in species composition (as high as 93.4% similarity) was found for adjoining habitats (i.e. mangrove creeks and mangrove channel), while habitats that were far apart showed low overlap (i.e. 6.6% similarity for Marumbi seagrass beds and mangrove creeks). On average 58.4% in terms of abundance and 63.2% in terms of biomass of the fish assemblage of Chwaka Bay were of commercial fishery importance. 76% of fishes observed in this study were small juveniles. Chwaka Bay thus appears to be an important juvenile habitat for various commercially important fish species.

INTRODUCTION

Coastal habitats harbouring mangroves and seagrasses are known to be important habitats for juvenile fishes, many of them commercially important to the reef fisheries.[1-6] These habitats are suspected to be nursery grounds for reef fishes (although real evidence has yet to be provided),[7,8] and as a result they are considered of higher conservation value than other unvegetated habitats.[7] Nagelkerken *et al.*[9] point out that the use of different sampling strategies between different coastal habitats is one of the drawbacks in getting comparable data on densities of fish between different habitats, and hence making it difficult to ascertain the importance of different coastal habitats such as mangroves and nearby habitats.

Studies on the structure of fish assemblages utilizing mangroves and seagrass beds along the east African coast is limited to studies done in Kenyan estuaries.[10-14] Hence it is not clear how non-estuarine embayments in this region are utilised by juvenile fish, a situation that could accelerate degradation and/or loss of these habitats by ignorance of these values.[15,16] Given the inconsistent information on the importance of these habitats by fishes in the Indo-Pacific region,[10,17,18] it is important to investigate each habitat individually in order to establish the possible importance of these habitats in a particular region.

This study explores the fish assemblages of various habitats including mangroves, seagrass beds and mud/sand flats within a Tanzanian embayment to describe the relative importance of each bay habitat in terms of abundance of fish species of commercial importance as well as size distributions of the fish faunas in these habitats. A similar sampling method was employed throughout the study area to be able to compare the habitats. This information is crucial in the management and enhancement of the value of these areas as potential nursery grounds, and in setting management priorities in situations of limited funding and man-power as it has been always the case in many tropical developing countries.

The aim of this paper is to assess the potential importance of these shallow water habitats for fisheries production. Therefore, this paper deals with the following questions: 1) what is the degree of similarity (in terms of density, biomass, diversity, species richness, evenness and species and guild composition) between the fish assemblages of different bay habitats? 2) Is the fish assemblage of Chwaka Bay similar to those of estuaries and non-estuarine habitats within the Indo-Pacific region and elsewhere?

MATERIALS AND METHODS

Study Area

Chwaka Bay is a shallow non-estuarine embayment located on the east coast of Unguja Island, Zanzibar, Tanzania (Fig. 1). It is an intertidal water body (average depth of 3.2 m) and its water area varies with tide: the estimated area during high spring tide is 50 km^2 and during low spring tide 20 km^2.[19] Air temperature ranges between 27-30°C and rainfall between 1000-1500 mm per annum. There are two rainy seasons in Zanzibar: the long rains that occur during the months of March, April and May, and the short rains which extend from October to December.[20] Winds are northeast monsoons (October-March) and southeast monsoons (March-October), with short intermediate periods.

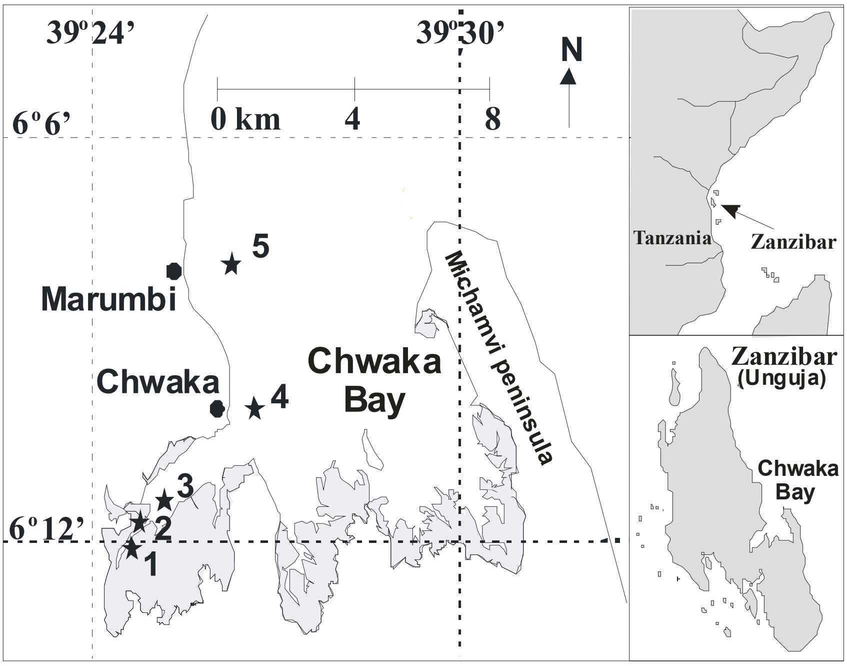

Fig. 1 Map of Unguja Island, Zanzibar, showing the location of Chwaka Bay and the sampled habitats. 1, mangrove creeks, 2, mangrove channel, 3, mud/sand flats, 4, Chwaka seagrass beds, 5, Marumbi seagrass beds. Gray areas in Chwaka Bay indicate mangrove forests.

Chwaka Bay is bordered by a dense mangrove forest of approximately 3000 ha.[21] A number of tidal creeks characterise this mangrove forest, with Mapopwe Creek (approximately 2 m deep) being the largest and the main water exchange route between the forest and the embayment. These creeks are intertidal in nature and none have any significant fresh water input other than rain. During heavy rains in the rainy season, salinity gradients develop and the mangrove creeks and channel temporarily acquire estuarine characteristics with salinities as low as 5 ppt.[22,23] This part of the bay is characterised by a relatively low water clarity and low oxygen levels.[23] On the seaward side, immediately adjacent to the forest, the embayment opens up to large intertidal flats that are characterised by mixed assemblages of algae and seagrasses and scattered monospecific seagrass stands. The outer and middle parts of bay (about 4 m deep) are oceanic in character with salinities rarely below 35 ppt and relatively high water clarity of 6.3 to 15.8 m horizontal Secchi distance.[23] The bay is relatively sheltered since it 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).

Field sampling

Fish samples were collected bi-monthly (at each spring low tide) for a period of one year (November 2001 - October 2002) from five habitats in Chwaka Bay: (1) mangrove creeks, (2) mangrove channel, (3) intertidal mud/sand flats located 2 km away from the mangroves, (4) Chwaka seagrass beds located about 6 km away from the mangroves, and (5) Marumbi seagrass beds situated about 8 km away from the mangroves (Fig. 1). Characterised by a muddy substratum and prop roots of the mangrove *Rhizophora mucronata*, the mangrove creeks and channel habitats harboured few algae and seagrasses. In contrast, the mud/sand flats were largely bare, except for some patches of algae and some seagrasses. The two sampled seagrass habitats consisted of vast fields of *Enhalus acoroides* interrupted by small patches of *Thalassodendron ciliatum* and the calcareous algae *Halimeda* spp.

A seine net measuring 35 m in length, 3 m in height, with a stretched mesh size of 1.8 cm was used to collect fish from all habitats, except in the creeks, with a sampled area of approximately 480 m^2 per haul. The narrowness of the creeks hindered a similar net deployment. Instead, an alternative method was used where the mouth of the mangrove creeks (about 4 m wide) was closed by the net and the whole net laid out upstream at one side of the creek (about 30 m) and then closed again, sampling an area of approximately 120 m^2. In each habitat, four replicate hauls were randomly taken during each spring tide.

To make sure that the net remained vertically stretched and touched the bottom, a metal chain was attached at the middle part of the sinker line. In addition, plastic floats were attached to the float line so that the upper side of the net remained afloat. Concurrently, snorkelling observations were made for net efficiency during deployment to check whether the net trailed over the substratum and if any fish escaped. We observed that the lower part of the net remained on the bottom throughout the exercise and no fish escaped below the net. Only some individuals of Mugilidae jumped over the net.

It was concluded that the procedure was well designed for most of the species under study. To standardize the methods, we involved the same two fishermen, using the same net, and similar net deployment procedures throughout the sampling period. Fish fork lengths were measured to the nearest 0.1 cm and biomass weighed to the nearest 0.1 g.

It should be noted that the majority of the juveniles collected in this study were larger than 2.5 cm in length. The smaller fishes (< 2.5 cm) tended to pass through the net. This may possibly have lead to an underestimation of the total density of early juveniles under study. It is known that seine nets have a limitation in sampling adult and fast swimming fishes, a problem that could result into them being underrepresented in this study. However, since the same mesh size was used throughout the bay habitats, the effect of the net (if any) applies for all the habitats and hence the observations from this study are representative for the different bay habitats.

The different size classes of fishes used in the present study were distinguished as follows: small juveniles (< one third of the maximum species' length), large juveniles and sub-adults (one third − two third of the maximum species' length), and adults (> two third of the max. species' length) following Nagelkerken and van der Velde.[4] Information on the maximum length that an individual species can attain, residence status, feeding guild, and the fishery importance of different fish species were obtained from Dorenbosch *et al.*[24], Froese and Pauly[25], Lieske and Myers[26], and other miscellaneous sources.[24-26]

The temporal variation in the fish community structure, abiotic variables and size-frequency data of some commercially important fish species of Chwaka Bay has already been reported.[6,23]

Statistical Analysis

The choice for a parametric test was made after the data were tested for homogeneity of variances using a Levene's test. Mean species richness and mean density for the entire fish community were compared among different bay habitats using a one-way ANOVA on log-transformed data, followed by multiple comparisons of means with a Tukey's HSD post-hoc test, using the programme SPSS for Windows.[27] Shannon's diversity index (H') and Pielou evenness index (J') were used to assess the diversity and distribution of species within each habitats. The overlap in species composition between different bay habitats was assessed using a Chao's abundance-based Sørensen index (L_{abd}) which is not only incidence-based (presence/absence) but also takes into account the relative abundance of the shared species.[28] The Chao's abundance-based Sørensen index was used to compare each pairwise combination of two habitats and was calculated as follows:

$$L_{abd} = 2UV/(U + V)$$

Where L_{abd}: Chao's abundance-based Sørensen index (higher values indicate a higher similariy), U: total relative abundance of shared individuals of assemblage 1, and V: total relative abundance of shared individuals of assemblage 2.

RESULTS

A total of 150 species belonging to 55 families were collected (Table 1). The mean number of species was significantly different between the bay habitats (1-way ANOVA; $p < 0.001$), and was higher in Chwaka seagrass beds (79) than in the mangrove creeks (44) and mangrove channel (62) (Tukey's HSD post-hoc test, $p < 0.001$, and $p < 0.005$, for mangrove creeks and mangrove channel, respectively) but similar to the mud/sand flats (78) and the Marumbi seagrass beds (58). The Shannon's diversity index was also highest in Chwaka seagrass beds ($H' = 3.4$), and was lowest on the mud/sand flats ($H' = 1.9$; Table 1). The evenness (J') followed the same trend as H', with $J' = 0.8$, and $J' = 0.4$, for Chwaka seagrass beds and mud/sand flats, respectively.

In the embayment as a whole, the contribution in terms of density to the total catch throughout the sampling period was highest for *Gerres oyena* (22.6%), *Ambassis gymnocephalus* (9.5%), *Apogon lateralis* (8.9%), *G. filamentosus* (7.5%), *Leptoscarus vaigiensis* (6.2%) and *Leiognathus equulus* (5.4%). In the mangrove creeks *Ambassis gymnocephalus* and *Apogon lateralis* were the most abundant species with a relative abundance of 22.2% and 20.6%, respectively. While *Gerres oyena* was the most dominant species in the mangrove channel (25.6%), in the mud/sand flats (62.6%) and in Chwaka seagrass beds (37.6%), *Leptoscarus vaigiensis* dominated the catches in Marumbi seagrass beds with a relative abundance of 48.0% (Table 1).

Gobiidae contributed the highest number of species to the fish fauna of Chwaka Bay, with 14 species. Labridae, Mullidae, Pomacentridae and Tetraodontidae were represented by eight species each, while Apogonidae and Scaridae had six species each (Table 1). While 21 families were represented by 2 to 5 species, 25 families were represented by just 1 species each.

With respect to the overlap in fish species for the five habitats, only 8 species (*Acanthurus blochii*, *Gerres oyena*, *Lethrinus harak*, *L. lentjan*, *Lutjanus fulviflamma*, *Saurida gracilis*, *Scarus russelii* and *Sphyraena barracuda*) out of the 150 recorded fish species were found in all five habitats (Table 1). The Chao's Sørensen similarity coefficient (Fig. 2) showed that neighbouring habitats harboured a more similar fish assemblage than habitats which were located far apart. Neighbouring habitats showed a similarity of 85.0 - 93.5% in fish community structure, whereas the most distantly located habitats (mangrove creeks vs. Marumbi seagrass beds) showed a similarity of just 6.6%. The same trend was seen for the overlap in number of species (Fig. 2).

Table 1 Mean densities (ind. 1000 m^{-2}), respective families, fishery importance (HC, highly commercial, C, commercial, MC, minor commercial, NC, non commercial, based on Froese & Pauly[25], residence group (R = reef-associated species: fish species that predominantly occur in reefs and use bay habitats as additional habitat[24-26]), N, nursery species: reef species that use bay habitats as juvenile habitat[24-25], B, bay associated species: species that are known to use particular bay habitats like seagrass and mangroves during their entire lifetime[25,26], OI, occasional visitors/intruders: pelagic predators, and R, rare species: reef species with less than 5 individuals in the whole bay for the whole sampling period), and feeding guilds (H, herbivore, I, insectivore, O, omnivore, PL, zooplanktivore, PS, piscivore, Z, zoobenthivore) of each fish species in each bay habitats. The total mean density, total mean biomass, total number of species, total number of families, Shannon's diversity and Pielou's evenness indices for each bay habitat are also provided. Gray boxes highlight mean densities which are > 5% of the relative abundance within a habitat

Families/species	Fishery importance	Residence group	Feeding guild	Mangrove creeks	Mangrove channel	Mud/sand flats	Chwaka seagrass	Marumbi seagrass
Acanthuridae								
Acanthurus blochii	C	R	H	0.3	0.2	0.1	0.1	0.0
Ctenochaetus striatus	C	OI	O					0.0
Zebrasoma veliferum	MC	OI	H				0.1	
Ambassidae								
Ambassis gymnocephalus	MC	B	Z/PS	53.1	0.4	0.1		
Antennariidae								
Antennarius hispidus	NC	OI	Z/PS	0.1				
Antennarius pictus	NC	OI	Z/PS					0.0
Antennarius striatus	NC	OI	Z/PS			0.0		
Histrio histrio	MC	R	Z/PS		0.0	0.2	0.0	
Apogonidae								
Apogon lateralis	NC	B	PL/Z	49.2	0.9			
Apogon nigripes	NC	R	O					0.4
Archamia mozambiquensis	NC	OI	Z					0.0
Cheilodipterus quinquelineatus	NC	R	Z				5.9	0.0
Fowleria aurita	NC	R	Z			0.0	0.1	
Sphaeramia orbicularis	MC	B	PL/Z	3.5		0.1	0.5	
Atherinidae								
Atherinidae sp.	NC	OI	PL			0.0	0.0	0.0
Aulostomidae								
Aulostomus chinensis	MC	OI	Z/PS					0.0
Balistidae								
Balistidae sp.	C	R	Z			0.1		
Belonidae								
Strongylura leiura	C	B	Z/PS	0.1	0.1	0.0		
Tylosurus crocodilus crocodilus	C	B	PS		0.4	0.1	0.1	0.1
Blenniidae								
Petroscirtes breviceps	NC	R	D			0.7	0.1	
Petroscirtes mitratus	NC	OI	H			0.0		
Plagiotremus tapeinosoma	NC	B	PS				0.0	
Bothidae								
Bothus pantherinus	C	B	Z		0.1	0.0	0.2	0.0
Carangidae								
Alectis indicus	C	OI	Z/PS			0.2		
Caranx sexfasciatus	C	OI	Z/PS	9.3	3.2	0.9		
Scomberoides commersonnianus	MC	OI	Z/PS			0.1		
Trachinotus blochii	MC	OI	Z			0.0		
Centriscidae								
Aeoliscus punctulatus	NC	B	PL					5.2
Chaetodontidae								
Heniochus acuminatus	NC	OI	PL	0.1	0.0		0.0	
Chaetodon auriga	MC	OI	O				0.1	
Chaetodon melannotus	NC	OI	Z			0.0	0.1	
Chaetodon xanthocephalus	NC	OI	O				0.0	
Chanidae								
Chanos chanos	HC	B	O			0.1		
Clupeidae								
Herklotsichthys spp.	MC	B	PL	0.2	0.0	0.0	0.0	
Dactylopteridae								
Dactyloptena macracanthus	MC	OI	Z			0.0		
Dactyloptena orientalis	MC	OI	Z		0.0	0.0		
Dasyatidae								
Taeniura lymma	C	OI	Z/PS				0.0	
Diodontidae								
Diodon liturosus	NC	OI	Z					0.0
Eleotridae								
Butis butis	MC	B	Z/PS	1.2	0.1	0.5		
Eleotris fusca	MC	B	Z	0.9	0.0	0.3		
Engraulidae								
Thryssa baelama	MC	B	PL		0.0	0.1		
Ephippidae								
Platax orbicularis	MC	R	O	0.2	0.1	0.0	0.1	
Platax teira	MC	R	O			0.0	0.4	0.0
Fistulariidae								
Fistularia commersonii	MC	R	Z/PS		0.1		0.6	0.1
Gerreidae								
Gerres acinaces	C	B	Z	0.9	1.7	1.8		
Gerres filamentosus	MC	B	Z	22.9	18.4	0.7		
Gerres oblongus	C	OI	Z		0.1			
Gerres oyena	C	B	Z	17.1	19.4	56.5	34.7	0.0
Gobiidae								
Acentrogobius audax	NC	B	Z	1.2		0.3		
Amblygobius albimaculatus	NC	B	H		0.0	0.2	0.4	
Amblygobius semicinctus	NC	OI	O				0.0	
Amblygobius sp. 1	NC	R	O	1.0		0.1		
Amblygobius sp. 2	NC	OI	O	0.1				
Amblygobius sphynx	NC	OI	O			0.0	0.0	
Bathygobius fuscus	MC	OI	Z		0.0			
Cryptocentrus cryptocentrus	NC	OI	Z				0.0	
Glossogobius callidus	NC	OI	Z				0.0	
Glossogobius giuris	MC	R	Z/PS	0.2	0.0	0.0		
Gnatholepis sp.	NC	OI	D				0.1	
Oxyurichthys ophthalmonema	NC	OI	Z		0.0	0.3		
Psammogobius knysnaensis	NC	B	Z	0.5		0.3	1.5	
Yongeichthys nebulosus	NC	B	Z		0.1	0.8		
Haemulidae								
Diagramma pictum	C	OI	Z/PS		0.0			
Plectorhinchus gaterinus	C	OI	Z/PS	0.2		0.0		
Plectorhinchus plagiodesmus	C	OI	Z/PS	0.1	0.0			
Plectorhinchus vittatus	C	OI	Z/PS			0.0		
Pomadasys multimaculatum	C	B	Z	2.2	0.9			
Hemiramphidae								
Zenarchopterus dispar	C	B	Z	19.5	2.2		0.0	
Holocentridae								
Neoniphon sammara	MC	OI	Z/PS				0.1	
Kyphosidae								
Kyphosus vaigiensis	C	OI	Z			0.1		

Table 1 continued

Labridae								
Cheilinus chlorourus	MC	R	Z				0.0	0.2
Cheilinus trilobatus	MC	OI	Z					0.1
Cheilio inermis	MC	B	Z				0.2	4.5
Epibulus insidiator	MC	R	Z/PS			0.3		0.0
Halichoeres scapularis	MC	OI	Z				0.0	0.0
Oxycheilinus bimaculatus	MC	R	Z					0.3
Stethojulis albovittata	NC	R	Z				0.1	1.3
Stethojulis strigiventer	NC	B	Z				0.0	0.2
Leiognathidae								
Leiognathus equulus	MC	B	Z	14.2	13.2	2.9		
Lethrinidae								
Lethrinus harak	C	B	Z/PS	0.2	0.1	0.2	0.1	0.1
Lethrinus lentjan	HC	N	Z/PS	2.6	1.8	6.2	3.6	1.1
Lethrinus variegatus	MC	B	Z		0.2	0.0	1.7	0.2
Lutjanidae								
Lutjanus argentimaculatus	C	N	Z/PS	1.2	0.1			
Lutjanus ehrenbergii	MC	N	Z/PS	2.3	0.3		0.0	
Lutjanus fulviflamma	C	N	Z/PS	1.8	1.1	3.5	4.8	0.2
Lutjanus fulvus	C	R	Z/PS	0.5	0.0	0.0		
Monacanthidae								
Aluterus scriptus	NC	OI	O			0.1	0.0	
Paramonacanthus barnardi	NC	OI	Z					0.0
Stephanolepis auratus	NC	R	Z			0.2	0.0	
Monodactylidae								
Monodactylus argenteus	MC	N	O	13.1	4.1	0.2	0.0	
Mugilidae								
Valamugil buchanani	C	B	O	1.6	1.0	0.2		
Mullidae								
Mulloidichthys flavolineatus	C	OI	Z				0.1	
Parupeneus barberinus	C	N	Z			0.0	1.4	0.2
Parupeneus indicus	C	OI	Z				0.0	
Parupeneus macronema	C	R	Z				0.1	0.4
Parupeneus rubescens	C	B	Z				0.4	0.1
Upeneus sulphureus	MC	OI	Z		0.0			
Upeneus tragula	C	R	Z	0.3	0.1	0.0		
Upeneus vittatus	C	OI	Z			0.0		
Muraenidae								
Lycodontis sp.	NC	OI	Z/PS		0.0			0.0
Nemipteridae								
Scolopsis ghanam	MC	N	Z/PS				2.5	0.0
Scolopsis lineata	MC	OI	Z/PS				0.0	
Ostraciidae								
Lactoria cornuta	NC	R	Z		1.2	0.0	0.0	0.0
Lactoria fornasini	NC	R	Z			0.5		0.0
Platycephalidae								
Thysanophrys sp.	NC	OI	Z/PS		0.0			
Plotosidae								
Plotosus lineatus	C	R	Z/PS			0.0	0.2	2.8
Poeciliidae								
Pantanodon podoxys	C	B	Z	12.9				
Pomacentridae								
Abudefduf sordidus	MC	OI	O				0.0	
Abudefduf vaigiensis	MC	OI	O					0.0
Chromis dasygenys	NC	R	O		0.0	0.2		
Pomacentridae								
Chrysiptera annulata	NC	B	O				0.1	3.1
Dascyllus aruanus	NC	R	O				0.2	
Pomacentrus pavo	MC	OI	O				0.0	
Pomacentrus trilineatus	NC	R	O				0.5	0.1
Stegastes nigricans	MC	R	O				0.4	
Scaridae								
Calotomus carolinus	C	OI	H					0.0
Calotomus spinidens	C	B	H				0.4	2.5
Hipposcarus harid	C	N	H			0.0	7.8	0.0
Leptoscarus vaigiensis	C	B	H				2.2	32.5
Scarus ghobban	C	N	H		0.1	0.5	0.8	0.1
Scarus russelii	C	R	H	0.1	0.1	0.3	3.1	1.1
Scorpaenidae								
Dendrochirus brachypterus	MC	R	Z			0.8	0.1	0.2
Dendrochirus zebra	MC	OI	Z		0.0			0.0
Pterois miles	NC	R	Z/PS		0.1	0.1	0.1	
Parascorpaena mossambica	NC	OI	Z/PS					0.1
Serranidae								
Epinephelus lanceolatus	MC	OI	Z/PS		0.0			
Epinephelus suillus	C	R	Z/PS			0.1	0.0	
Siganidae								
Siganus argenteus	C	OI	H				0.0	
Siganus rivulatus	MC	OI	H					0.1
Siganus stellatus	C	N	H		0.4	0.3	0.1	0.0
Siganus sutor	C	N	H		0.0	1.2	2.6	5.0
Sillaginidae								
Sillago sihama	C	B	Z		0.1			
Soleidae								
Pardachirus marmoratus	C	OI	Z				0.0	
Sphyraenidae								
Sphyraena barracuda	MC	N	Z/PS	2.2	0.9	1.3	0.6	0.1
Sphyraena forsteri	C	R	Z/PS	0.1	0.0	0.2		
Syngnathidae								
Hippichthys spicifer	NC	OI	Z/PS	0.4				
Hippocampus histrix	NC	B	PL/Z	0.1				0.1
Syngnathoides biaculeatus	NC	B	PL/Z	0.5	0.0		0.2	0.4
Synodontidae								
Saurida gracilis	C	R	PS	0.4	0.2	0.5	0.2	0.0
Teraponidae								
Pelates quadrilineatus	MC	B	Z/PS	0.2		2.6	11.4	
Terapon jarbua	MC	B	O		0.1	1.6		
Terapon theraps	MC	B	Z/PS			0.0		
Tetraodontidae								
Arothron hispidus	MC	B	O		0.0	0.3	0.1	
Arothron immaculatus	MC	B	O	0.4	1.7	0.7	0.1	
Arothron stellatus	NC	OI	Z			0.0		
Canthigaster bennetti	NC	R	O				0.0	0.1
Canthigaster solandri	NC	R	O			0.1	0.3	0.8
Canthigaster valentini	NC	R	O				0.1	3.1
Lagocephalus guentheri	NC	OI	O		0.0			
Sphoeroides pachygaster	C	OI	Z/PS		0.0			
Unknown								
Unidentified sp.	?	?	?			0.0		

Total number of individuals	**2614**	**3232**	**3996**	**4474**	**2839**
Total number of species	**44**	**62**	**78**	**79**	**58**
Total number of families	**27**	**38**	**41**	**36**	**29**
Shannon's diversity index (H')	**2.5**	**2.3**	**1.9**	**3.4**	**2.1**
Pielou's evenness index (J')	**0.7**	**0.6**	**0.4**	**0.8**	**0.5**
Mean density (ind. 1000 m^{-2})	**238.7**	**75.7**	**90.2**	**92.2**	**67.7**
Mean biomass (kg 1000 m^{-2})	**1.7**	**0.6**	**0.9**	**1.1**	**1.6**

Distance gradient

Distance gradient

km	km	0	0	2	6	8
	Habitat	Mangrove creeks	Mangrove channel	Mud/sand flats	Chwaka seagrass beds	Marumbi seagrass beds
0	Mangrove creeks	44	33	31	19	10
0	Mangrove channel	93.5%	62	42	28	19
2	Mud/sand flats	73.8%	92.8%	78	40	24
6	Chwaka seagrass beds	38.6%	51.7%	85.0%	79	39
8	Marumbi seagrass beds	6.6%	19.1%	30.1%	86.4%	58

Fig. 2 Matrix showing the overlap in number of fish species (right) and Chao's abundance-based Sørensen indices (left) between bay habitats. The shaded boxes show the total number of species in each bay habitat. The distance gradient (km) of each bay habitat in relation to the mangroves is also given.

Apogonidae, Ambassidae and Gerreidae contributed the most to the fish densities in the mangrove creeks, but Ambassidae did not contribute much to the biomass (Fig. 3). Apogonidae, Gerreidae, Gobiidae and Hemiramphidae contributed the most to the biomass in the mangrove creeks. Gerreidae dominated highly in terms of both densities and biomass within the mangrove channel, mud/sand flats and Chwaka seagrass beds. On the other hand, Scaridae was the single most important family in the Marumbi seagrass beds (Fig. 3).

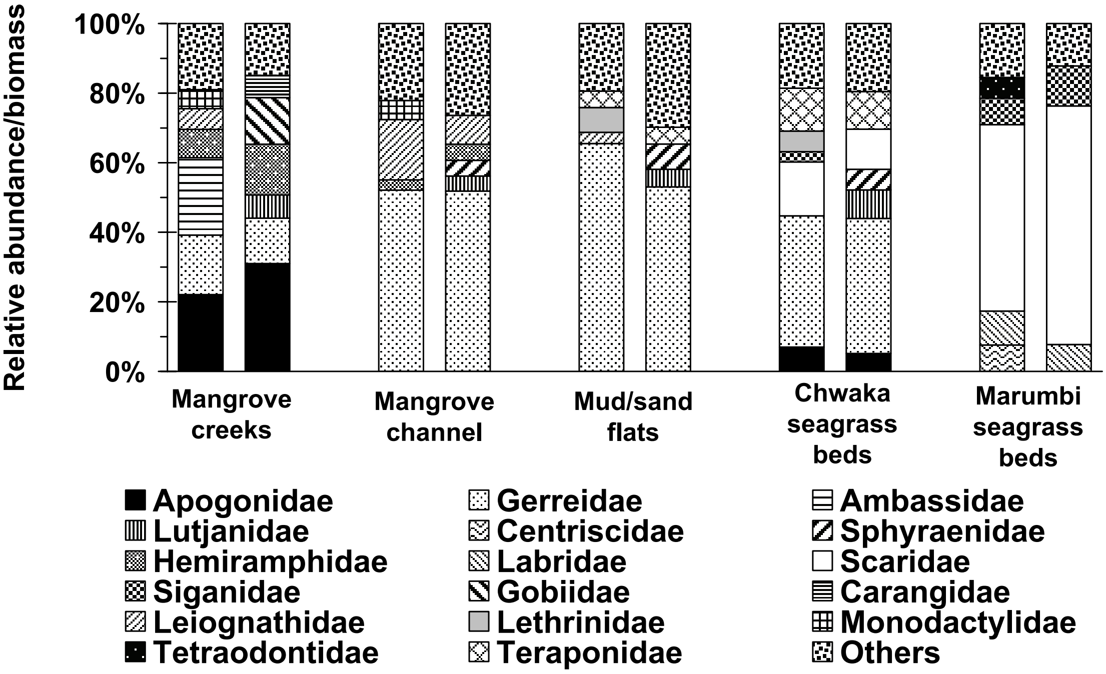

Fig. 3 Relative share of the most abundant fish families in each bay habitat in terms of density (left) and biomass (right).

The total mean fish density was significantly higher in the mangrove creeks (mean ± SE = 238.7 ± 1.7 ind. 1000 m^{-2}) than the other habitats (Tukey's HSD post-hoc test, $p < 0.01$), which showed comparable values (Table 1). The mean biomass (± SE) was highest in the mangrove creeks (1.7 ± 2.5 kg 1000 m^{-2}) and in the Marumbi seagrass beds (1.6 ± 2.5 kg 1000 m^{-2}), and lowest in the mangrove channel (0.6 ± 0.6 kg 1000 m^{-2}). These differences in mean biomass were not significant (1-way ANOVA, d.f. = 4, $p > 0.05$), however, due to the higher within_habitat variability.

The major proportion of fishes from the mangrove creeks was of minor or non- commercial fishery importance in density (70%) and biomass (60%; Fig. 4). Also in the mangrove channel a large part of the fishes were of minor or non-commercial fishery importance (density: 56%), although 59% in biomass was of commercial fishery importance. In contrast, commercially important fish species formed the major proportions (> 68%) of both density and biomass of fishes from the mud/sand flats, and the Chwaka and Marumbi seagrass beds. Of the total fish assemblage of Chwaka Bay, 58.4% in terms of abundance and 63.2% in terms of biomass were of commercial fishery importance.

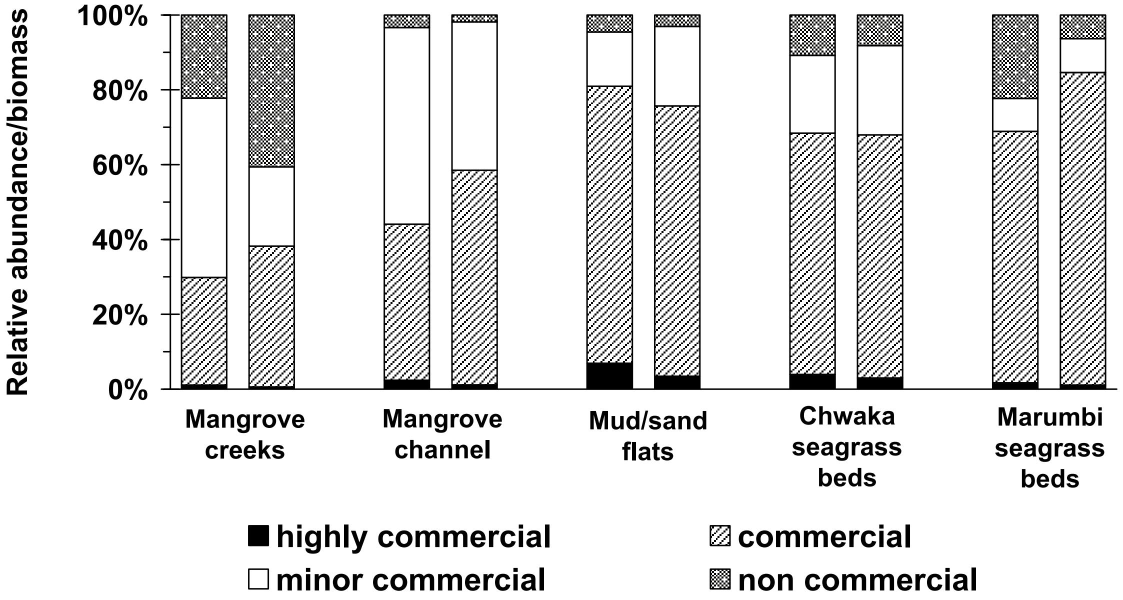

Fig. 4 Relative abundance (left) and relative biomass (right) of fishes in different bay habitats with respect to their fishery importance.

Zoobenthivores were the most abundant feeding guilds in relative density (> 38.8%) in all habitats except in Marumbi seagrass beds where herbivores dominated (Fig. 5). Herbivores also formed a small proportion (19%) of the fish assemblage of the Chwaka seagrass beds (19.4%), but they were almost absent in the mud/sand flats and mangrove habitats (<3%). Zoobenthivores/ piscivores accounted for a considerable proportion (31.8%) of the fish assemblage within the mangrove creeks and in Chwaka seagrass beds (26.4%). While zoobenthivores/ zooplanktivores were almost only found in the mangrove habitats, zooplanktivores were almost only present in the Marumbi seagrass beds (located relatively near to the open ocean).

The major proportions of the fishes in terms of relative density (59-85%) in all habitats were species considered to spend most of their life cycle within the bay (i.e. bay residents, Fig. 6). The proportion of nursery species was highest in the Chwaka seagrass habitats (26.4%) and was lowest in the mangrove creeks (9.8%) and in the Marumbi seagrass beds (10.1%). The proportion of reef species increased from the mangroves (deep within the bay) towards the seagrass beds of Marumbi (near the mouth of the bay), but interestingly, occasional visitors and intruders increased in relative density towards the mangrove habitats (Fig. 6).

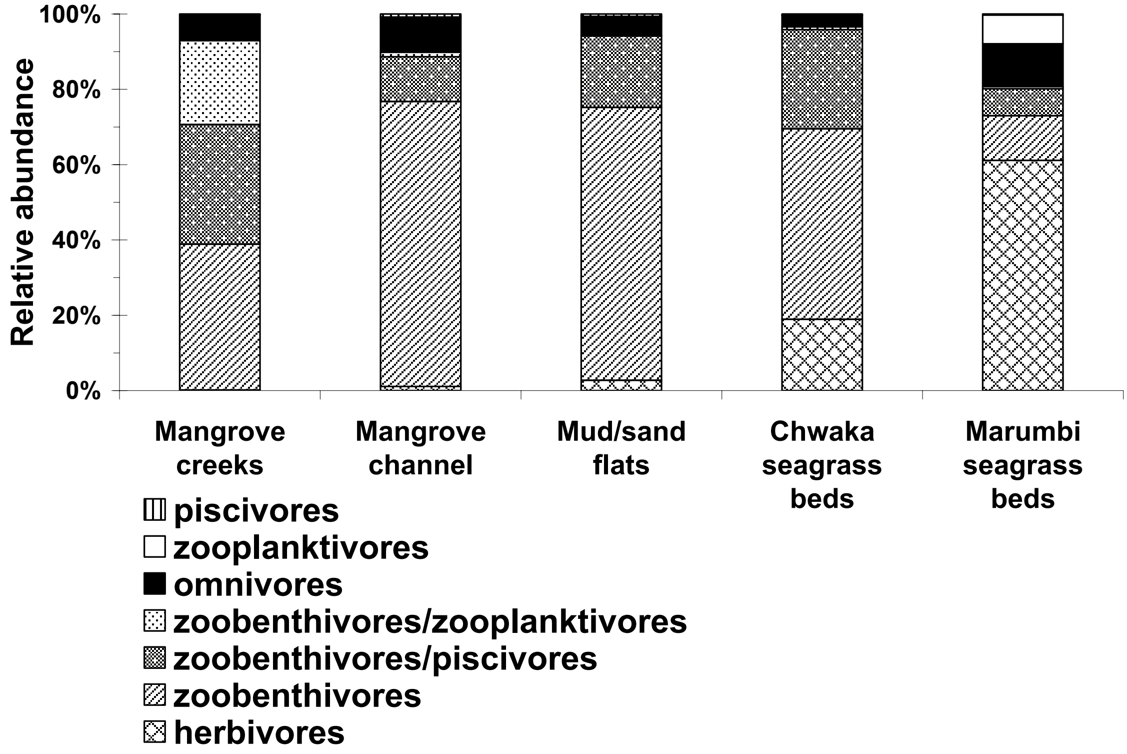

Fig. 5 Relative abundance of various feeding guilds of fishes in different bay habitats.

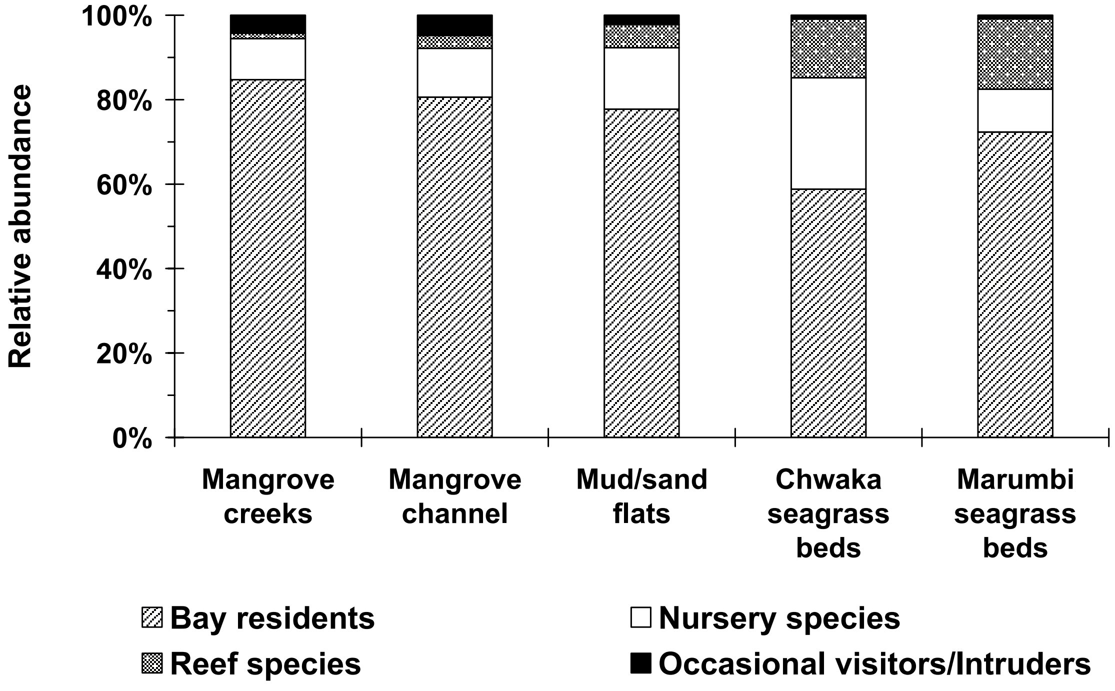

Fig. 6 Relative abundance of different ecological groups of fishes in different bay habitats based on their degree of residence in the bay; the definition for each category is given in Table 1.

Over 49.2% in relative abundance of the fishes occurring within the various bay habitats consisted of small juveniles (Fig. 7). The proportion was highest within the mud/sand flats (93.9%), followed by the mangrove channel (86.6%) and the Chwaka seagrass beds (82.1%). The mangrove creeks and the Marumbi seagrass beds had the highest proportion of adults and large juvenile/sub-adults (49.2% and 50.8%, for mangrove creeks and Marumbi seagrass beds, respectively). Overall, 75.7% of the relative abundance of all fishes caught in Chwaka Bay were small juveniles; the remaining fraction was composed of large juveniles/sub-adults (16.4%) with adults contributing 7.9% only.

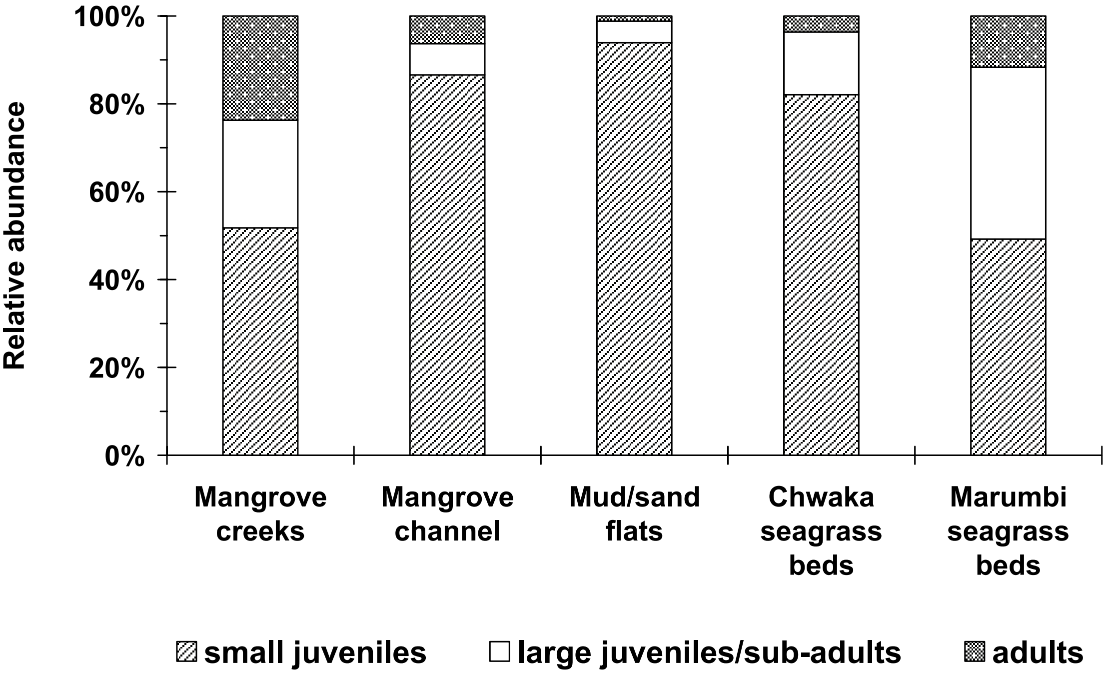

Fig. 7 Relative abundance of different size classes of fishes in different bay habitats.

DISCUSSION

Despite the relatively high number of species, the fish assemblage in Chwaka Bay was composed of a few dominant species only, both in terms of density and biomass. As noted by Quinn[29] this is a common feature of bay, inshore and estuarine fish assemblages in both temperate and sub-tropical environments, where less than six species comprise approximately 70% of the total abundance, even though many more species are caught.[29] In the present study, a slightly higher number of species (nine) comprised 70% of the total catch from Chwaka Bay as a whole. Similar observation (with number of species comprising 70% of the catch) include those of Tudor Creek, Kenya (7 species),[10] Sarodrano mangrove creek, Madagascar (5 species), [30] Cockle Bay, North Queensland, Australia (3 species),[31] and

Caete River estuary, Brazil (6 species)[32]. From the above studies and the present study, it can be generalized that bays and estuaries from tropical environments follow a similar trend as those of temperate and sub-tropical environments where few species dominate despite many species that are encountered in these environments.

Mud/sand flats had the lowest species diversity and evenness, despite having (almost) the highest number of fish species and families. This is probably due to the dominance of one species, viz. *Gerres oyena*. The low species diversity and evenness indices in this habitat are possibly related to the lack of structural complexity as compared to the seagrass and mangrove habitats. Vegetated habitats have been reported to support a high diversity of fishes compared to unvegetated habitats.[33-36]

The Chwaka seagrass beds harboured the highest number of fish species. Higher numbers of species in seagrass habitats compared to mangrove habitats have also been reported in Tudor Creek and Gazi Bay, Kenya[10,11] and in Negombo estuary, Sri Lanka;[37] the opposite has been documented in Australia and in Florida.[38-40] On the other hand, no significant difference in species richness was found between the mangroves and seagrass bed of a non-estuarine bay in the Caribbean.[4] The higher number of fish species, species diversity and evenness in the Chwaka seagrass beds compared to the other habitats, is possibly explained by its location in-between the mangroves in the deeper part of the embayment and the coral reef. Lugendo *et al.*[6] suggest that fish species from adjacent habitats may school together in the seagrass channels of Chwaka during low tides since these channels are always inundated with water. Dorenbosch *et al.*[5] reported the utilisation of Chwaka seagrass channels by fishes from adjacent rocky habitats during low tide.[5] It is furthermore known that fishes use transient habitats during certain phases of tidal cycles.[18,41] Additionally, the Chwaka seagrass beds could also form a corridor for fishes if they undertake an ontogenetic migration from the mangroves to the deeper and outer parts of the embayment.[6]

There was a strong negative relationship between distance and similarity in species composition among habitats. Nevertheless, it is possible that habitat type could be more responsible for the similarity and differences in species diversity and community characteristics observed in the present study than distance alone. Similar habitat types (e.g. mangrove creeks and mangrove channel) showed more similarity compared to that between mangrove habitats and the seagrass beds. However, a relatively large proportion of reef species in Marumbi and Chwaka seagrass beds than in the mangrove habitats which were located deep inside the bay could be an indication of an interaction with the reef. A decrease in the influence of coral reef species with increasing distance away from the reefs has been also observed in Caribbean and Japanese bays.[42,43]

The ichthyofauna of the Chwaka Bay shows similarities but also some marked differences with that of estuaries in the east African region. Gerreidae, Gobiidae, Plotosidae and Siganidae dominated Tudor mangrove creeks[10] whereas Atherinidae, Clupeidae and Gerreidae dominated Gazi Bay.[13] In the present study, Gerreidae and Scaridae dominated the bay as a whole while Ambassidae, Apogonidae and Gerreidae dominated catches from the mangrove habitats. Furthermore, relatively fewer species (44 and 62 for mangrove creeks and mangrove channel, respectively) were collected from the mangroves habitats in the present study compared to the 83 species from Tudor Creek in Kenya.[10] The differences in dominant species and in species richness between these studies are possibly be related to differences in physical conditions that prevail in these various habitats. The seasonal salinity gradient that was recorded in the mangrove habitats of Chwaka Bay, particularly during the rainy season,[23] make mangrove creeks in Chwaka Bay different from Tudor Creek which lacked any marked gradients in salinity between the creek and the ocean.[10] This salinity gradient in Chwaka Bay may possibly have acted as a physiological barrier to stenohaline fishes, resulting in avoidance of the mangrove creeks. Equally important could be the differences in mesh size used, i.e. 0.6 cm in Tudor Creek[10] and 1.8 cm in the present study.

The mean density of fishes was about three times higher in the mangroves than in any of the other habitats. As pointed out by Lugendo *et al.*[6], this is similar to the observation from tropical Queensland (Australia), where 4 − 10 times higher densities of fish were observed in mangroves than in adjacent habitats.[38] The high density of fish in mangroves is probably explained by the high structural complexity formed by the prop-roots.[38,40,44-46] On the contrary, Ikejima *et al.*[47] found no significant differences in abundance between the mangroves and the adjacent habitats.

The greatest proportion of fishes in the bay was formed by small juveniles (75.7%), with adults comprising 7.9% only. Also, the largest proportion of fish species (58.4%) in the bay was composed of species of commercial fishery importance. These findings suggest that the Chwaka Bay habitats are potential nurseries for economically important fish species. Many species that are assumed to utilise these nearshore habitats as nurseries,[24,25] were found throughout the bay, sometimes in relatively high densities. These included species like *Lutjanus fulviflamma*, *Hipposcarus harid*, *Monodactylus argenteus*, *Scolopsis ghanam*, *Siganus sutor* and *Sphyraena barracuda*.

Herbivorous fish species were most abundant in the seagrass beds where they could evidently obtain their preferred food (algae and seagrasses), but they were nearly absent from the mangrove habitats where these food types were largely lacking. The most abundant species found in our study were zoobenthivores. The abundance of zoobenthivores is not unexpected due to the high abundance of invertebrates (an important food resource to zoobenthivores) which are known to occur in these shallow water habitats.[48,49] Zoobenthivore/piscivores represented 19.3% of the fish assemblage in Chwaka Bay; this proportion is consistent with that observed for piscivores in Sarodrano mangroves in Madagascar (18%),[30] but lower than the one observed in the Dampier region, North-western Australia (37%).[50] The proportion of zoobenthivores/piscivores was comparatively higher in the mangrove creeks (31.8%) than in any other bay habitat and was basically made up of mangrove resident species (i.e. large juveniles/sub-adults and adults of *Ambassis gymnocephalus*). Furthermore, occasional visitors/intruders (mainly the reef species *Caranx sexfasciatus*, size range 4.4-14.5 cm, mean size 6.9 cm) which could be potential predators on small juvenile fishes were relatively more abundant within the mangrove creeks than in any other bay habitat. We do not have information on the occurrence of juveniles of this species on the nearby reef. Their size range indicates that all individuals caught were small juveniles, suggesting that they possibly use also the mangrove habitats as a juvenile habitat.

In conclusion, the fish assemblage of all bay habitats was mainly composed of juveniles including many of commercial importance, showing the potential of Chwaka Bay as a juvenile or nursery habitat. All bay habitats were dominated by bay residents. Zoobenthivores dominated the fish assemblages of all habitats except Marumbi seagrass beds where herbivores dominated. The overlap in species composition between bay habitats that was observed in the present study was probably influenced by similarities/differences in habitat type and distance to the reef.

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Chapter 3

Spatial and temporal variation in fish community structure of a marine embayment in Zanzibar, Tanzania

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(*In press-Hydrobiologia*)

Abstract: Spatial and temporal variation in the fish community structure were studied in a tropical non-estuarine embayment in Chwaka Bay, Zanzibar (Tanzania). Fish samples were collected bi-monthly (at each spring low tide) for 1 year (November 2001–October 2002) from a range of bay habitats ranging from mangroves deep inside the bay to seagrass beds close to the mouth of the bay. Additionally, environmental variables were examined to determine their relationship with the fish community structure. Being a non-estuarine embayment, the environmental variables as well as the fish community structure in each habitat remained relatively constant for most part of the year; however, a marked decline was observed during the rainy period (April–May). Significant variations in fish community variables (density, biomass and species richness) and in water temperature and salinity were observed during the rainy season in all habitats, with larger changes in the mangroves and mud/sand flats habitats than in the seagrass beds. Seasonal variations in water clarity and dissolved oxygen were not significant, though. Many species disappeared from the mangrove and mud/sand flats habitats during the rainy season and those which persisted showed a remarkable decrease in density. Moreover, the results indicate that mangroves were the preferred settling habitats for *Gerres filamentosus*, *Gerres oyena*, *Lethrinus lentjan* and *Monodactylus argenteus*, especially during the dry period (December–February) before the rainy season. This observation is contrary to what has been reported from some other tropical regions where greater abundance and species richness was observed during the rainy season. A significant relationship was found between density of fish and temperature, salinity and visibility. Since salinity was the most conspicuously changing environmental variable with seasons, we propose that salinity, alone or in combination with low visibility and temperature, was probably the most important environmental factor structuring the fish assemblage in the mangroves and mud/sand flats habitats, particularly during the rainy season.

INTRODUCTION

In many studies around the world, estuaries have been reported to harbour juveniles of various reef fish species. For some species the utilisation of estuaries is an important phase during their life cycle (Day, 1981). Consequently, these habitats are referred to as nursery areas in several studies (Parrish, 1989). While few marine species spawn in estuaries, many fry enter estuaries shortly after hatching in adjacent marine waters (Blaber, 2000). Mangroves, mudflats and seagrass beds in these estuaries appear to offer an attractive habitat for many species of fish and may offer some advantages over coral reefs for early survival of young juveniles. Several reasons explaining the high abundances of juvenile reef fish species in estuaries in these habitats have been proposed: food abundance (Nagelkerken et al., 2000; Laegdsgaard & Johnson, 2001), protection against predation (Parrish, 1989; Robertson & Blaber, 1992; Laegdsgaard & Johnson, 2001; Cocheret de la Morinie`re et al., 2004; Verweij et al., 2006), and interception of planktonic fish larvae due to their large areas (Parrish, 1989).

The abundance of larvae and juvenile fish can, however, be influenced by physical conditions like salinity, turbidity and temperature that vary in time, largely due to seasonal variations in freshwater input (Cyrus & Blaber, 1987; Barletta et al., 2000; Barletta-Bergan et al., 2002a, b; Barletta et al., 2003, 2005). However, due to the relative stability of temperature in annual patterns within the tropics, physical conditions other than temperature influence larval fish occurrence in tropical estuaries (Barletta-Bergan et al., 2002b).Studies from tropical estuaries show that salinity and freshwater input are important factors associated with fish community structure including larval fish abundance (de Morais & de Morais, 1994; Barletta-Bergan et al., 2002a, b; Barletta et al., 2003, 2005). In Southern African estuaries, salinity and turbidity have been reported to be important factors influencing larval fish abundance (Cyrus & Blaber, 1987; Whitfield, 1994). Other environmental factors like oxygen (Louis et al., 1995) and monsoon-driven coastal currents may influence seasonal dispersal and community structure of estuarine larval fish (Tzeng et al., 2002). However, the response to environmental variables has been shown to be species-specific (Tzeng & Wang, 1992; Barletta-Bergan et al., 2002b).

Comparable to estuaries, marine embayments harbouring mangroves and seagrasses have been reported to play a similar role for juvenile fish (Nagelkerken & van der Velde, 2002; Lugendo et al., 2005). Depending on the configuration of the area, these bays could as well receive a considerable freshwater input during just the rainy season, which will consequently result into (short-term) changes in environmental variables similar to those occurring in estuarine habitats. Being a non-estuarine embayment, the study site at Chwaka Bay in Unguja Island (Zanzibar, Tanzania) maintains a stable marine environment for a large part of the year, except during the rainy season when part of the bay acquires estuarine characteristics.

Many fish species seagrass and mangrove habitats as feeding and/or nursery areas in a way which generally leads to the use of different habitats in different seasons of the year, for example, during periods of highest primary production. In many tropical estuaries, high primary production occurs in the warm and wet season, but in high-salinity fringing mangroves highest primary production occurs during the hot and dry season (Yáñez-Arancibia et al., 1988). This can result into seasonal and spatial variation in fish densities and recruitment (Robertson & Duke, 1987; Ya´n˜ ez-Arancibia et al., 1988) as well as in fish community structure (Robertson & Duke, 1990). The knowledge concerning the utilisation by fish of mangroves and seagrass habitats in East Africa is limited to a few studies done in Kenya (Little et al., 1988; van der Velde et al., 1995a, b; De Troch et al., 1996; Kimani et al., 1996) and in Tanzania (Lugendo et al., 2005). Worldwide, most studies have been done in (temperate) estuaries, and little is known of how environmental variables influence fish communities in marine embayments.

The present study investigated the fish community structure in a tropical marine embayment harbouring mangroves, mud/sand flats and seagrass habitats, in relation to seasonal variation in environmental variables, to answer the following questions: (1) Are there seasonal variations in physico-chemical variables and in fish density, biomass, size, and species richness in different bay habitats? (2) Is there a correlation between presence of fish species and environmental variables? (3) In which bay habitat and season does recruitment of fish occur?

MATERIALS AND METHODS

Study site

Chwaka Bay harbours several marine habitats, including mangrove creeks, mangrove channel, mud/sand flats and seagrass beds. It is a shallow non-estuarine embayment located on the east coast of Unguja Island, Zanzibar, Tanzania (Fig. 1). Chwaka Bay is an intertidal water body (average depth of 3.2 m) and its area varies with the tide: the estimated area during high spring tide is 50 km2 and during low spring tide it is 20 km2 with a mean tidal range of 3.2 m (Cederlo¨ f et al., 1995). Air temperature ranges between 27 and 30°C and rainfall between 1,000 and 1,500 mm per annum. There are two rainy seasons in Zanzibar: the long rains that occur during the months of March, April and May, and the short rains which extend from October to December (McClanahan, 1988). During the study period in 2001 the short rains of October–December were very restricted (maximum 64.2 mm) and are therefore considered a dry season here. The maximum amount of rainfall during the sampling period was 705.4 mm and was recorded in April 2002; for the rest of the year an average (±SD) of 88.6 ± 38.1 mm was recorded. Winds are northeast monsoons (October–March) and southeast monsoons (March–October), with short intermittent periods.

On the landward side, Chwaka Bay is bordered by a dense mangrove forest of approximately 3,000 ha (Mohammed et al., 1995). A number of tidal creeks characterise this mangrove forest, with Mapopwe Creek (approximately 2 m deep) being the largest and the main water exchange route between the forest and the embayment. These creeks are intertidal in nature and none have any significant freshwater input other than rain. During the rainy season, salinity gradients develop and they temporarily acquire estuarine characteristics with salinities as low as 5 ppt (Johnstone & Mohammed, 1995). This part of the bay is characterised by low visibility (range 0.3–1.7 m) and oxygen levels (range 2.9–5.9 mg/l). On the seaward side, immediately adjacent to the forest, the embayment opens up to large intertidal flats that are characterised by mixed assemblages of algae and seagrasses and scattered monospecific seagrass stands. The outer and middle parts of bay (about 4 m deep) are oceanic in character with salinities rarely below 35 ppt and a relatively high visibility (horizontal Secchi disk visibility) of 6.3–15.8 m. The mangrove part of the bay is characterised by higher ammonium concentrations as compared to the rest of the bay, as well as a higher ammonium concentration during the dry season as compared to the wet season (Johnstone & Mohammed, 1995; Mohammed & Johnstone, 2002). Similarly, the mangrove part of the bay is characterised by higher primary productivity than the rest of the bay with significantly higher levels during November–December period (Kyewalyanga, 2002). The bay is relatively sheltered since it 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).

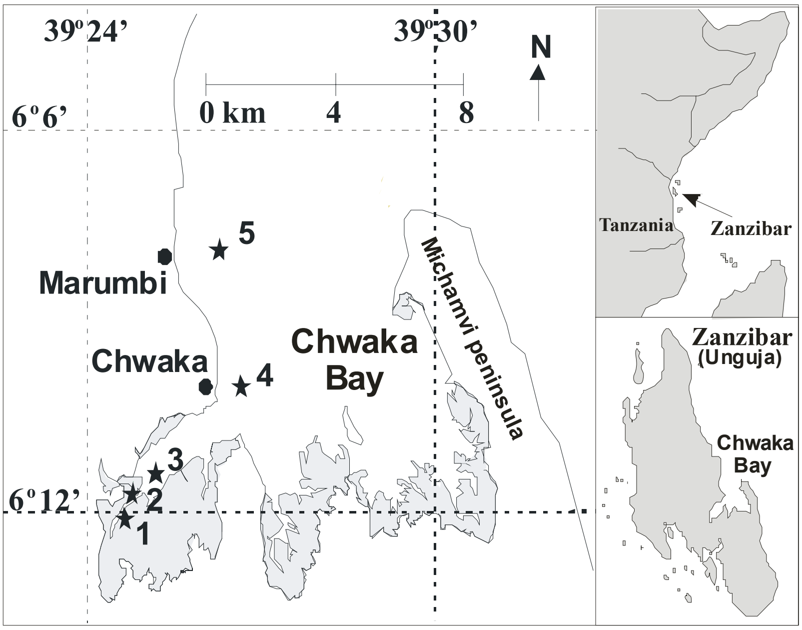

Fig. 1 Map of Chwaka Bay showing the locations of the sampled habitats (1 = mangrove creeks, 2 = mangrove channel, 3 = mud/sand flats, 4 = Chwaka seagrass bed, 5 = Marumbi seagrass bed). Gray areas in Chwaka Bay indicate mangrove forests

Field sampling

Prior to fish sampling, water temperature, pH, salinity and dissolved oxygen were measured using a temperature-compensated Multi Parameter Analyser (Eijkelkamp, model 18.28). Furthermore, visibility was determined using a line extended to the maximum horizontal distance at which a snorkeller in the water could discern a black and white coloured Secchi disk (44 cm diameter). Environmental variables could not be measured during some months due to equipment failure and no possibilities for repair or replacement.

Fish samples were collected bi-monthly (at each spring low tide) for a period of 1 year (November 2001–October 2002) from five habitats in Chwaka Bay: (1) mangrove creeks, (2) mangrove channel, (3) intertidal mud/sand flats located 2 km from the mangroves, (4) Chwaka seagrass beds located about 6 km from the mangroves, and (5) Marumbi seagrass beds situated about 8 km from the mangroves (Fig. 1). Characterised by a muddy substratum and prop roots of the mangrove *Rhizophora mucronata* (Lamarck), the mangrove creeks and channel habitats had few algae and seagrasses. The mud/ sand flats were characterised by a higher cover of algae and some seagrasses. The sampled seagrass beds consisted of vast fields of *Enhalus acoroides* (L.) Royle, interrupted by small patches of *Thalassodendron ciliatum* (Forsskål) den Hartog and the calcareous algae *Halimeda* spp.

A seine net measuring 35 m in length, 3 m in height and with a stretched mesh size of 1.8 cm was used to collect fish from all habitats, except in the creeks, with a sampled area of approximately 480 m^2 per haul. The seine net could not be used in the creeks due to their narrowness. Instead, an alternative method was used where the mouth of the mangrove creeks (about 4 m wide) was closed by the net and the whole net laid out upstream at one side of the creek (about 30 m) and then closed again, sampling an area of approximately 120 m^2. In each habitat, four replicate hauls were randomly taken during each spring tide.

To make sure that the net remained vertically stretched and touched the bottom, a metal chain was attached at the middle part of the sinker line. In addition, plastic floats were attached to the float line so that the upper side of the net remained afloat. Concurrently, snorkelling observations were made for net efficiency during deployment to check whether the net trailed over the substratum and if any fish escaped. We observed that the lower part of the net remained on the bottom throughout the exercise and no fish escaped below the net. Only some individuals of Mugilidae jumped over the net. It was concluded that the procedure was well designed for the species under study. To standardize the methods, we involved the same two fishermen, using the same net, and similar net deployment procedures throughout the sampling period.

Fish fork lengths of caught specimens were measured to the nearest 0.1 cm and their wet weight established to the nearest 0.1 g as a measure of biomass. In order to describe the overall picture of the bay, the variation in total density, total biomass and species richness is presented for each bay habitat. In addition, based on their high frequency of occurrence, numerical dominance, their commercial value, their potential as nursery species (Dorenbosch et al., 2005) and their occurrence in more than one habitat, the following species were studied in more detail to investigate the influence of seasonal variations on individual species and size classes: *Gerres filamentosus* (Cuvier), *Gerres oyena* (Forsskål), *Lethrinus lentjan* (Lacepède), *Lutjanus fulviflamma* (Forsskål), *Monodactylus argenteus* (Linnaeus), *Siganus sutor* (Valenciennes) and *Sphyraena barracuda* (Walbaum).

It should be noted that the majority of the juveniles collected in this study were larger than 2.5 cm in length. The smaller fish (<2.5 cm) were mostly fish larvae about to settle and tended to pass through the net and this may possibly have lead to a small underestimation of the total density of very young juveniles under study. However, since the same mesh size was used throughout the bay habitats, the effect of the net (if any) applies for all the habitats and hence the observations from this study are representative for the different bay habitats. Detailed information (density, biomass, etc.) at species level on the fish community structure of Chwaka Bay can be found in Lugendo et al. (in press, in revision).

Statistical analysis

A choice for a parametric or a non-parametric test was made after the data were tested for homogeneity of variances using a Levene’s test. In case variances were homogeneous, a one-way ANOVA was employed to test differences in both fish community variables and environmental variables across the range of habitats and among seasons (dry season before rainy season, rainy season, and dry season after rainy season). Habitat and season were tested separately. 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 kind of data compared to other tests (Field, 2000). All data that did not show homogeneous variances were log-transformed, and a Levene's test was performed once again. A Kruskal–Wallis test was used as a non-parametric test equivalent to a one-way ANOVA when variances were not homogeneous, even after log-transformation. In this case, a Games–Howell post-hoc was used because this test is more powerful and specifically designed for lack of homogeneity of variances (Field, 2000).

To examine the relationship between fish community and environmental variables in different bay habitats, two sets of multiple linear regression analyses were performed; (1) for mean density, biomass and species richness of all species pooled, (2) for total density of each of the seven selected species. All analyses were performed using the programme SPSS for Windows (Field, 2000). Semi-partial (Part) correlations are provided to show the correlations of the separate independent variables with the dependent variable, taking the effect of the other independent variables into account. A significance level of $P < 0.05$ was used in all tests. Correlations between environmental variables and the fish densities were also examined with a Principal Component Analysis, using the Canoco 4.0 ordination program (ter Braak & Smilauer, 1998). Scaling was focused on inter-species distances, and species scores were divided by the standard deviation.

RESULTS

Temporal and spatial variation in physico-chemical variables

The measured abiotic variables varied both spatially and seasonally. While pH, water temperature and oxygen levels were lowest just after the rainy season (June–July), salinity and visibility were lowest during the rainy season (April–May; see Supplementary material). There was a marked seasonal variation in salinity for mangrove and mud/sand flats habitats with lowest values (as low as 5‰ in the mangrove channel) recorded during the rainy season. Variations in salinity were less pronounced in Marumbi seagrass beds where levels remained close to that of oceanic water throughout the year (average 35.5‰; see Supplementary material). Nevertheless, the variations in salinity were significant between seasons in all habitats, with salinity during the rainy season being significantly different from those of the other two seasons (Hochberg's GT2, $P < 0.05$ for mangrove creeks, Games–Howell, $P < 0.05$, for the other habitats). Significant seasonal variations were also observed for water temperature (Kruskal–Wallis, $P < 0.001$) in all habitats.

Lowest values for salinity, oxygen and visibility were recorded within mangrove habitats (i.e. mangrove creeks and mangrove channel) and mud/sand flats, whereas highest values were recorded for the seagrass habitats (Chwaka and Marumbi seagrass beds; see Supplementary material). While water temperature and pH did not vary significantly across habitats, salinity, oxygen and visibility did

(Kruskal–Wallis; P = 0.030, P = 0.001 and P < 0.001, for salinity, oxygen and visibility, respectively). Significantly higher values (Games–Howell; P < 0.05) were recorded within the seagrass habitats as compared to either the mangrove habitats only (for salinity and oxygen), or the mangrove habitats as well as mud/sand flats (for visibility).

Temporal variation in total fish density, biomass and species richness

In the mangrove creeks, two peaks for both density and biomass were observed during the two dry periods: before (in December) and after (in July) the rainy period (Fig. 2). During the rainy season, a sharp drop in total density and biomass was observed. For the mangrove channel and mud/sand flats only a high peak was observed for fish biomass and density in the dry period before the rainy season, with a sharp drop during the rainy period and only a slight increase afterwards. Also Chwaka and Marumbi seagrass beds showed only a high peak in fish biomass and density before the rainy season, viz. around November/December. Significant differences among seasons were found for fish densities in all habitats (mangrove creeks: one-way ANOVA, P = 0.001; mangrove channel: one-way ANOVA, P < 0.001; mud/sand flats: Kruskal–Wallis, P < 0.0010; Chwaka seagrass beds: one-way ANOVA, P < 0.001; and Marumbi seagrass beds: one-way ANOVA, P < 0.001), with significant differences between the rainy season and the two dry seasons (for mangrove habitats, Hochberg's GT2; P < 0.001), between the dry season after the rainy season and either the rainy season or the dry season before the rainy season (for mud/sand flats, Games–Howell; P < 0.001, for Marumbi, Hochberg's GT2; P = 0.024, and for Chwaka seagrass beds, Hochberg's GT2; P = 0.006).

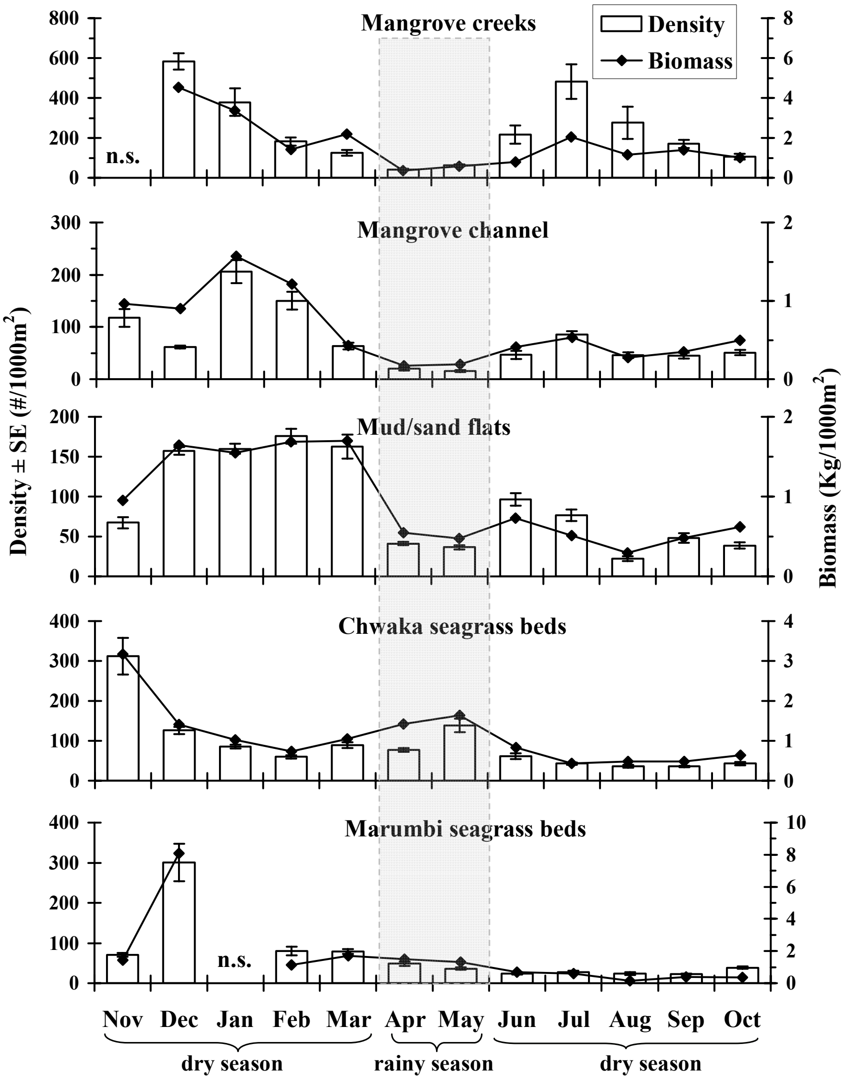

Fig. 2 Temporal variation in mean total fish biomass and mean total density (± SE) in different bay habitats in Chwaka Bay. No sampling (n.s.) was done during November in the mangrove creeks and during January in the Marumbi seagrass beds

Species richness also varied over the year with a marked decrease during the rainy season for all habitats except Marumbi seagrass beds, which also had few species during the dry period following the rainy season (Fig. 3). Generally, the highest number of species was observed during the dry period before the rainy season. The seasonal variation in species richness was significant in all habitats (mangrove creeks: oneway ANOVA, $P < 0.001$; mangrove channel: oneway ANOVA, $P = 0.006$; mud/sand flats: Kruskal–Wallis, $P = 0.002$; Chwaka seagrass beds: one-way ANOVA, $P < 0.001$; and Marumbi seagrass beds: one-way ANOVA, $P = 0.006$). The significant seasonal variation in species richness was always present between the rainy season and the dry season before the rainy season, for the mangroves creeks (Hochberg's GT2; $P < 0.001$), mangrove channel (Hochberg's GT2; $P = 0.004$) and mud/sand flats (Games–Howell; $P < 0.001$), and between the two dry seasons for the mud/ sand flats (Games–Howell; $P < 0.001$), and Chwaka and Marumbi seagrass beds (mud/sand flats, wochberg's GT2; $P < 0.001$).

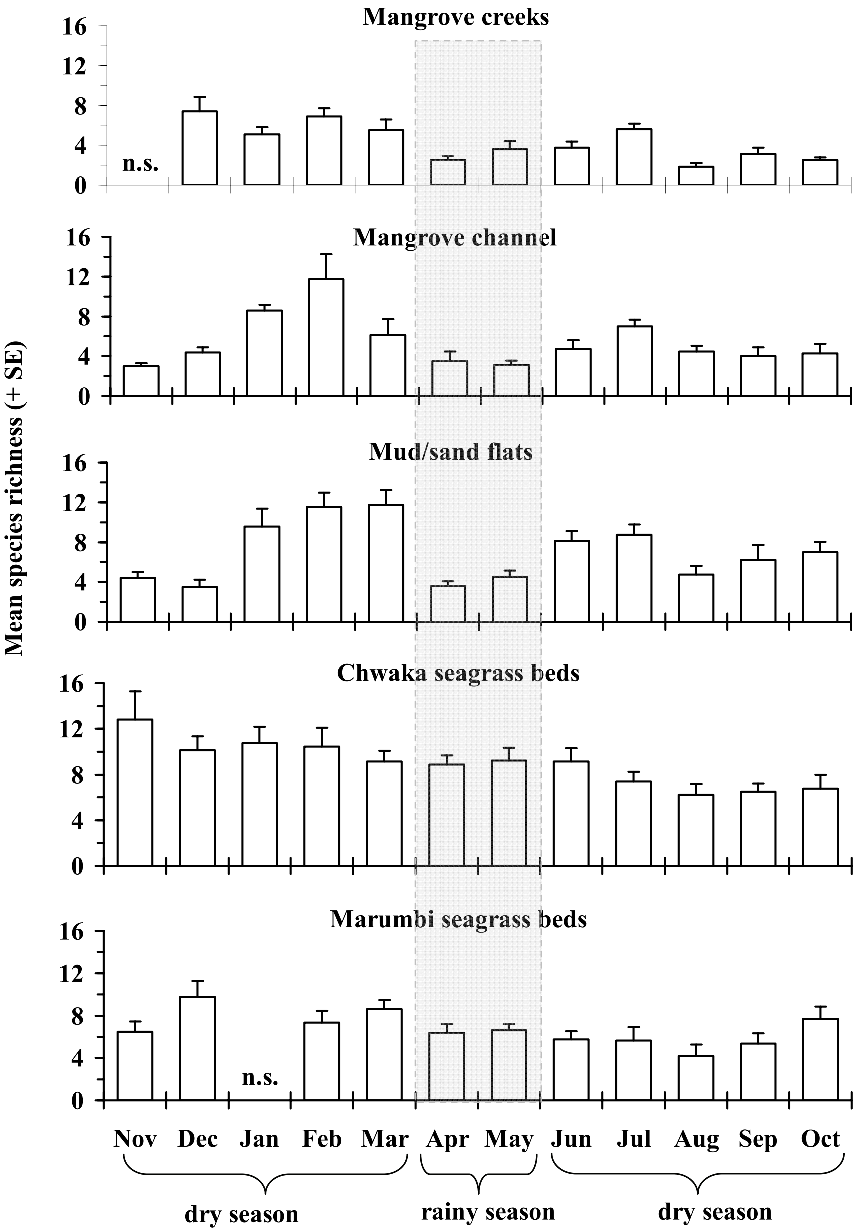

Fig. 3 Temporal variation in mean species richness (+SE) in different bay habitats in Chwaka Bay. No sampling (n.s.) was done during November in the mangrove creeks and during January in the Marumbi seagrass beds

Temporal variation in density and size of target species

The majority of fish caught within the bay habitats were larger than 4 cm; however, in four of the seven common species (i.e. *G. filamentosus*, *G. oyena*, *L. lentjan*, and *M. argenteus*) also recruits (< 4 cm) were recorded, although in low densities (Fig. 4). The majority of these smallsized juveniles were found within the mangrove creeks and channel, and sometimes also in the mud/sand flats. They were most abundant during the dry seasons, especially the one before the rainy season (Fig. 4). *G. oyena* additionally showed a high peak of small juveniles after the rainy season.

Generally, regardless of size, there was a sharp drop in density of species during the rainy season in the mangrove habitats and mud/sand flats. Many species disappeared from these habitats and those which persisted showed a remarkable decrease in density (Fig. 4). This was also revealed at family level where Apogonidae, Gerreidae, Leiognathidae, Lethrinidae and Teraponidae, which were abundant families in the mangrove and mud/sand flat habitats, peaked during the dry season before the rain and disappeared during the rainy season. There were two exceptional families: Ambassidae (*Ambassis gymnocephalus* (Lacepède)) and Cyprinodontidae (*Pantanodon podoxys* (Myers)) which peaked just after the rain season in the mangrove creeks (Fig. 5a). In Chwaka seagrass beds Teraponidae showed a decrease in density during the rainy season, whereas Gerreidae, abundant in four out of the five studied habitats, together with medium and/or large-sized fishes of two other species (i.e. *Lutjanus fulviflamma* and *Sphyraena barracuda*), showed elevated densities during the wet season (Fig. 4). The Marumbi seagrass beds did not show a pattern of low densities of the above-mentioned families during the rainy season versus high densities during the dry seasons.

Correlation with environmental variables

Multiple regression analysis showed that in three of the five studied habitats (mangrove channel, mud/sand flats and Chwaka seagrass beds), environmental variables showed significant relationships with fish community variables (see Supplementary material). In the mangrove channel mean density and species richness showed a negative relationship with temperature ($r^2 = 0.697$, $P = 0.032$, and $r^2 = 0.795$, $P = 0.022$, for mean density and species richness, respectively). In the mud/sand flats mean density of fish had negative relationships with temperature, visibility and salinity (full model: $r^2 = 0.997$, $P = 0.007$) while species richness showed a negative relationship with temperature, salinity, oxygen and visibility (full model: $r^2 = 0.992$, $P = 0.017$). In Chwaka seagrass beds mean species richness showed a negative relationship with temperature and visibility (full model: $r^2 = 0.982$, $P = 0.037$). No significant relationship was found between mean biomass and environmental variables in any of the habitats (see Supplementary material).

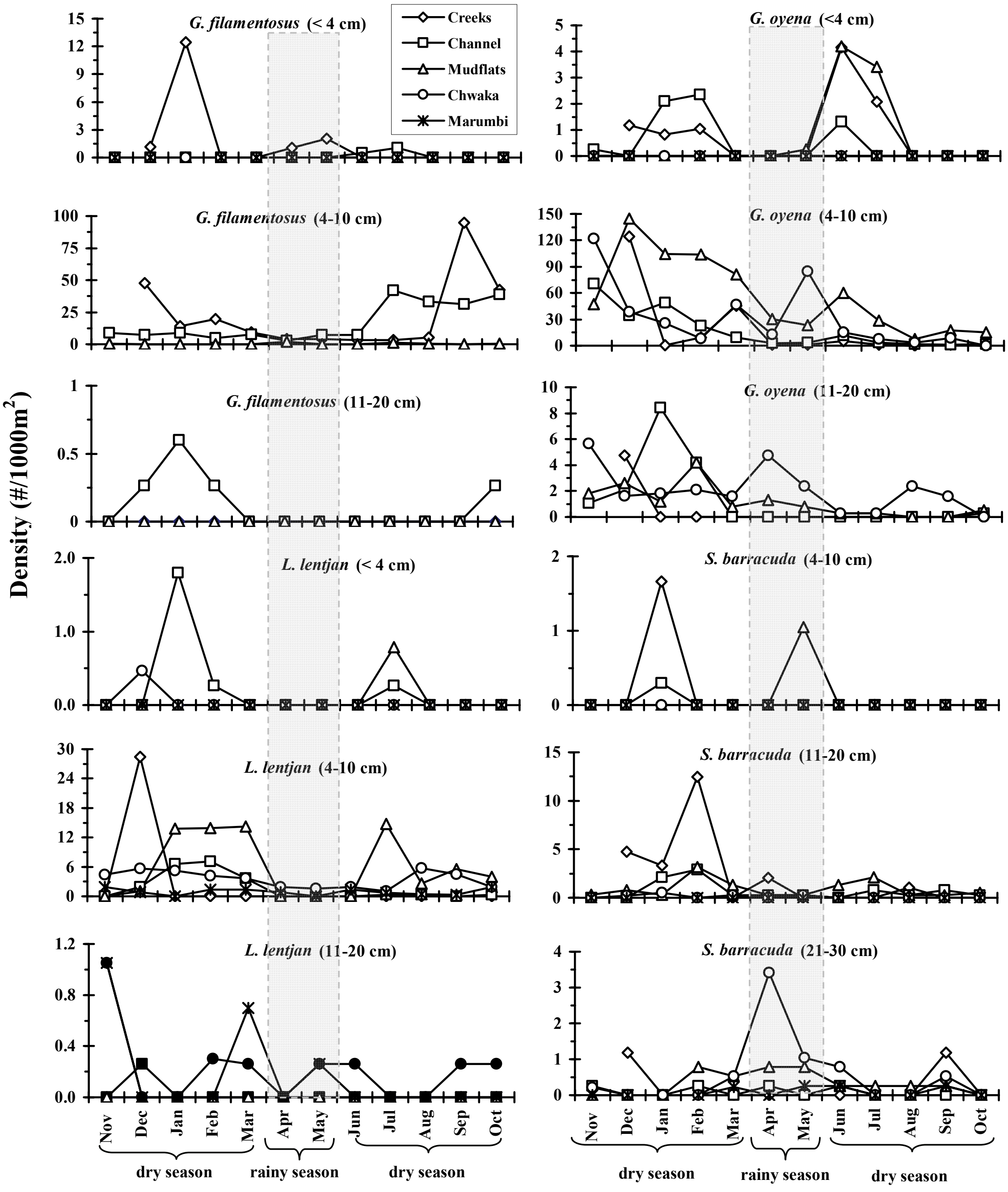

Fig. 4 Temporal variation in density of different size classes (<4, 4–10, 11–20, and 21–30 cm) of common fish species in different bay habitats

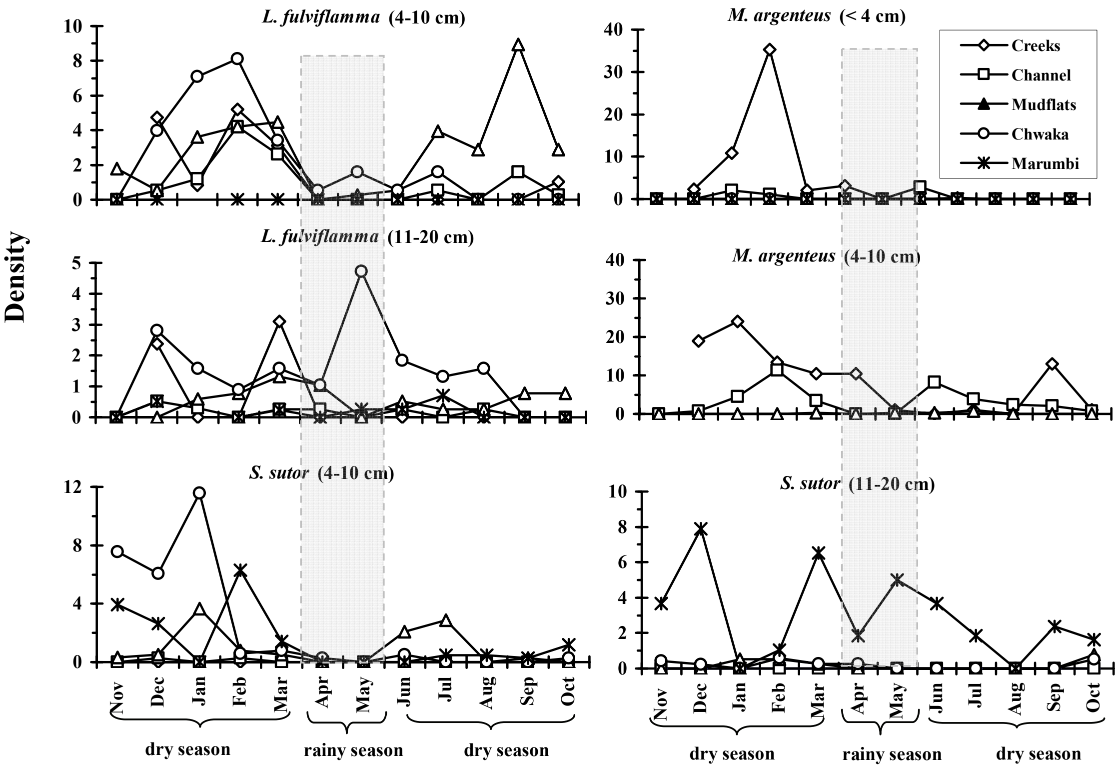

Fig. 4 continued

Significant relationships were also discerned at species level in different bay habitats (see Supplementary material). In the mangrove channel *Gerres filamentosus* and *Lethrinus lentjan* showed a negative relationship with visibility (r^2 = 0.695, P = 0.018 and r^2 = 0.756, P = 0.045, for *G. filamentosus* and *L. lentjan*, respectively). *Monodactylus argenteus* showed a negative relationship with temperature (r^2 = 0.416, P = 0.026) and salinity (r^2 = 0.458, P = 0.021), and a positive relationship with visibility (r^2 = 0.652, P = 0.011. In mud/sand flats *G. filamentosus* showed a negative relationship with visibility (r^2 = 0.731, P = 0.032), while *G. oyena* had a negative relationship with temperature (r^2 = 0.912, P = 0.032). A significant negative relationship was also found between density of Sphyraena barracuda and salinity in Chwaka seagrass beds (r^2 = 0.815, P = 0.033).

Principal component analysis (PCA) showed a clear separation between species in the mangrove habitats and those in the other habitats (Fig. 6). The eigenvalues of the first and second PCA axis were 0.686 and 0.225, respectively, indicating that a high proportion of the variation in species density data could be explained by the hypothetical axes. The PCA graph shows that *G. filamentosus* and *M. argenteus* were present in the mangrove habitats regardless of seasons, and that their densities in both seasons were negatively correlated with all measured environmental variables (Fig. 6). The remaining species, viz. *G. oyena*, *L. lentjan*, *L. fulviflamma* and *S. barracuda*, showed a change in highest densities during the rainy season from either the mangrove habitats or mud/sand flats to the seagrass beds, with exception of *S. sutor* which changed from Chwaka to Marumbi seagrass beds (Fig. 6).

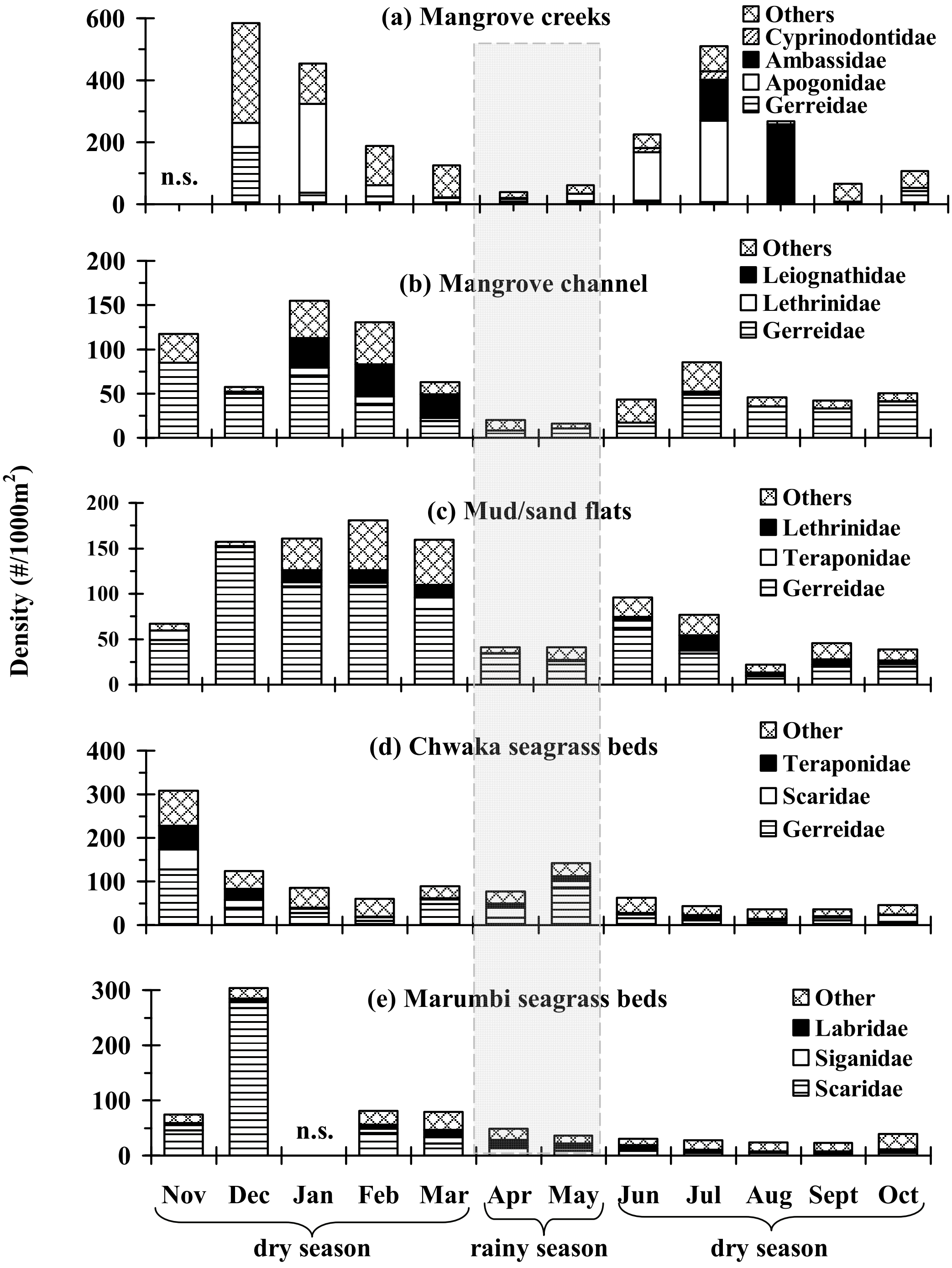

Fig. 5 Temporal variation in density of abundant families of fish in different habitats in Chwaka Bay. No sampling (n.s.) was done during November in the mangrove creeks and during January in the Marumbi seagrass beds

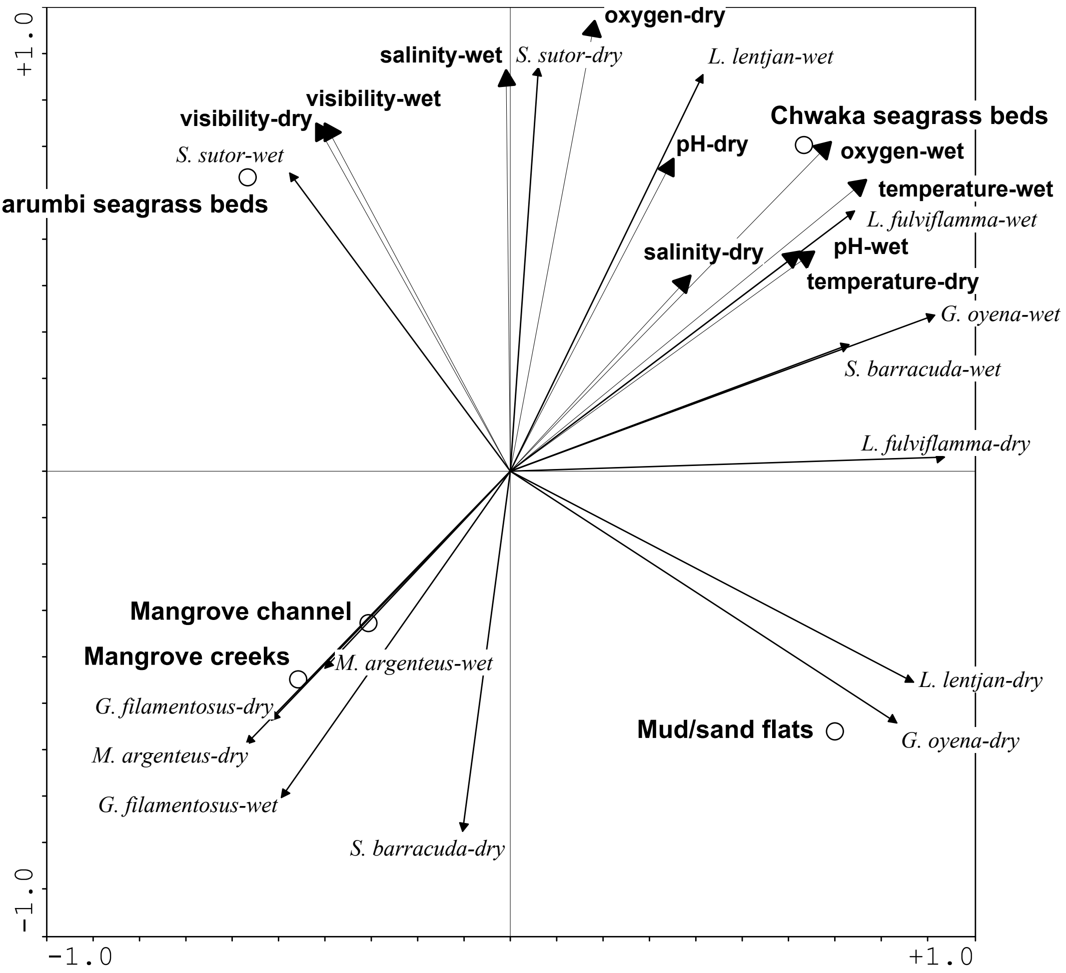

Fig. 6 Principal component analysis (PCA) graph showing correlation between density of common fish species and abiotic variables in dry and wet seasons in different bay habitats

DISCUSSION

Fish community as well as abiotic variables showed temporal variations in Chwaka Bay. Density, biomass and species richness remained constant for most part of the year but declined significantly during the rainy season. Likewise, environmental variables remained constant for most part of the year, however, there was a conspicuous change during the rainy season especially in the mangrove habitats and mud/ sand flats. Despite the absence of evident surface freshwater inflow into Chwaka Bay, surface flow from the heavy rains during April caused significant changes in environmental variables in the mangroves and mud/sand flats habitats. These effects decreased farther out towards the seagrass beds because these were located further away from the rain water outflow. A relationship was present between density of fish and temperature, salinity and visibility. Salinity was the most conspicuously changing environmental variable with seasons. Therefore, salinity, alone or in combination with low visibility and temperature, was likely the most important environmental factor structuring the fish assemblage deep within Chwaka Bay (i.e. in the mangrove habitats and mud/sand flats), particularly during the rainy season. This probably explains the decline in fish density and biomass in the mangrove habitats and mud/sand flats during the rainy season. This effect is also known from temperate South African estuaries (Strydom & d'Hotman, 2005), and from a northern Brazilian tropical estuary (Barletta-Bergan et al., 2002b; Barletta et al., 2003, 2005).

Fish found in true estuarine habitats are believed to be generally more tolerant of low salinities than of high salinities (Weerts & Cyrus, 2002). The opposite seems to be the case for Chwaka Bay fishes since this bay exhibits marine conditions for most part of the year. As the fish species here are marine species adapted to ocean water salinities (which is constant for most part the year), they probably do not withstand the low salinities, perhaps coupled by low visibility, in the mangrove habitats brought about with the surface run-off from the rain. As a result they appeared to move away from these habitats. Indeed, low salinities (below 16 ppt) have been reported to be stressful to marine fish with a possibility of restricting the type and number of species in a particular area (Bulger et al., 1993). Hence, marine embayments appear to be different from estuaries in that they contain mostly marine species which appear to migrate away when salinities reach estuarine characteristics. Barletta et al. (2003) suggested the possibility of the tidal channel of a lower estuary being used as refuge habitats for species that seek shelter when the estuary is strongly influenced by freshwater. Similarly, Chwaka seagrass beds may probably serve as a refuge habitat for fishes coming from the mangroves and mud/sand flats habitats when these habitats are strongly influenced by freshwater. The decline in fish density and biomass during the rainy period within the mangrove habitats and the increase in density of some fish species (Gerres oyena, Lutjanus fulviflamma and Sphyraena barracuda) in Chwaka seagrass beds where fluctuation in abiotic variables was less severe could explain a seasonal migration of fish in search for an optimal environment. Studies by Barletta-Bergan et al. (2002b) and Barletta et al. (2003) in the Caete´ Estuary, Brazil, reported seasonal fish movement and migration during the rainy season due to increase in freshwater runoff which resulted in a decline in salinity.

The most striking observation in the present study is the extent to which short term (April–May) changes in environmental variables brought about such significant changes in fish densities. According to Blaber (1980), substrate type, depth and turbidity may be important factors in determining the distribution of juvenile fish in tropical estuaries rather than salinity. However, given the fact that Chwaka Bay is not an estuary but has stable environmental variables during most part of the year, the short-term seasonal variation in salinity here was probably a more important factor in explaining the temporal variations in fish community structure observed. In this case, other factors like water depth and substrate type probably have a minor or secondary influence. However, in agreement with Blaber (1980) under relatively stable environmental conditions, the other factors (water depth and substrate type) are much more important in explaining the distribution of juvenile fish.

Our results do not address factors that influence recruitment of fish in Chwaka Bay. However, the seasonal variation in densities of recruits (< 4 cm) of the four target species (*Gerres filamentosus*, *G. oyena*, *Lethrinus lentjan* and *Monodactylus argenteus*) suggests a possible timing of settlement during favourable conditions. Factors like high primary production (Ya´n˜ ez-Arancibia et al., 1988), favourable temperature, turbidity and salinity (Cyrus & Blaber, 1987) seem to be related to the patterns observed for recruits in the bay habitats. Timing of spawning to match the spatial and temporal coincidence of recruits and food items has been pointed out to be among possible reasons for seasonal variations in the abundance of fish larvae (Dickey-Collas et al., 1996). Johnstone & Mohammed (1995) and Mohammed & Johnstone (2002) report high ammonium concentration (the form of nitrogen taken up most readily by phytoplankton) within the mangroves of Chwaka Bay as compared to the rest of the bay, as well as high ammonium concentrations during the dry season as compared to the wet season. In addition, Kyewalyanga (2002) reported a higher primary productivity within the mangrove habitats in Chwaka Bay as compared to seagrass beds, and a general high primary productivity during the November–December period. These observations coincide with higher densities of recruits within mangrove habitats around this time, suggesting that high primary production could be among the factors that favours settlement of fish during this period of the year. Cyrus & Blaber (1987) mention increased turbidity as one of the factors associated with larval fish abundance. This factor is possibly also important in Chwaka Bay where recruits were abundant in the mangrove and mud/ sand flats habitats during the dry season, where turbidity was significantly higher compared to seagrass beds. However, during the rainy season enhanced turbidity and reduced oxygen levels coupled with osmotic stress due to very low salinities in these areas likely made these habitats hostile for recruits to survive. These are possibly among the reasons why recruits were abundant in the mangrove habitats during the dry season and not found here during the rainy period. Four of the seven studied species showed recruits within the mangroves during January–February period, suggesting that these species have similar requirements as far as recruitment is concerned. Possible differences in breeding season or in the habitat preference for recruitment for the other fish species (e.g. *Lutjanus fulviflamma*, *Siganus sutor* and *Sphyraena barracuda*) need further research as they can not be substantiated by this study. The dominance of juveniles of Gerreidae in the mangrove habitats is consistent with other studies done within Indian Ocean and elsewhere (Little et al., 1988; Laroche et al., 1997; Nagelkerken et al., 2000; Vidy, 2000) while those of *Lethrinus lentjan* and *Monodactylus argenteus* are known to be brackish spending their early life time in mangroves (Froese & Pauly, 2004).

The questions that were set at the beginning of this study can be answered as follows: (1) There was a significant seasonal variation in physicochemical variables specifically in temperature and salinity, and in fish density, biomass and species richness in different bay habitats, (2) Water temperature, salinity and visibility are the environmental variables that showed the highest correlation with the fish community variables, (3) Settlement of small juveniles (<4 cm) of several common species occurred mainly in the mangrove habitats and to a lesser extent within the mud/sand flats, and was highest in the dry season before the rainy season (December–February) when environmental conditions were probably most favourable. Similar to fish density, the species richness of fishes in Chwaka Bay was also significantly higher in the dry season (before the rainy season) than in the rainy season. This observation is contrary to what has been reported from some other tropical regions where higher abundance and species richness was observed during the wet season (West Atlantic: Stoner, 1986; Australia: Robertson & Duke, 1990; Thailand: Ikejima et al., 2003).

Acknowledgements

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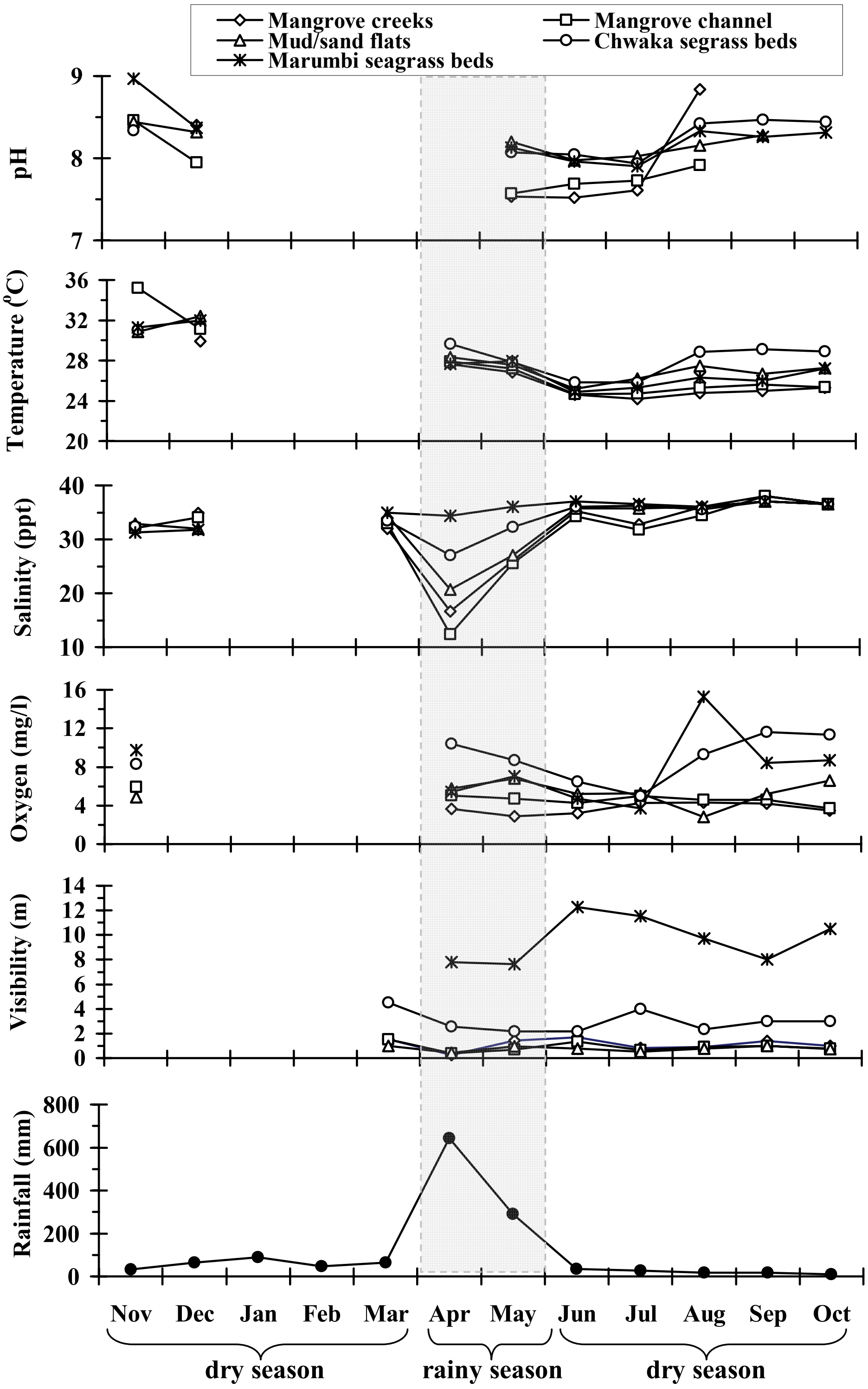
SUPPLEMENTARY MATERIAL



Temporal variation in environmental variables in different bay habitats in Chwaka Bay. Total monthly rainfall for Zanzibar was provided by the Department of Meteorology, Zanzibar.

Results of the multiple linear regression analyses showing the R^2 and P-value of the full model and the part (semi-partial) correlation of the separate environmental variables, for the total mean density, biomass and species richness of all species and for density of the common species in each habitat. * = Significant at 0.01<p<0.05, ** = significant at p<0.01.

	Part Correlations				Full model	
	Temperature	Salinity	Oxygen	Visibility	R2	P
Creek						
Mean Density	-0.669	-0.412	0.138	0.060	0.926	0.143
Mean Biomass	-0.356	-0.142	0.260	0.055	0.794	0.370
Mean Species	-0.732	-0.679	0.005	0.284	0.642	0.587
G. filamentosus	0.642	0.507	0.423	0.205	0.676	0.543
G. oyena	-0.713	-0.577	-0.209	0.288	0.787	0.381
L. fulviflamma	0.244	0.805	-0.710	-0.823	0.917	0.160
M. argenteus	0.473	-0.034	0.586	0.288	0.629	0.604
S. barracuda	0.435	-0.019	0.543	0.122	0.774	0.400
Channel						
Mean Density	-0.697*	-0.069	0.095	-0.410	0.968	0.063
Mean Biomass	-0.535	-0.021	-0.245	-0.334	0.848	0.280
Mean Species	-0.795*	-0.244	0.173	-0.339	0.972	0.056
G. filamentosus	-0.328	0.371	0.014	-0.695*	0.982	0.036*
G. oyena	-0.303	-0.633	-0.151	0.768	0.922	0.150
L. fulviflamma	0.324	0.566	0.453	0.029	0.428	0.817
L. lentjan	-0.681	-0.050	-0.073	-0.756*	0.944	0.108
M. argenteus	-0.416*	-0.458*	0.006	0.652*	0.991	0.018*
S. barracuda	-0.080	0.299	0.602	-0.294	0.554	0.693
Mud/sand flats						
Mean Density	-0.827**	-0.219*	0.128	-0.225*	0.997	0.007**
Mean Biomass	-0.380	-0.180	0.649	-0.157	0.866	0.438
Mean Species	-0.365*	0.418*	0.329*	-0.371*	0.992	0.017*
G. filamentosus	0.168	-0.139	-0.054	-0.731*	0.964	0.070
G. oyena	-0.912*	-0.557	0.020	-0.051	0.945	0.108
L. fulviflamma	0.261	0.495	0.050	0.083	0.399	0.841
L. lentjan	0.132	0.557	0.238	-0.618	0.594	0.647
M. argenteus	-0.338	0.073	0.202	-0.483	0.502	0.748
S. barracuda	-0.534	-0.361	0.197	-0.166	0.499	0.751
S. sutor	-0.472	0.188	0.234	-0.564	0.930	0.136
Chwaka						
Mean Density	-0.294	-0.542	0.197	-0.266	0.564	0.682
Mean Biomass	-0.285	-0.704	0.241	-0.233	0.845	0.285
Mean Species	-0.529*	-0.762*	0.333	-0.195	0.982	0.037*
G. oyena	-0.206	-0.332	0.121	-0.309	0.340	0.885
L. fulviflamma	-0.054	-0.250	-0.151	-0.297	0.726	0.524
L. lentjan	0.618	0.761	-0.450	-0.472	0.846	0.284
S. barracuda	-0.216	-0.815*	0.217	0.035	0.953	0.091
S. sutor	0.467	0.640	-0.697	-0.004	0.790	0.375
Marumbi						
Mean Density	0.474	-0.324	-0.307	0.244	0.958	0.082
Mean Biomass	0.132	-0.306	-0.600	-0.138	0.870	0.243
Mean Species	0.803	0.371	-0.554	0.407	0.896	0.197
L. fulviflamma	-0.073	0.038	-0.503	0.171	0.533	0.716
L. lentjan	0.553	0.111	-0.052	0.789	0.677	0.541
S. barracuda	-0.100	0.576	-0.362	-0.509	0.623	0.612
S. sutor	0.467	0.640	-0.697	-0.004	0.790	0.375

Chapter 4

Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania

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***Abstract*:** Habitat utilisation by juveniles of 13 commercially important fish species was studied in five habitats located in Chwaka Bay, Zanzibar: mangrove creeks, mangrove channel, sand/mud flats, a seagrass area close to mangroves, and a seagrass area far from mangroves. Fish samples were collected from each habitat using a seine net, and fish abundance and size were measured to determine habitat utilisation. The seagrass beds near to mangroves showed the most diverse fish assemblage of all habitats, possibly because it functions as a corridor between the mangroves and deeper parts of the embayment. Juveniles of *Cheilio inermis*, *Hipposcarus harid, Leptoscarus vaigiensis*, and *Scolopsis ghanam* inhabited seagrass beds only. Juveniles of *Gerres filamentosus* and *Monodactylus argenteus* were mainly found in the mangrove habitats. *Lethrinus variegatus*, *Pelates quadrilineatus* and *Siganus sutor* were found in more than two habitats, with highest abundances in seagrass beds. Juveniles of *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma* and *Sphyraena barracuda* were the most generalist species and were found in all studied embayment habitats. Visual census surveys supported the seine net data showing that most fishes in the embayment habitats were juveniles or sub-adults. In terms of habitat utilisation by different size classes, five of the 13 species (*Lethrinus lentjan*, *L. variegatus*, *P. quadrilineatus*, *Siganus sutor* and *Sphyraena barracuda*) were found as small-sized individuals in shallow and turbid mangrove areas, whereas large-sized individuals were observed in deeper and less turbid seagrass beds. A possible explanation for this pattern could be an ontogenetic shift in habitat utilisation, although this could not be proven. The patterns observed in the present study show a high similarity to those observed in marine embayments in the Caribbean, indicating that similar mechanisms are at work which make these systems attractive juvenile habitats.

INTRODUCTION

Lagoonal and bay habitats containing mangroves and seagrasses are known to be important habitats for juvenile fish, many of them commercially important to reef fisheries (Blaber & Blaber 1980; Parrish 1989; Nagelkerken et al. 2000b; Nagelkerken & van der Velde 2002; Dorenbosch et al. 2004a). It is suspected that they act as nurseries for juvenile fish, although some evidence has yet been provided (Beck et al. 2001; Chittaro et al. 2004). At a certain stage, most fish probably outgrow the protection of these habitats and likely migrate permanently from their nursery habitats to deeper water, such as adjacent coral reefs (Cocheret de la Morinière et al. 2002; Nagelkerken & van der Velde 2002; Nagelkerken et al. 2002; Dorenbosch et al. 2004a).

The present knowledge concerning the nursery potential of habitats with mangrove and seagrasses is mostly based on research conducted in North America, Australia and the Caribbean (see for example Robertson & Duke 1987; Thayer et al. 1987; Morton 1990; Nagelkerken et al. 2000a,b; Cocheret de la Morinière et al. 2002), with most studies carried out in estuaries. The general situation in the Indo-Pacific region may differ considerably from Caribbean islands, since bays and estuaries along the continental coastline in the former area are often characterised by turbid waters, a larger tidal range and a muddy substratum (Blaber 2000). Given that the functioning of mangroves as juvenile fish habitats is not the same in all areas across the globe (see for example Chong et al. 1990), it is of importance to study these areas separately to understand the potential variations in the role of mangroves as fish habitats.

In East Africa hardly any fish studies have been done in shallow tropical habitats, knowledge of the utilisation of mangroves and seagrass beds by fishes is limited to a few studies done in Kenyan estuaries (Little et al. 1988; van der Velde et al. 1995; De Troch et al. 1996; Kimani et al. 1996; Wakwabi 1999). Hence it is not clear how marine embayments in this region (and others) are utilized by juvenile fish. The scarcity of such studies world-wide could lead to an underestimation of the importance of such habitats, a situation that could lead to degradation and/or loss of these habitats (Morton 1990; Nagelkerken 2000).

In this study we present a detailed description of habitat use by juveniles of selected commercially important fish species that are found within a marine embayment in Zanzibar, Tanzania. The study was designed to answer the following key questions: (1) Do selected commercially important fish species use the bay habitats as juvenile habitats? (2) What is the spatial variation in habitat utilization by the selected fishes? (3) Which bay habitat contains the most species of juvenile fish? (4) Is the distribution of fish related to environmental variables?

MATERIALS AND METHODS

Study area

This study was carried out in Chwaka Bay, a shallow system on the east coast of Unguja Island, Zanzibar, Tanzania (Fig. 1). This embayment is an intertidal water body with an average depth of 3.2 m and an estimated area of 50 km^2 at high spring tide and 20 km^2 at low spring tide (Cederlöf et al. 1995). The region receives between 1000 and 1500 mm of rainfall per annum. Air temperatures are tropical and range from 27-30°C. Predominantly north-easterly winds occur between October and March, and mainly south-easterly winds from March to October. There are two rainy seasons in Zanzibar: the extended rainy season that occurs during the months of March, April and May, and the short rainy season which extend from October to December (McClanahan 1988).

On the east side, Chwaka Bay is protected from high-wave action from the ocean by a reef system running along the coastline, as well as the Michamvi peninsula (Fig. 1). On the landward side, this embayment is fringed by a dense mangrove forest of approximately 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 acting as the main water exchange route between the forest and the embayment. All the creeks are intertidal in nature and none have any significant fresh water input from rivers or streams. Only during heavy rains, salinity gradients develop and these creeks temporarily acquire estuarine characteristics, with salinities as low as 5 psu (Johnstone & Mohammed 1995). The mangrove part of the bay is characterised by low water clarity (Table 1) and fluctuations in oxygen levels. On the seaward side, immediately adjacent to the forest, the embayment opens up onto large intertidal flats that are overgrown by mixed assemblages of algae and seagrasses, including scattered monospecific seagrass stands. The outer and middle parts of the embayment (about 4 m deep) are oceanic in character with salinities rarely below 35 psu (Table 1). Due to proximity of this part of the embayment to the open ocean, it is characterised by relatively high water clarity (Table 1). Furthermore, salinity and oxygen levels in this part of the embayment are relatively constant, even during the rainy seasons.

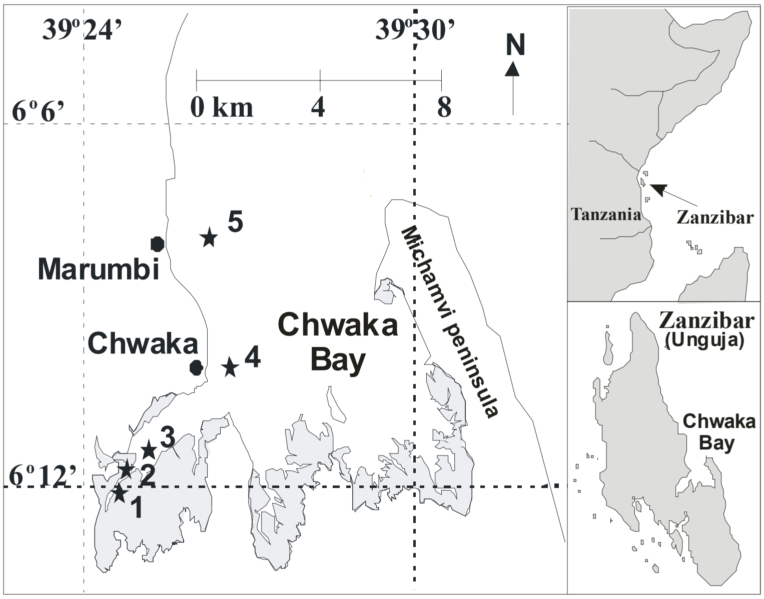

Fig. 1 Map of Unguja Island (Zanzibar) showing the location of Chwaka Bay and the sampled habitats. 1: mangrove creeks, 2: mangrove channel, 3: mud/sand flats, 4: Chwaka seagrass beds, 5: Marumbi seagrass beds. Gray areas in Chwaka Bay indicate mangrove forest.

Study design

Bimonthly sampling was conducted during the day at spring low tide (two spring tides per month) for a period of one year (November 2001 - October 2002). Fish samples were collected from five habitats in Chwaka Bay, including: (1) mangrove creeks, (2) mangrove channel, (3) intertidal mud/sand flats located within 2 km of the mangroves, (4) Chwaka seagrass beds located approximately 6 km from the mangroves, and (5) Marumbi seagrass beds situated about 8 km from the mangroves (Fig.1). The mangrove creeks and the channel were characterised by mangrove prop roots (*Rhizophora mucronata*), with a muddy substratum harbouring few algae and seagrasses. The mud/sand flats were characterised by a higher cover of algae and some seagrasses. The seagrass habitats consisted of vast fields of *Enhalus acoroides* interspersed by patches of *Thalassodendron ciliatum* and the calcareous algae *Halimeda* spp.

Fish samples were collected from each habitat using a seine net measuring 35 m in length, 3 m in height, and with a stretched mesh size of 1.8 cm. The sampled area of each haul was approximately 480 m^2. In each habitat, four replicate samplings were randomly conducted during each spring low tide. A consistent net deployment (purse seining) was used in all habitats, except the creeks where narrowness restricted similar deployment of the net. Instead, the mouth of the mangrove creeks (about 4 m wide) was closed by the net and the whole net laid out upstream along one side of the creek (about 30 m) and then closed, sampling an area of approximately 120 m^2.

To make sure that the net remained vertically stretched and touching the bottom, a metal chain was attached to the middle section of the sinker line. In addition, plastic floats were attached to the float line so that the entire water column was enclosed. Snorkelling observations during net deployment indicated that the lower part of the net remained on the bottom throughout the exercise and no fish were observed escaping under the net. Although some individuals belonging to the family Mugilidae were observed jumping over the net, it was concluded that the procedure was well designed for the study species.

To improve standardisation, the sampling was carried out by the same two fishermen, using the same net, and similar net deployment procedures. All fish sampled by the seine net were collected (see Figs. 2 and 3) but 13 commercially important fish species (Jiddawi & Stanley 1997, see Table 2) that were most common and represented over 60% of the total catch are studied in more detail, so that the results can contribute to effective management and conservation of the fisheries in this embayment. The role of the studied embayment habitats as a feeding area by these fish species will be reported elsewhere. In the laboratory, fish fork lengths were measured to the nearest 0.1 cm and analysed in class intervals of 2.5 cm, except for two large-sized species (viz. *Sphyraena barracuda* and *Cheilio inermis*) where a 5 cm class interval was used.

In another study during September - December 2003, visual census surveys of the fish communities in the mangroves near Chwaka (different from the beach seine surveys) and in the seagrass beds of Chwaka and Marumbi were performed during neap tides in quadrats of 5 x 5 m using SCUBA. Visual census surveys could not be done within the mangrove creeks, mangrove channel and mud/sand flats habitats due to high turbidity in these habitats. Water depth at the Marumbi and Chwaka seagrass beds was on average 4.5 m. After marking the quadrat with a line, the observer waited 3 min to minimise fish disturbance in the quadrat, after which fishes were counted during 10 min. Fish surveys were performed by two independent observers that were simultaneously trained in fish identification and size class estimation prior to the surveys. Care was taken not to count fishes that moved in and out of the quadrats more than once.

The majority of juveniles collected in this study were larger than 2.5 cm in length and did not include larval stages. The smaller juveniles (<2.5 cm) and larvae tended to pass through the net, thus leading to an underestimation of the total density and size composition of early juveniles captured during this study. However, since the same mesh size was used throughout the embayment habitats, the selectivity of the net applies equally to all habitats, thus resulting in comparable data being collected. It is known that seine nets have a limitation in sampling adult fish, a problem that could result into them being underrepresented in this study. The visual census survey was used as an additional technique to determine whether adults are present in the embayment habitats.

Table 1 Environmental characteristics (mean values ± SD) of different embayment habitats, depth and seaward distance of different embayment habitats from the mangroves. Different fishing pressure intensities (- = rare or nearly absent, + = present but insignificant, ++ = regular and significant, +++ = irregular but intense) are also documented.

Environmental factors	Mangrove creeks	Mangrove channel	Mud/sand flats	Chwaka seagrass beds	Marumbi seagrass beds
pH	8.0 (0.7)	7.9 (0.4)	8.1 (0.2)	8.2 (0.2)	8.2 (0.3)
Temperature (^{o}C)	26.3 (2.5)	26.8 (3.0)	27.6 (2.2)	28.1 (2.1)	27.3 (2.4)
Salinity (psu)	30.9 (6.9)	29.9 (8.6)	32.2 (5.8)	33.8 (3.4)	35.5 (1.9)
Oxygen (mg/l)	3.6 (1.2)	4.8 (1.1)	5.5 (2.6)	8.6 (4.6)	6.9 (4.3)
Water clarity (m)	1.0 (0.7)	0.9 (0.4)	0.7 (0.2)	2.8 (0.9)	9.4 (2.9)
Habitat structure	Mud Mangrove prop roots Few algae Few seagrasses	Mud Mangrove prop roots Few algae Few seagrasses	Mud and sand Brown algae Few seagrasses	Seagrasses Seaweed farms (red algae) Other algae	Seagrasses Calcareous algae (*Halimeda* spp.) Other algae
Distance from the mangroves (km)	0	0	2	6	8
Maximum depth (m)	2	2	2	4	4
Fishing Pressure	-	-	+	++	+++

Table 2 Families, species names, common names, percentage composition of different categories of fish (following Nagelkerken & van der Velde 2002): small juveniles (<1/3 max. species' length), large juveniles and sub-adults (1/3-2/3 of max. species' length), and adults (> 2/3 of max. species' length), maximum length an individual species can reach (source: Froese & Pauly 2004). Habitats where fishes were most abundant are also documented (1: mangrove creeks, 2: mangrove channel, 3: mud/sand flats, 4: Chwaka seagrass beds, 5: Marumbi seagrass beds, *habitat with high fish density).

Family	Species	Common names	% small juveniles in the bay	% large juveniles in the bay	% adults in the bay	Maximum size attained by adult fish (cm)	Habitat observed
Gerreidae	*Gerres filamentosus*	Whipfin silver biddy	100	0	0	35	1*, 2*, 3
Gerreidae	*Gerres oyena*	Common silver biddy	94.7	5.3	0	30	All, 2*, 3*, 4*
Labridae	*Cheilio inermis*	Cigar wrasse	55.8	44.2	0	50	4, 5*
Lethrinidae	*Lethrinus lentjan*	Redspot emperor	100	0	0	52	All, 1*, 2*, 3*, 4*
Lethrinidae	*Lethrinus variegatus*	Variegated emperor	26.4	73.4	0	20	2, 3, 4*, 5
Lutjanidae	*Lutjanus fulviflamma*	Blackspot snapper	87.1	12.9	0	35	All, 3*, 4*
Monodactylidae	*Monodactylus argenteus*	Silver moon	97.8	2.2	0	25	1*, 2*, 3
Nemipteridae	*Scolopsis ghanam*	Arabian monacle bream	87.0	13.0	0	30	4*
Scaridae	*Hipposcarus harid*	Candelamoa parrot fish	100	0	0	75	4*
Scaridae	*Leptoscarus vaigiensis*	Marbled parrotfish	45.3	54.7	0	35	4, 5*
Siganidae	*Siganus sutor*	Whitespotted rabbitfish	88.9	11.1	0	45	2, 3, 4*, 5*
Sphyraenidae	*Sphyraena barracuda*	Great barracuda	100	0	0	200	All*
Teraponidae	*Pelates quadrilineatus*	Fourlined terapon	93.6	6.4	0	30	1, 3, 4*

Table 3 Mean density (# fish 100 m^{-2}) and standard error (between brackets) of different size classes (cm) of fish observed during visual census surveys (n = number of transects surveyed). The maximum size that can be reached by individual fish species is shown in Table 2.

	Chwaka mangroves (n=9)				Chwaka seagrass beds (n=31)				Marumbi seagrass beds (n=29)			
Species	0-10	10-20	20-30	>30	0-10	10-20	20-30	>30	0-10	10-20	20-30	>30
Gerres filamentosus	-	-	-	-	-	-	-	-	-	-	-	-
Gerres oyena	-	-	-	-	-	-	-	-	-	-	-	-
Cheilio inermis	-	-	-	-	0.6 (0.4)	2.6 (1.2)	1.8 (0.8)	0.6 (0.4)	0.8 (0.3)	5.5 (1.2)	4.6 (1.3)	-
Lethrinus lentjan	-	-	-	-	3.0 (1.2)	0.3 (0.3)	-	-	1.9 (0.9)	16.1 (4.1)	-	-
Lethrinus variegatus	-	-	-	-	0.1 (0.1)	-	-	-	-	0.1 (0.1)	-	-
Lutjanus fulviflamma	-	0.4 (0.4)	-	-	-	0.8 (0.8)	-	-	-	0.3 (0.3)	-	-
Monodactylus argenteus	5.3 (4.9)	-	-	-	-	-	-	-	-	-	-	-
Scolopsis ghanam	-	-	-	-	2.1 (1.0)	1.0 (0.8)	-	-	-	4.0 (2.8)	-	-
Hipposcarus harid	-	-	-	-	10.8 (2.2)	11.6 (4.7)	0.1 (0.1)	-	-	-	-	-
Leptoscarus vaigiensis	-	-	-	-	3.0 (1.4)	9.9 (3.6)	0.6 (0.3)	-	3.9 (2.7)	28.1 (8.2)	4.6 (2.8)	-
Siganus sutor	-	2.7 (2.7)	-	-	3.5 (0.9)	1.7 (0.7)	0.6 (0.5)	-	2.6 (1.3)	11.7 (4.4)	-	-
Sphyraena barracuda	-	0.4 (0.4)	0.4 (0.4)	-	-	-	-	-	-	-	-	-
Pelates quadrilineatus	-	-	-	-	-	-	-	-	-	-	-	-

Since variations in environmental variables can have profound effects on the distribution and consequently catches of fish, these variables were recorded before each catch. Water temperature, pH, salinity and dissolved oxygen were measured using a temperature-compensated Multi Parameter Analyzer (Eijkelkamp, model 18.28). To determine water clarity, a line was extended to the maximum horizontal distance at which a snorkeller in the water could discern a black and white coloured stationary held Secchi disk (44 cm diameter).

Data analysis

Using the monthly environmental data, mean and standard deviations for each of the variables were determined (Table 1).

Mean species richness and mean density for the entire fish community were compared between different embayment habitats using a one-way ANOVA on log-transformed data, followed by a multiple comparisons of means with a Gabriel's Post Hoc test, using the programme SPSS for Windows (Field 2000). To examine associations between fish densities in different embayment habitats and environmental variables, two analyses were done: 1) Multiple linear regression analysis for each target species (all size classes pooled), and 2) Correspondence Analysis (CA) on log-transformed data of the various size classes of all target species (ter Braak & Smilauer 1998). First of all, simple linear regressions were done among the environmental variables to detect co-linearity. Temperature was significantly correlated to oxygen; to prevent over-parameterisation we therefore excluded temperature from the model and used only oxygen as a variable. Distance was significantly correlated to salinity, and we used only salinity as a variable. We excluded pH from the model because this factor hardly varied within the habitats. The final multiple linear regression model thus included three independent variables (predictors): oxygen, salinity and water clarity. Each of the 13 target species was set as a dependent variable in 13 separate multiple regression analyses. Semi partial (Part) correlations are provided which show the correlations of the separate independent variables with the dependent variable, taking the effect of the other independent variables into account.

RESULTS

The number of all fish species and of target species both showed a similar trend across the embayment habitats, increasing from the mangrove creeks to Chwaka seagrass beds and then decreasing in Marumbi seagrass beds (Fig. 2a). The pattern for densities of all fish species pooled was the same as that of target species alone, except in the mangrove creeks (Fig. 2b). The density of all species pooled was significantly higher in the mangrove creeks than in any other habitats (1-way ANOVA and Gabriel's post-hoc test, $p < 0.05$). Non-target species, which contributed most to the high fish densities in the mangroves, included members of the family Ambassidae, Apogonidae and Leiognathidae. The highest densities of the target species pooled were recorded on the mud/sand flats and in Chwaka seagrass beds, but the differences in their density over the habitat gradient was not significant (1-way ANOVA, $F_{4,53} = 2.127$, $p = 0.09$).

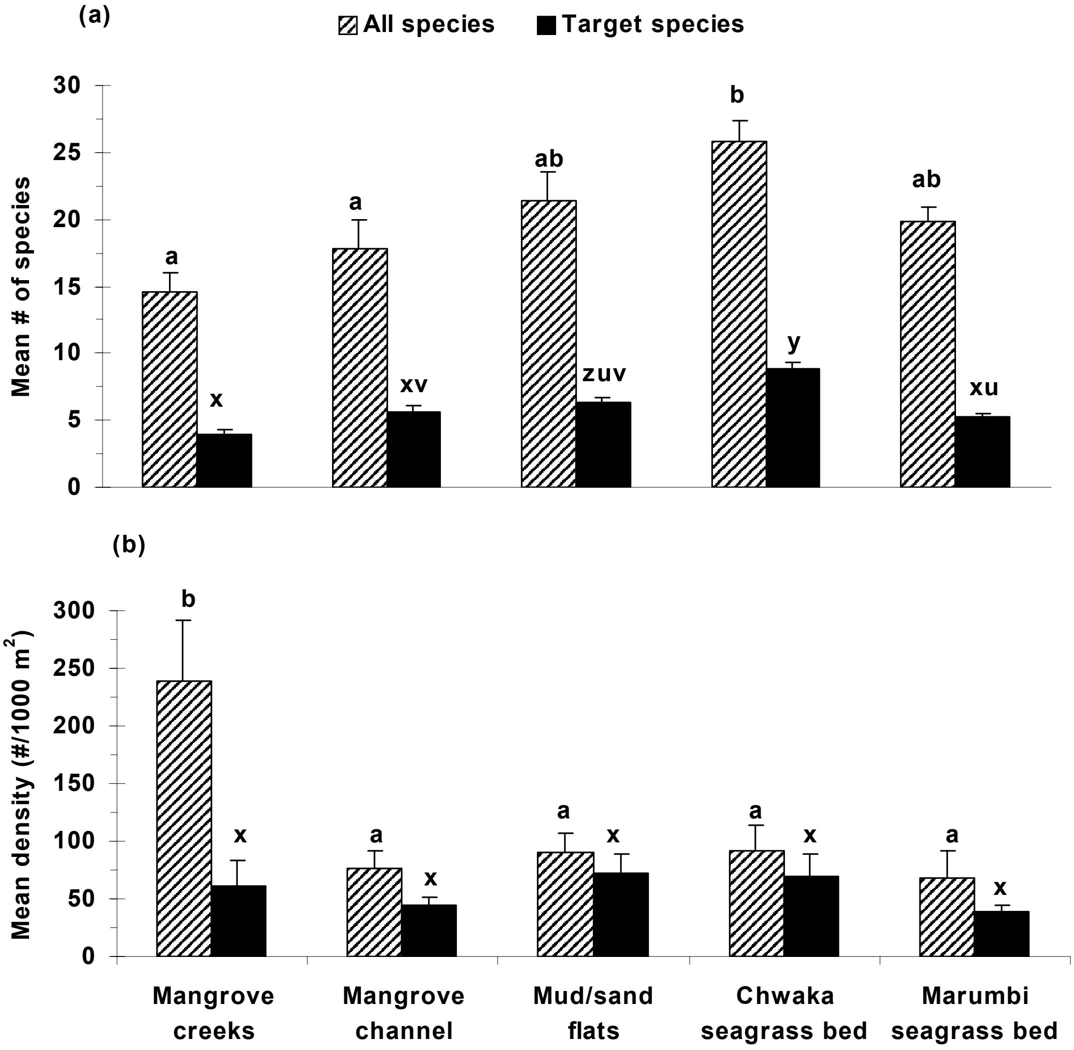

Fig. 2 Variations (+ SE) in (a) mean number of species and (b) mean densities along a gradient of habitats in Chwaka Bay for all species and for target species. Values that are significantly different (Gabriel's post-hoc test) have different letters (*a*, *b* for all species; *x*, *y*, *z*, *u* for target species). Mean number of species is calculated by pooling the 8 beach seine hauls of each month and taking the average of the different months.

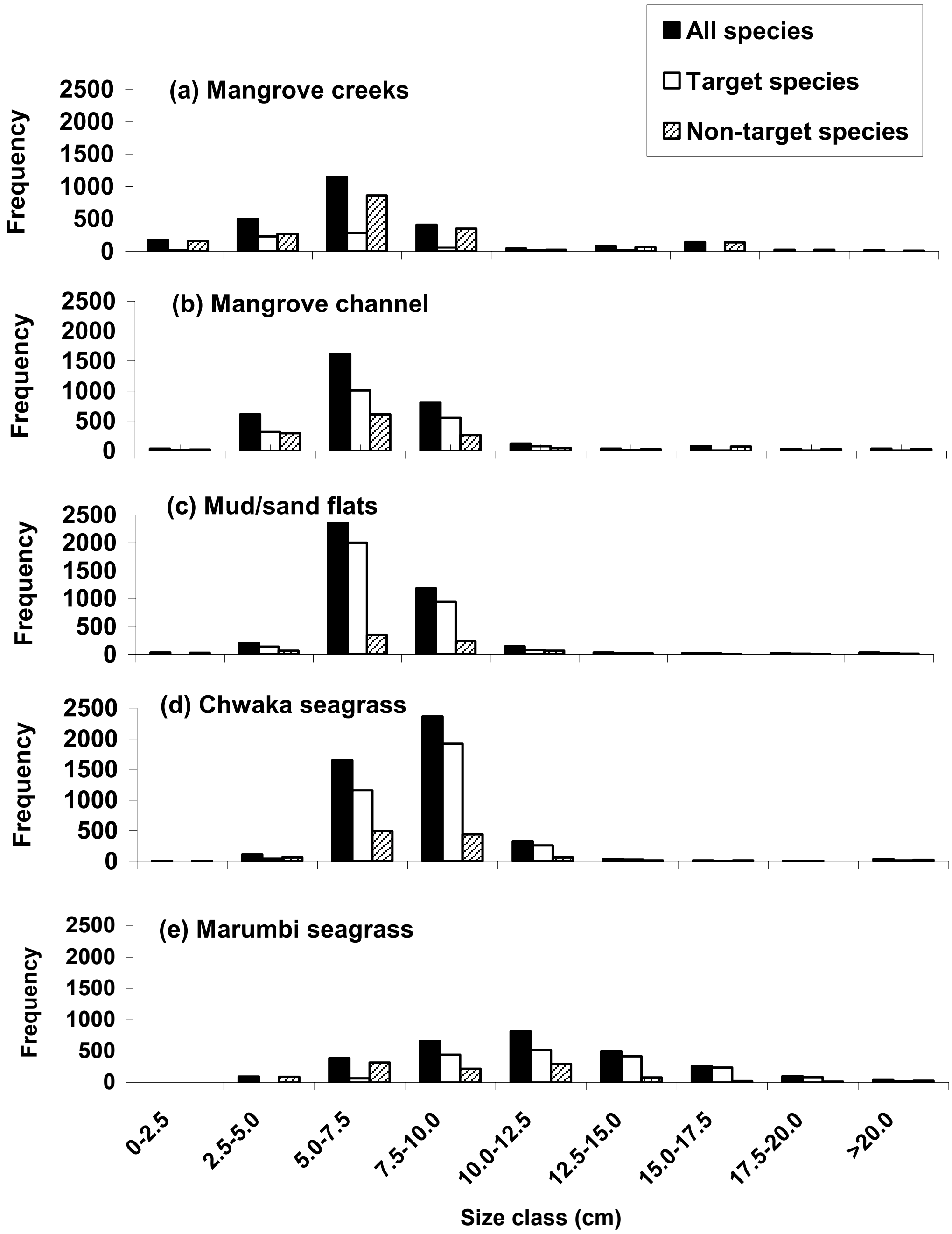

Fig. 3 Length frequency distribution of fish in different habitats in Chwaka Bay. Non-target species refers to all species minus target species.

Considering target species alone, the majority of small juveniles (< 5 cm) were found within the mangrove habitats (i.e. creeks and channels) although other size classes were also represented (Fig. 3a,b). Mud/sand flats and Chwaka seagrass beds mainly harboured intermediate sized juveniles (5 – 10 cm) while in Marumbi seagrass beds large-sized juveniles (>10.0 cm) dominated (Figs. 3c-e). Non-target species which mainly included small-body species did not show a distinctive pattern in size distribution over habitats (Fig. 3).

Considering the embayment as a whole and using the beach seine data, 11 out of 13 target species were recorded mainly as small juveniles, with the other 2 species predominantly occurring in the embayment as large juveniles (Table 2). No target species were recorded in the embayment as adults. Also visual census surveys revealed that the majority of the target fish species occurred in the embayment habitats as juveniles and sub-adults (Table 3). In contrast to the beach seine data, the visual census surveys showed presence of *Siganus sutor* in the mangroves, and absence of *Gerres filamentosus*, *G. oyena* and *Pelates quadrilineatus* in all habitats.

Correspondence Analysis showed a clear separation of species and size classes of the target species in the different habitats (Fig. 4). The Eigenvalues of the first and second CA axis were 0.66 and 0.37, respectively, indicating that a high proportion of the variation in species density data could be explained by the hypothetical axes. Four distinct groups could be identified. The first group occupied the mangrove habitats (creeks and channel) and were characterised by small-sized individuals of *Gerres filamentosus*, *G. oyena*, *Lethrinus lentjan, Monodactylus argenteus* and *Sphyraena barracuda*. In addition, the whole size range of *M. argenteus* was found in these habitats, together with large individuals of *Lutjanus fulviflamma*. The second group was found on the mud/sand flats and were characterised by small-sized individuals of *L. fulviflamma*, *Lethrinus variegatus, Pelates quadrilineatus, Siganus sutor, Sphyraena barracuda* and intermediate-sized individuals of *G. filamentosus* and *G. oyena*. Chwaka seagrass beds were occupied by the third group which was characterised by intermediate-sized individuals of *P. quadrilineatus* and *S. barracuda* and all size classes of *Hipposcarus harid* and *Scolopsis ghanam*. The last group, comprising mainly large individuals (≥ 10.0 cm) of *Cheilio inermis*, *Leptoscarus vaigiensis*, *Lethrinus lentjan*, *L. variegatus, Siganus sutor* and *Sphyraena barracuda* were found in Marumbi seagrass beds.

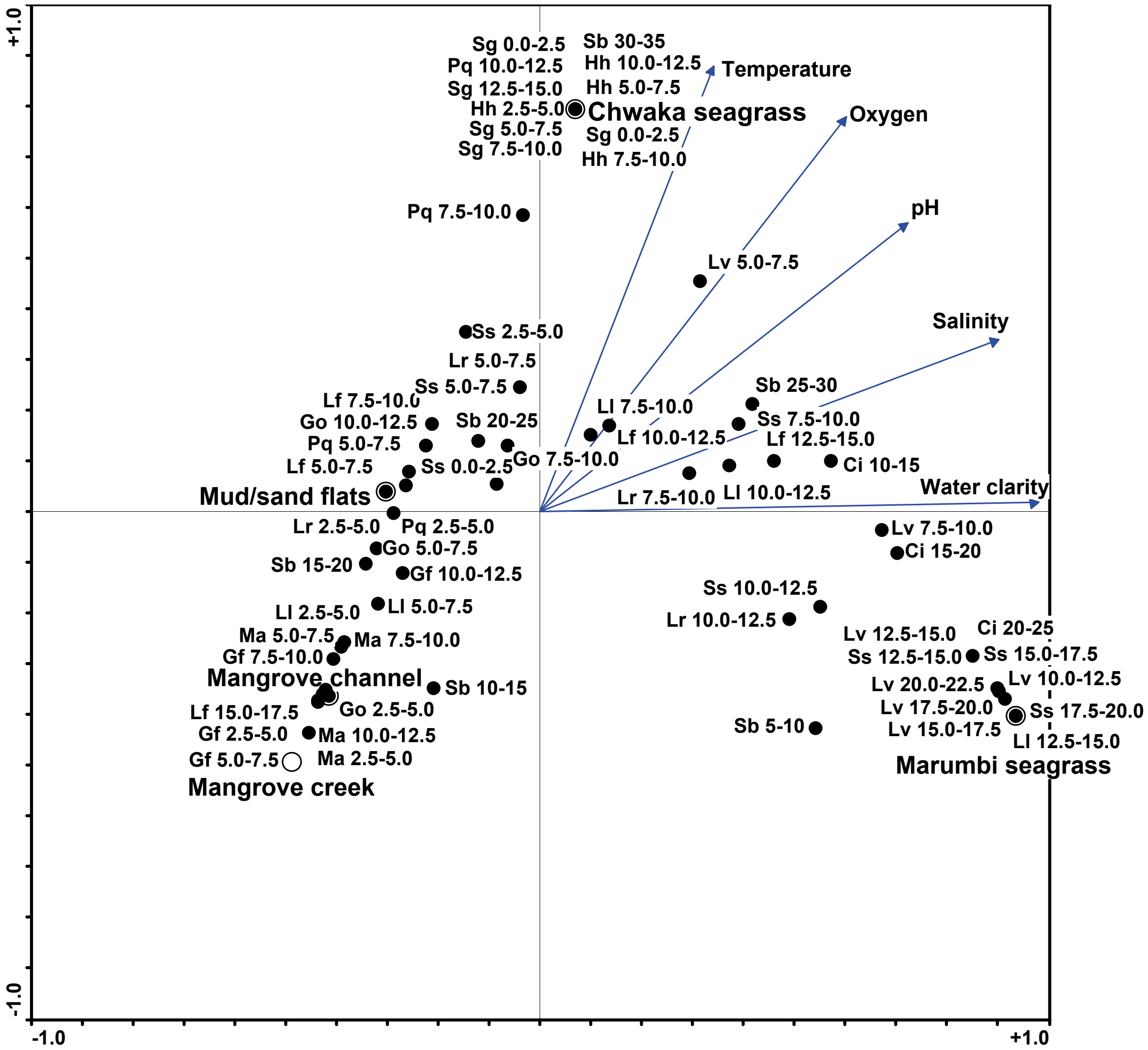

Fig. 4 Correspondence Analysis (CA) graph showing habitat utilisation of different size classes of target fish species and their relationship with environmental variables. Go: *Gerres oyena*, Gf: *Gerres filamentosus*, Ma: *Monodactylus argenteus*, Sb: *Sphyraena barracuda*, Ci: *Cheilio inermis*, Ll: *Lethrinus lentjan*, Lr: *Lethrinus variegatus*, Lv: *Leptoscarus vaigiensis*, Ss: *Siganus sutor*, Sg: *Scolopsis ghanam*, Hh: *Hipposcarus harid*, Pq: *Pelates quadrilineatus*, Lf: *Lutjanus fulviflamma*.

The density distribution of the various size classes of the target species was highly correlated to all environmental variables (Fig. 4). The size distribution of the target species as well as the environmental variables increased from the mangroves to the seagrass beds of Chwaka and Marumbi. At species level, salinity (and/or distance), oxygen (and/or temperature) and water clarity were correlated to the fish density distribution (Table 4), although few conditions were significant. Only two species (*C. inermis* and *L. variegatus*) showed significant results.

At the species level, several species showed a difference in habitat utilization for small versus large juveniles (Fig. 5, Table 2): (1) small-sized individuals of *Lethrinus lentjan, Pelates quadrilineatus* and *Sphyraena barracuda* were found in the mangrove habitats, whereas the large-sized individuals of these species were recorded in the seagrass beds (2) small-sized individuals of *L. variegatus* and *Siganus sutor* were found in the mangroves and mud/sand flats, whereas the large individuals were recorded in the seagrass habitats. The other target species did not show such a pattern, with all life stages found in the mangroves (*Gerres filamentosus*, *Monodactylus argenteus*), seagrass beds (*Cheilio inermis*, *Hipposcarus harid*, *Leptoscarus vaigiensis*, *Scolopsis ghanam*), or in a variety of habitats (*G. oyena*, *Lutjanus fulviflamma*).

Table 4 Results of the multiple linear regression analysis, showing the R^2 and p-value of the full model, and the part (semi partial) correlation of the separate environmental variables. *significant at 0.01<p<0.05, **significant at p<0.01.

	Part Correlation			R^2	p
Species	Salinity	Oxygen	Water clarity		
Cheilio inermis	0.009	0.036*	0.426**	1.000	0.001**
Gerres filamentosus	-0.651	0.153	0.453	0.994	0.101
Gerres oyena	0.249	0.087	-0.620	0.689	0.671
Hipposcarus harid	-0.027	0.604	-0.212	0.828	0.513
Leptoscarus vaigiensis	0.013	-0.050	0.454	0.997	0.074
Lethrinus lentjan	0.493	-0.718	-0.551	0.853	0.476
Lethrinus variegatus	-0.310*	0.807*	0.202	1.000	0.024*
Lutjanus fulviflamma	0.379	0.276	-0.640	0.972	0.214
Monodactylus argenteus	0.068	0.215	-0.538	0.874	0.442
Pelates quadrilineatus	0.341	0.291	-0.625	0.927	0.339
Scolopsis ghanam	-0.027	0.604	-0.212	0.828	0.513
Siganus sutor	0.129	0.198	0.135	0.866	0.456
Sphyraena barracuda	0.894	-0.415	-0.882	0.979	0.183

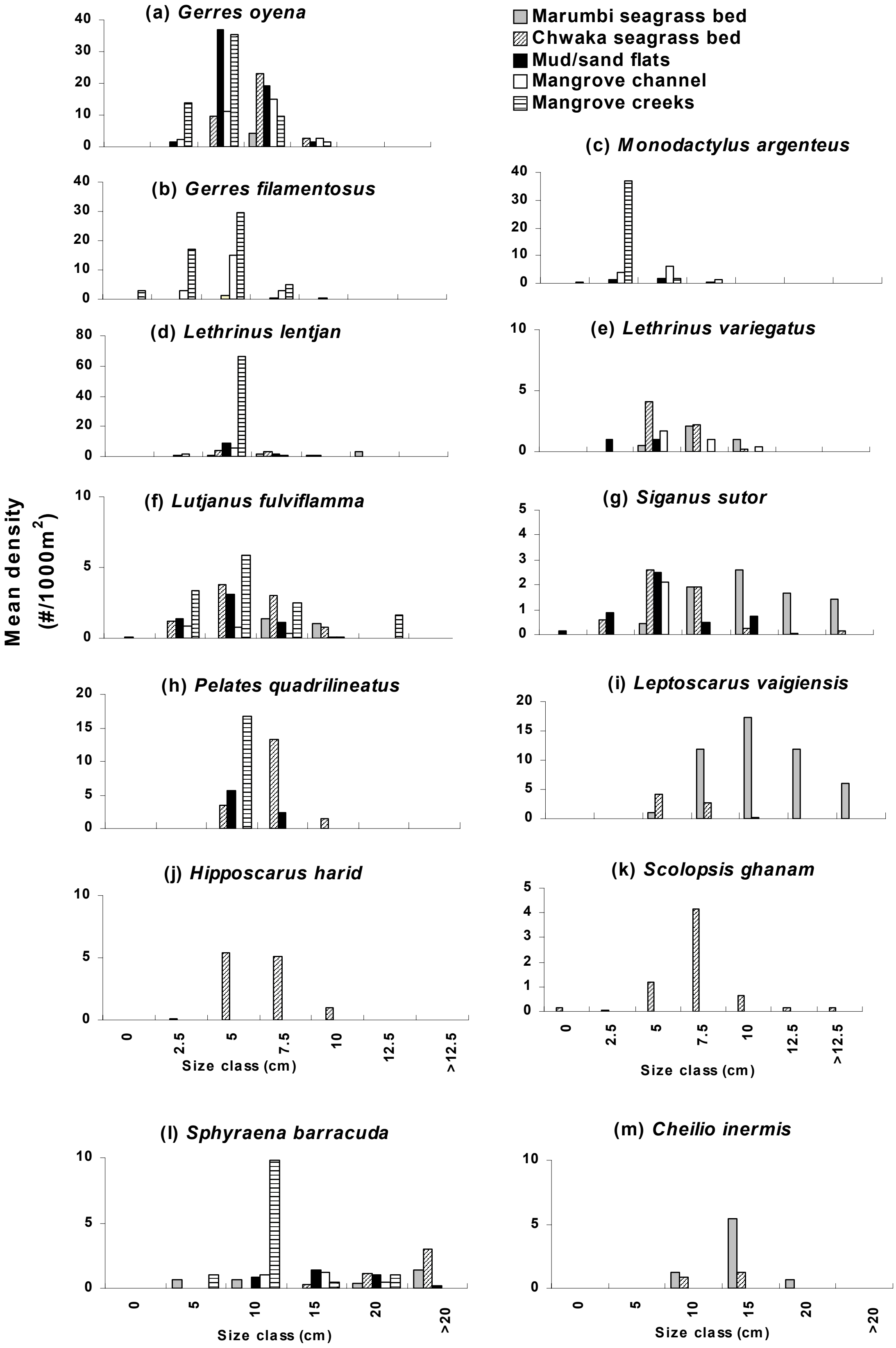

Fig. 5 Mean densities per size class of the target fish species in the five embayment habitats.

Discussion

Most fish caught in the present study were juveniles, indicating that an Indo Pacific marine embayment may have similar a function as juvenile habitats as Indo Pacific estuaries. In addition, both tropical marine embayments as well as estuaries are dominated by relatively few species when compared to fish diversity in adjacent coastal waters.

The density of juveniles of all species pooled was about 3 times higher in the mangroves than in any of the other habitats. Similarly, in tropical Queensland (Australia), Robertson and Duke (1987) observed 4-10 times higher densities of fish in mangroves than in adjacent habitats. The high density of fish in mangroves is probably explained by the high structural complexity formed by the prop-roots (Robertson & Duke 1987; Thayer et al. 1987; Cocheret de la Morinière et al. 2004). However, the low density of target species (i.e. commercially important species) as opposed to the high density of non-target species in the mangrove creeks indicates that the majority of fish found in the mangroves are not commercially important. This does not necessarily lessen the importance of mangroves, as the density of target species was equal in all habitats and non-target species are important in supporting food webs that include commercially important species. For example, in Dampier region of Australia, Blaber (1986) observed that 60% of the diet of commercially important species such as *Caranx ignobilis*, *Carcharhinus limbatus*, *Scomberoides comersonianus* and *Scomberomorous semifasciatus* was composed of permanently resident mangrove species. Therefore, as argued by Robertson and Duke (1987), the value of mangroves is not limited to a possible nursery potential alone.

The high number of fish species encountered in Chwaka seagrass beds, when compared to the other habitats, may possibly be explained by its geographical location between the mangroves and the deeper part of the embayment/coral reef. Fish species from adjacent habitats may school together in the seagrass channels of Chwaka during low tides. These channels are always inundated with water and fishes are known to occupy transient habitats during certain phases of tidal cycles (Chong et al. 1990; Forward & Tankersley 2001; Dorenbosch et al. 2004b). The Chwaka seagrass beds could also form a corridor for fishes if they would undertake an ontogenetic migration from the mangroves to deeper parts of the embayment. Higher numbers of species in seagrass habitats compared to mangrove habitats have been reported in other studies (Little et al. 1988; van der Velde et al. 1995; Pinto & Punchihewa 1996), but the opposite situation has also been documented (Robertson & Duke 1987; Thayer et al. 1987; Laegdsgaard & Johnson 1995).

Individuals of the fish species that were found in mangrove areas were smaller in size when compared to individuals of the same species that were found in seagrass areas. This suggests either a possible habitat shift with growth, with some species appearing to utilise the sand/mud flats as intermediate life stage habitats or it could also be a result of tidal migration in search for more beneficial habitats during low tides. Although the present study did not focus on the adult life stages, the almost total absence of adults in the studied embayment habitats suggests that these large fish must be present elsewhere, possibly in the deeper parts of the embayment or on the adjacent coral reef. There is a possibility that adult fish were able to escape the seine net more readily than juveniles, which could result into their under representation, however, visual census surveys (which target the entire size range) indicated that the deeper parts of the seagrass beds consisted mainly of juveniles.

Most species occurred in multiple embayment habitats, but some species were most abundant in just one habitat. *Gerres filamentosus* and *Monodactylus argenteus* showed a strong preference for mangrove areas and may be attracted to the brackish water that was sometimes present in this habitat (Froese & Pauly 2004). *Cheilio inermis* and *Leptoscarus vaigiensis* are typical seagrass-associated species (Froese & Pauly 2004) and were only recorded in seagrass beds during this study. Similarly, in Mhlathuze estuary, South Africa, Weerts & Cyrus (2002) reported the occurrence of Labridae and Scaridae only in eelgrass habitats.

Most studies on utilisation of neighbouring tropical shallow-water marine habitats by juvenile reef fish species have been done in the Caribbean. It is striking that many results of the present study in the western Indian Ocean are highly comparable to those of similar studies done in marine embayments in the Caribbean. In both regions, 1) marine embayment habitats were dominated by juvenile fish with an almost complete absence of adults (Nagelkerken et al. 2000a), 2) marine embayment habitats showed highest juvenile fish densities in mangroves (Nagelkerken & van der Velde 2002); 3) some marine embayment habitats were used specifically as an intermediate life-stage habitat (Nagelkerken et al. 2000b; Nagelkerken & van der Velde 2003), and 4) multiple marine embayment habitats could be used by juvenile fish simultaneously (Nagelkerken et al. 2000a).These similarities indicate that irrespective of the geographical location, the same mechanisms are at work which make shallow-water marine embayment habitats favourable juvenile habitats.

Conclusion

The questions posed at the beginning of this study can be answered as follows: (1) All studied fish species used one or more embayment habitats as juvenile habitats. (2) Several species occurred as small juveniles in the mangrove areas and as large-sized juveniles in the seagrass areas. (3) Chwaka seagrass beds appeared to be the most widely utilised habitat probably due to its intermediate location between the mangroves and the deeper parts of the embayment. (4) Only two of the 13 species showed a significant correlation between density and the selected environmental variables, suggesting that the latter do not play a major role in the fish density distribution.

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Chapter 5

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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Abstract: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 d13C 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 fish 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 d13C 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.

INTRODUCTION

Mangrove and seagrass habitats are often characterised 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 Morinie`re *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.*, 2002a). 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 km2 at high spring tide and 20 km2 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 fresh water 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.) 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 mm 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).

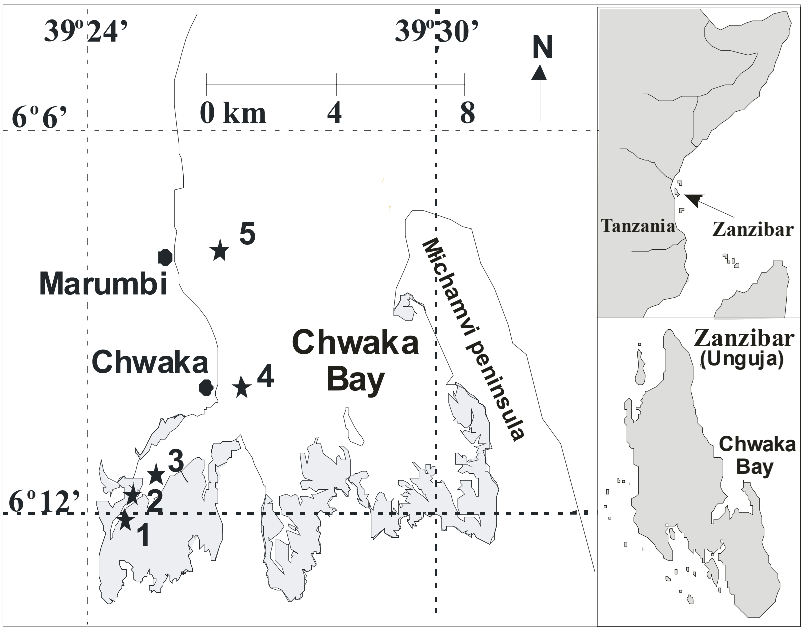


Fig. 1 Map of Unguja Island (Zanzibar) showing the location of Chwaka Bay and the sampled habitats (1, mangrove creeks; 2, mangrove channel; 3, mud and sand flats; 4, Chwaka seagrass beds; 5, Marumbi seagrass beds). Gray areas in Chwaka Bay indicate mangrove forests.

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 (δ^{13}C, δ^{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 (LF) 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 food item were scaled down to percentages, to give percentage composition of each food item in a diet of individual fish species examined.

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 shows relative proportions of each species for the whole bay. Different superscript letters and numbers represent statistical post hoc results and denote significantly different ($P < 0.05$) stable carbon isotope values of a fish species for similar LF 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	-21.2^{a} ± 0.4	9.6	5.8
Mangrove creeks	5-10	3	-21.1^{a} ± 0.5	8.0 ± 0.1	Mangrove channel	-21.6^{a} ± 0.5	24.3	17.0
Mangrove channel	5-10	5	-21.6^{a} ± 0.5	8.4 ± 0.1	Mud/sand flats	-19.2^{a} ± 1.0	0.8	1.1
Mud and sand flats	5-10	4	-19.2^{a} ± 1.0	8.0 ± 0.2				
Gerres oyena					***Gerres oyena***		**22.6**	**21.2**
Mangrove creeks	5-10	10	-19.4^{a} ± 0.3	7.5 ± 0.2	Mangrove creeks		7.1	7.1
Mangrove channel	5-10	10	-17.0^{b} ± 0.7	7.4 ± 0.1	Mangrove channel		25.6	35.0
Mud and sand flats	5-10	10	-13.8^{c} ± 0.3	6.6 ± 0.2	Mud/sand flats		62.6	56.2
Chwaka seagrass beds	5-10	10	-12.8^{c} ± 0.7	7.5 ± 0.1	Chwaka seagrass beds		37.6	38.8
Lethrinus lentjan					***Lethrinus lentjan***		**2.7**	**1.6**
Mangrove channel	5-10	10	-21.8^{a} ± 0.3	8.0 ± 0.1	Mangrove channel	-21.8^{a} ± 0.3	2.4	1.2
Mud and sand flats	5-10	9	-19.3^{b} ± 0.7	6.8 ± 0.2	Mud/sand flats	-19.3^{b} ± 0.7	6.8	3.4
Chwaka seagrass beds	5-10	10	-12.3^{c} ± 0.2	8.0 ± 0.1	Chwaka seagrass beds	-12.3^{c} ± 0.2	3.9	3.0
Marumbi seagrass beds	5-10	4	-12.4^{c} ± 0.6	8.3 ± 0.2	Marumbi seagrass beds	-12.0^{c} ± 0.4	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	-21.0^{1} ± 0.2	8.5 ± 0.1	Mangrove creeks	-20.1^{a} ± 0.9	0.8	2.0
Chwaka seagrass beds	5-10	4	-15.2^{2} ± 0.7	8.0 ± 0.2	Mangrove channel	-21.8^{a} ± 0.1	1.4	2.1
Mangrove creeks	10-15	3	-20.1^{ab} ± 0.9	8.6 ± 0.4	Mud/sand flats	-15.2^{b} ± 0.5	3.8	5.6
Mangrove channel	10-15	2	-22.6^{a} ± 0.0	9.2 ± 0.0	Chwaka seagrass beds	-14.5^{b} ± 0.4	5.2	8.2
Mud and sand flats	10-15	5	-15.2^{c} ± 0.5	7.6 ± 0.2	Marumbi seagrass beds	-11.2^{c} ± 0.4	0.3	0.4

TABLE I continued.

Species	L_F class (cm)	*N*	δ^{13}C	δ^{15}N	Species	Overall mean δ^{13}C	Relative abundance (%)	Relative biomass (%)
Chwaka seagrass beds	10-15	2	$-14.2^{bc} \pm 0.0$	9.0 ± 0.2				
Marumbi seagrass beds	10-15	4	$-11.2^{d} \pm 0.4$	9.0 ± 0.1				
Monodactylus argenteus					***Monodactylus argenteus***		**3.1**	**1.2**
Mangrove creeks	0-5	11	$-22.1^{a} \pm 0.2$	8.0 ± 0.1	Mangrove creeks		5.5	2.8
Mangrove channel	5-10	3	$-24.0^{b} \pm 0.6$	8.4 ± 0.4	Mangrove channel		5.5	3.8
Pelates quadrilineatus					***Pelates quadrilineatus***		**2.5**	**2.4**
Mud/sand flats	5-10	9	$-17.1^{a} \pm 0.1$	7.2 ± 0.1	Mud/sand flats		2.9	1.9
Chwaka seagrass beds	5-10	10	$-16.2^{b} \pm 0.4$	7.8 ± 0.2	Chwaka seagrass beds		12.3	10.8
Siganus sutor					***Siganus sutor***		**1.6**	**3.6**
Mud and sand flats	5-10	7	$-22.8^{a} \pm 0.5$	5.6 ± 0.3	Mud/sand flats	$-22.8^{a} \pm 0.5$	1.3	1.2
Chwaka seagrass beds	5-10	4	$-20.7^{a} \pm 0.8$	7.0 ± 0.2	Chwaka seagrass beds	$-19.5^{b} \pm 0.7$	2.8	2.0
Marumbi seagrass beds	5-10	4	$-15.5^{b} \pm 0.7$	6.7 ± 0.3	Marumbi seagrass beds	$-16.1^{c} \pm 0.5$	7.4	11.4
Chwaka seagrass beds	10-15	1	-15.4	6.1				
Marumbi seagrass beds	10-15	11	-16.2 ± 0.6	6.5 ± 0.1				
Marumbi seagrass beds	15-20	11	-16.5 ± 0.2	6.3 ± 0.1				
Sphyraena barracuda					***Sphyraena barracuda***		**0.9**	**3.8**
Mangrove creeks	10-15	2	$-20.6^{1} \pm 1.0$	9.2 ± 0.0	Mangrove creeks	$-20.6^{a} \pm 1.0$	0.9	3.1
Mangrove channel	10-15	5	$-19.9^{1} \pm 0.5$	9.8 ± 0.1	Mangrove channel	$-19.9^{a} \pm 0.5$	1.1	4.5
Mud/sand flats	15-20	5	-15.7 ± 0.2	8.5 ± 0.2	Mud/sand flats	$-15.9^{b} \pm 0.4$	1.5	7.2
Mud and sand flats	20-25	2	$-16.1^{a} \pm 0.5$	8.2 ± 0.4	Chwaka seagrass beds	$-14.6^{b} \pm 1.8$	0.7	5.9
Chwaka seagrass beds	20-25	2	$-14.6^{a} \pm 1.8$	9.1 ± 0.6				
Zenarchopterus dispar					***Zenarchopterus dispar***		**3.9**	**4.8**
Mangrove creeks	10-15	9	$-22.8^{a} \pm 0.1$	8.1 ± 0.1	Mangrove creeks		8.2	14.6
Mangrove channel	10-15	9	$-22.7^{a} \pm 0.1$	8.2 ± 0.1	Mangrove channel		2.9	4.9

N, sample size.

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) equaled 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 fish 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 log10-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 log10-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 mainly consisted 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 fish 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, $P < 0.001$) to those from the 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, $P < 0.01$) 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, $P > 0.05$). There were no significant differences (Hochberg's GT2, $P > 0.05$) in δ^{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).

TABLE II. Mean percentage composition of diet for different fish species and fork length (L_F) classes in different bay habitats. Gray 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 bed	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 bed	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 bed	5-10, 10-15	30		40.4	22.7			10.4	0.1						4.2	20.1		2.1
Marumbi seagrass bed		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 bed	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 bed	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.

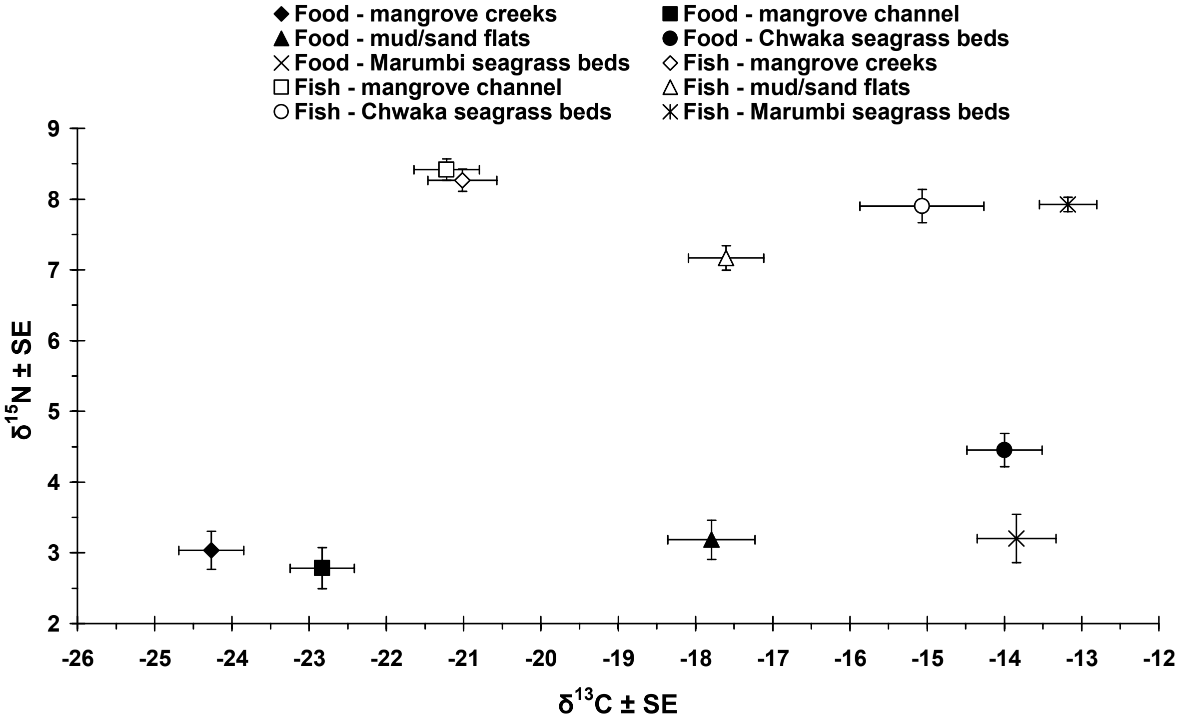


Fig. 2 Pooled mean stable carbon and nitrogen isotope values of fish (empty symbols and *) and food items (filled symbols and x) in different bay habitats. ◊ = mangrove creeks, □ = mangrove channel, Δ = mud/sand flats, ○ = Chwaka seagrass beds, * and x = Marumbi seagrass beds.

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 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 LF 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.

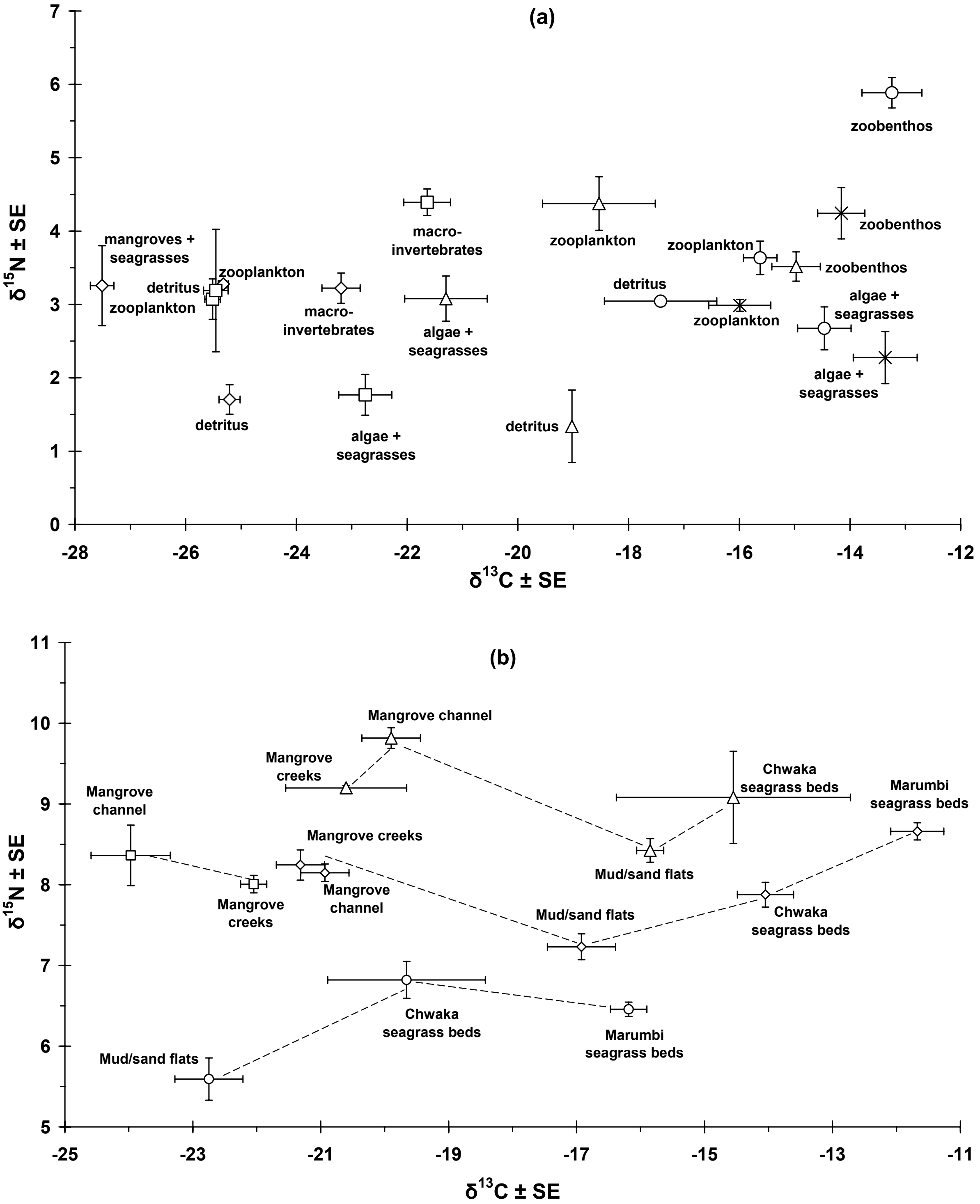


Fig. 3 Mean δ^{13}C and δ^{15}N values of different trophic groups of food items (a) in different bay habitats. ◊ = mangrove creeks, □ = mangrove channel, Δ = mud/sand flats, ○ = Chwaka seagrass beds and * = Marumbi seagrass beds, and feeding guilds of fish (b) in different bay habitats. Δ = piscivores, □ = omnivores, ◊ = zoobenthivores and ○ = herbivores.

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, $P < 0.001$ for *G. oyena*, Kruskal–Wallis, d.f. = 3, $P < 0.001$ for L. lentjan, Kruskal–Wallis, d.f. = 4, $P < 0.01$ for *L. fulviflamma*, t-test, d.f. = 1, $P < 0.05$ for *P. quadrilineatus* and one-way ANOVA, d.f. = 2,12, $P < 0.001$ 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, $P > 0.05$ for *G. filamentosus*, Mann–Whitney U-test, d.f. = 1, $P > 0.05$ for *Z. dispar*). Similar results were obtained when different LF 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, $P < 0.01$). 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 bed 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)].

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)].

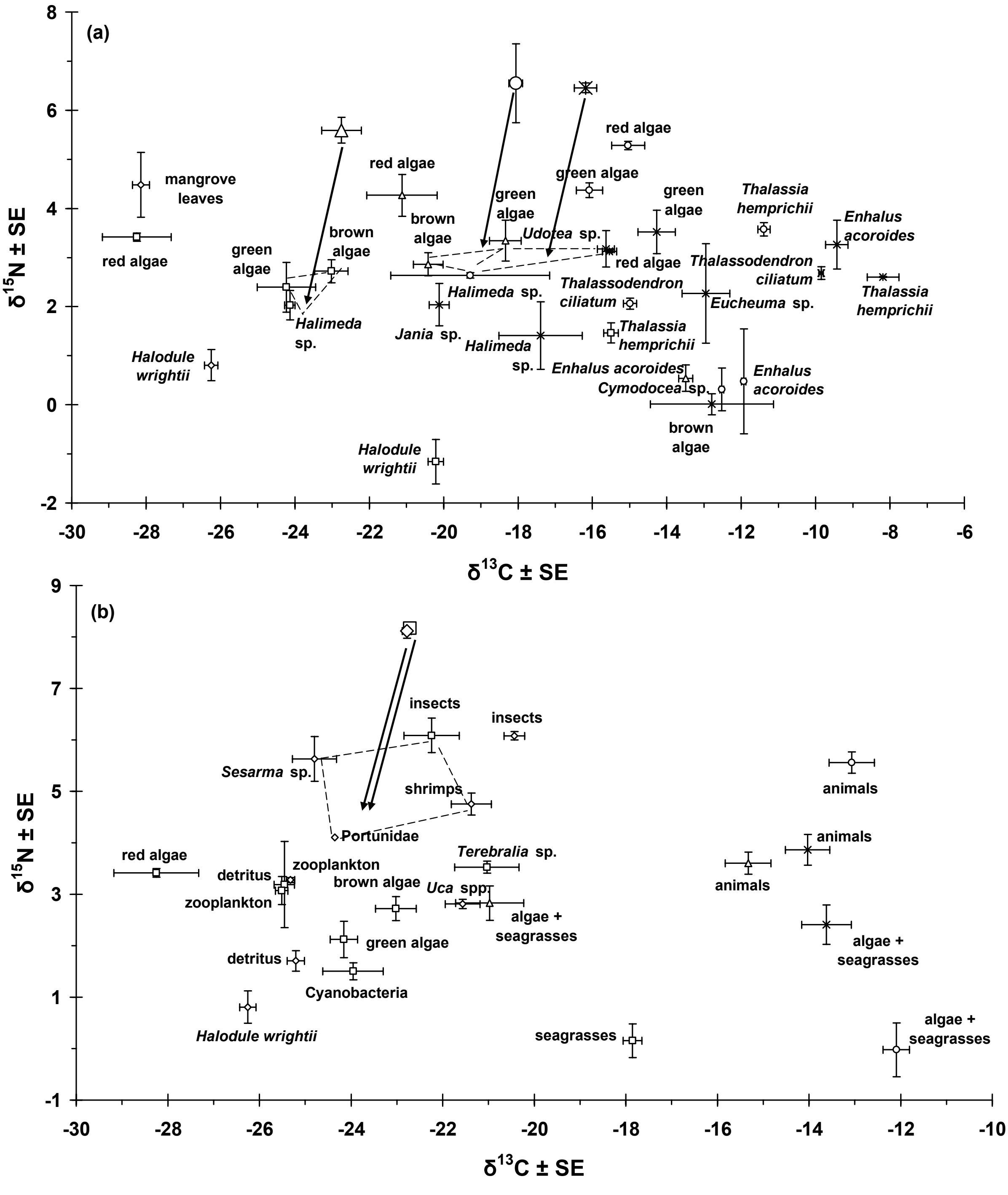


Fig. 4. Mean $\delta^{13}C$ and $\delta^{15}N$ values of fish species (a) *Siganus sutor*, (b) *Zenarchopterus dispar*, (c) Monodactylus argenteus, (d) *Sphyraena barracuda*, (e) *Gerres filamentosus*, (f) *Gerres oyena*, (g) *Lethrinus lentjan*, (h) *Lutjanus fulviflamma* and (i) *Pelates quadrilineatus* (large symbols) and potential food items (small symbols) in different bay habitats. ◊ = mangrove creeks, □ = mangrove channel, Δ = mud/sand flats, ○ = Chwaka seagrass beds and * = 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).

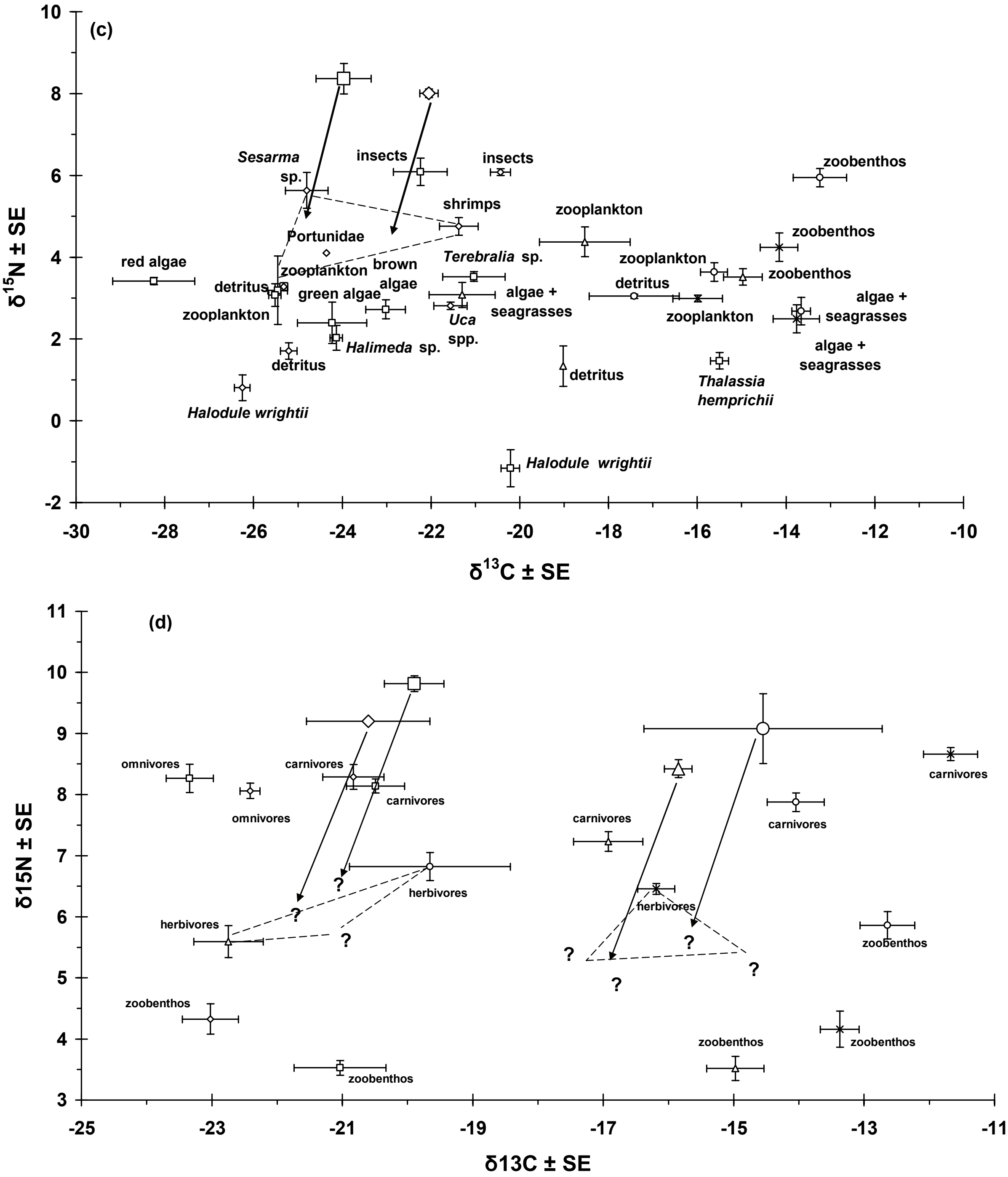
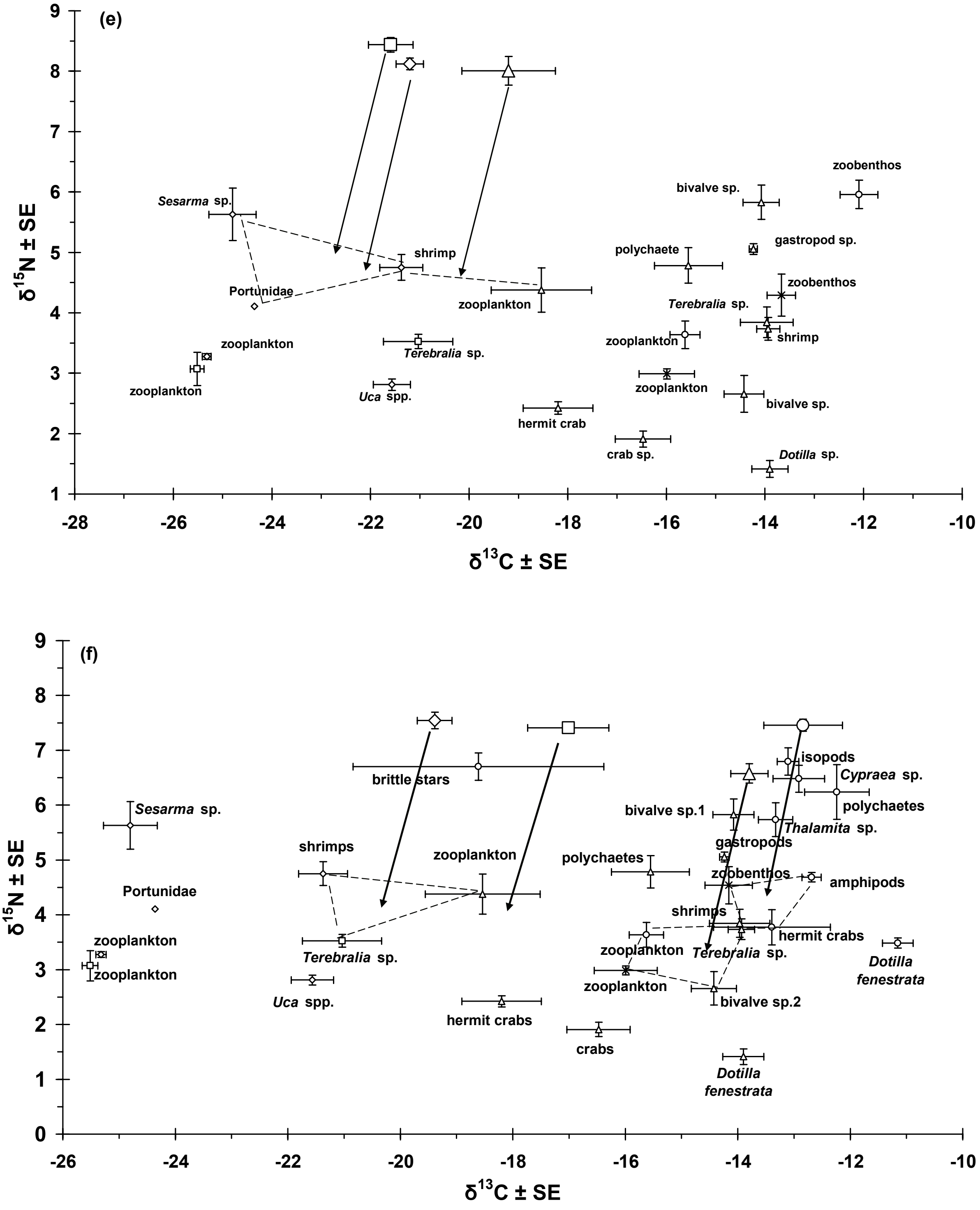


Fig 4. continued.

Although the gut content analysis shows that fishes formed the 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)].



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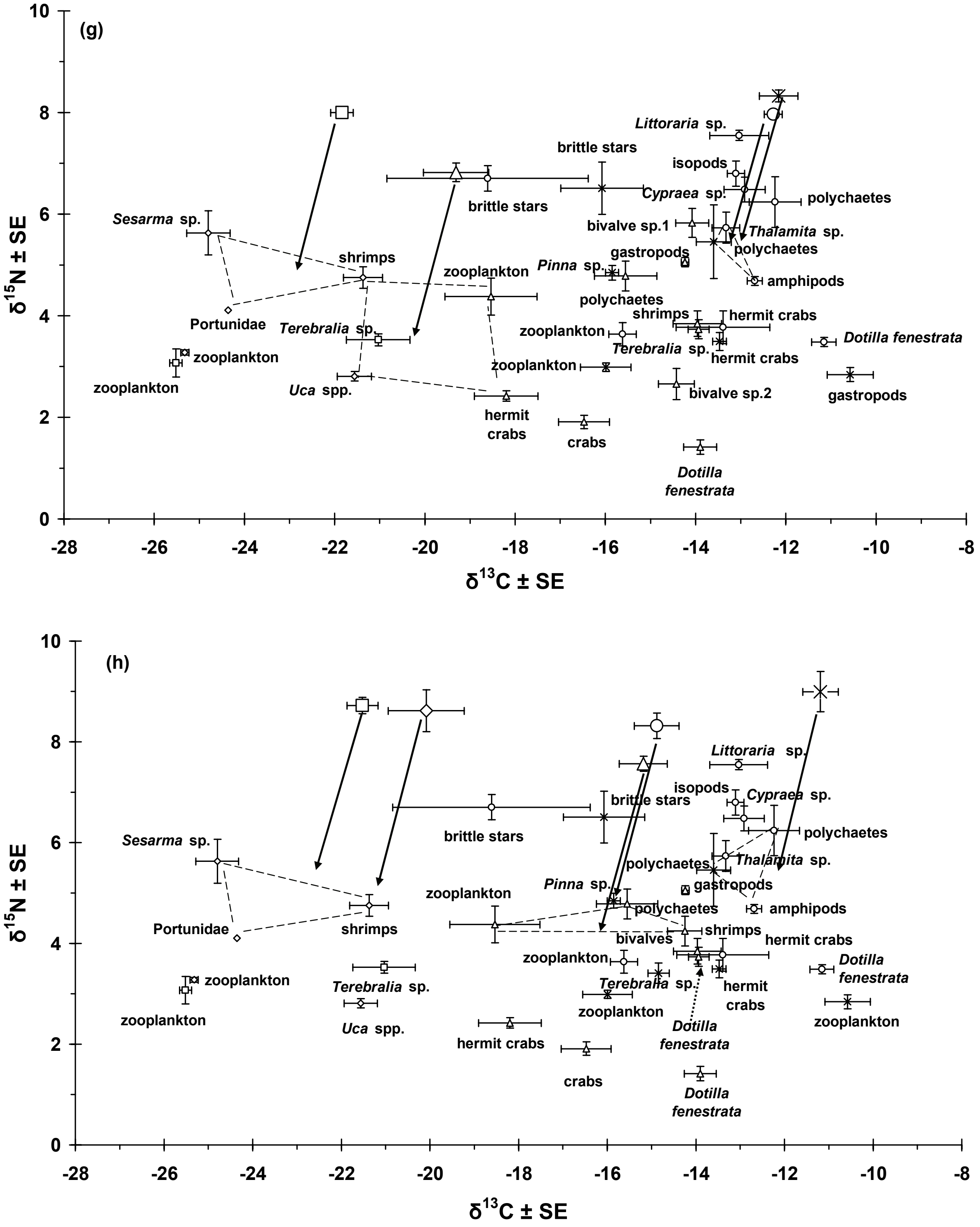

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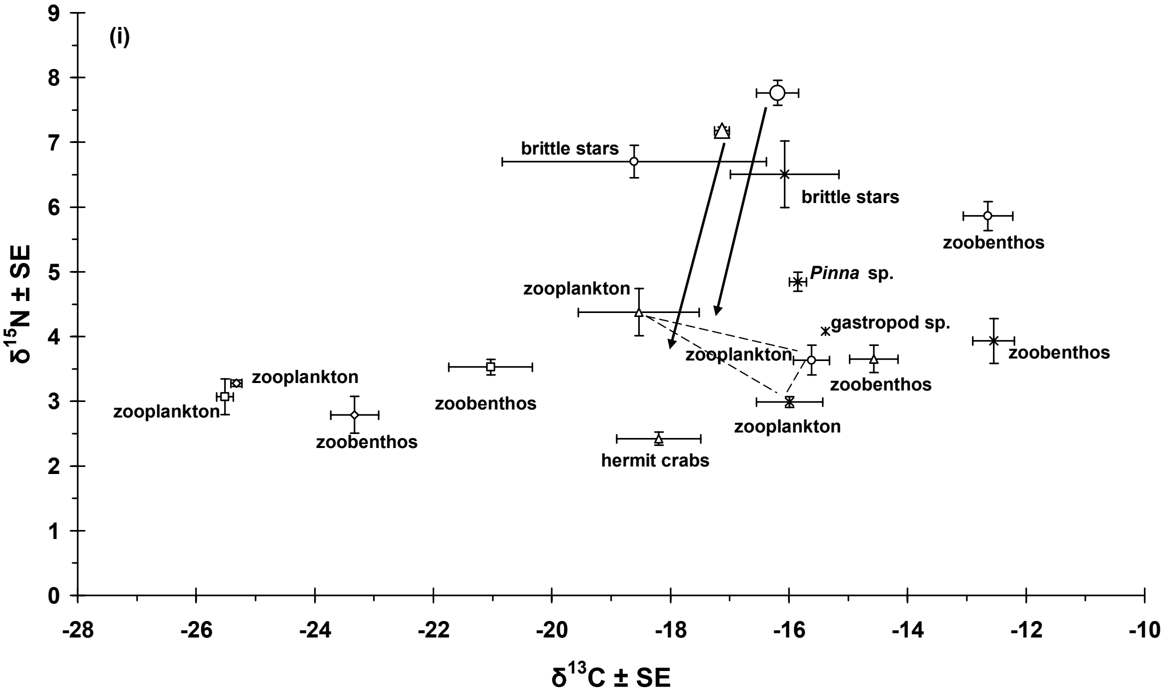

Fig 4. continued.

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 -28.1% 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*., 2002a; Cocheret de la Morinière *et al*., 2003). Similar to what was observed by Sheaves & Molony (2000), Bouillon *et al*. (2002b) 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*., 2002b; 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 δ^{13}C of -24.0%, 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 δ^{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 δ^{13}C of -26.3 and -20.2%, respectively) were too far enriched in δ^{13}C (-15.5 to -8.2%) 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 δ^{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 δ^{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 LF) 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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Chapter 6

The 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 utilised 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 mangroves 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.

INTRODUCTION

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 (in press). 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) 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 characterise 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 neighbouring habitats showing connectivity by tidally migrating fish (Nagelkerken and van der Velde, 2004b). However, mangrove swamps of the Caribbean, a region characterised in contrast by low tidal differences and slow tidal currents, have also been reported to be major feeding grounds for fish which could be 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 establish if 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 less adequate 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) it does not show 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 13C and an average of 3.5 ‰ enrichment of 15N 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 analysed 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? 2) To what degree do fishes present in the mangrove and adjacent habitats utilise food items associated with mangrove habitats?

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

MATERIALS AND METHODS

Study area.

This study was carried out in the 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* ((Forskal) 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 fresh water 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*, *Avicennia marina* and *Bruguiera gymnorhiza* ((L.) 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 characterised 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 characterised 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). 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 litres of seawater over a Whatman GF/C glass fibre filter. In the field, samples were put in a cool box and later frozen at -20^{o}C pending analysis. All caught fishes were identified, counted and their fork length measured to the nearest 0.1 cm. In the majority of the cases, a minimum of 3 samples were used to include a species in the analysis.

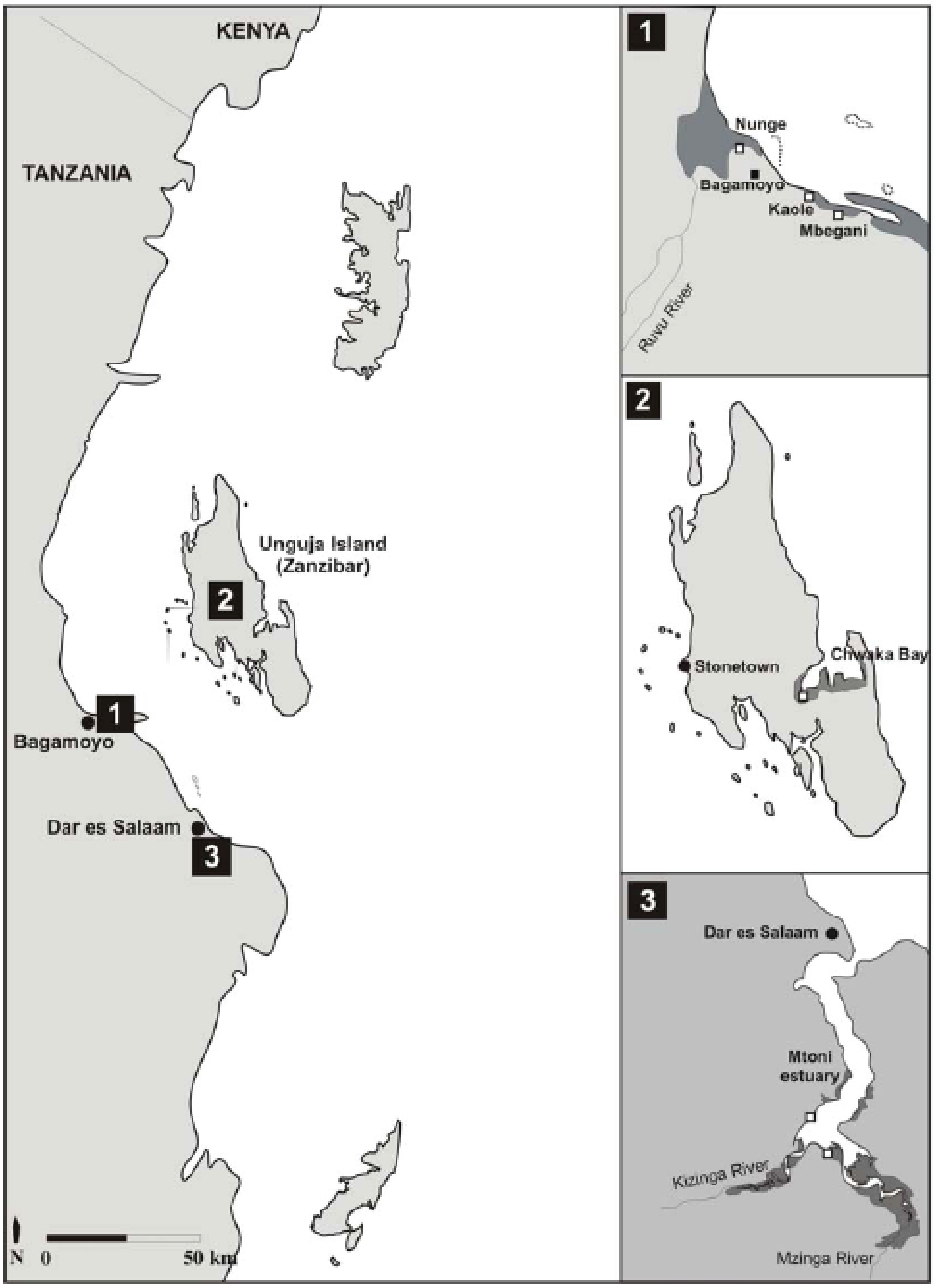


Fig. 1 Map of the coast of Tanzania showing the location of Chwaka Bay on Unguja Island (Zanzibar), Kaole, Mbegani and Nunge in Bagamoyo, and Mtoni estuary in Dar es Salaam. Dark gray areas in Bagamoyo, Chwaka Bay and Mtoni indicate mangrove forests, squares indicate the study sites.

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 h 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 which have been 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 case variances were homogeneous, a 1-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 kind of 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 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 *L. ehrenbergi* (Peters, 1869) from the large mangrove creek showed enriched δ^{13}C values compared to other species from the mangrove creeks. However, since δ^{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 δ^{13}C between the mangrove creeks and the mud/sand flats. The δ^{13}C of individuals of *G. filamentosus* (Cuvier, 1829), *G. oyena*, *Lethrinus lentjan* (Lacepède, 1802), *Lutjanus fulviflamma* and *Sphyraena barracuda* (Walbaum, 1792) differed significantly ($p < 0.01$) between the mangrove creeks and the mud/sand flats. The δ^{13}C values of the other species were not tested because these species occurred in one habitat only. The δ^{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 (*Siganus sutor*) to 9.8 (*Sphyraena barracuda*). These δ^{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, the range in average δ^{13}C values of macrofauna/flora from the mangrove creek ranged between -23.0‰ and -11.4‰ (Fig. 2C). Average δ^{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 a macrofauna/flora, however, there were clear differences in mean δ^{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 δ^{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 δ^{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 a single habitat only. For the whole Mbegani area, the δ^{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*) and 10.3 (*Sphyraena barracuda*) which clearly indicates the trophic positions of the different studied fish species (Fig. 2C & D).

Fringing mangroves

Although a clear difference in δ^{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 δ^{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 δ^{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 δ^{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 δ^{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*) to 9.4 (Atherinidae).

In Nunge, the mean δ^{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 δ^{13}C values of fishes in Nunge did not show a clear distinction between the different habitats, rather their mean δ^{13}C values were clustered between -16.0‰ and -10.3‰ and overlapped between habitats at species level (Fig. 3D). The δ^{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 δ^{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 δ^{13}C values of fishes from Mtoni did not show a clear distinction in δ^{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 δ^{13}C and/or δ^{15}N values from the cluster of other species (Fig. 3F). No significant difference was found between the δ^{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 a single habitat only. In the whole estuary, the δ^{15}N values of food items ranged between 3.4 (detritus) to 12.6 (shrimps) while those of fishes ranged from 8.2 (Carangidae) to 15.2 (Apogon sp.). These δ^{15}N values are relatively higher compared to δ^{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).

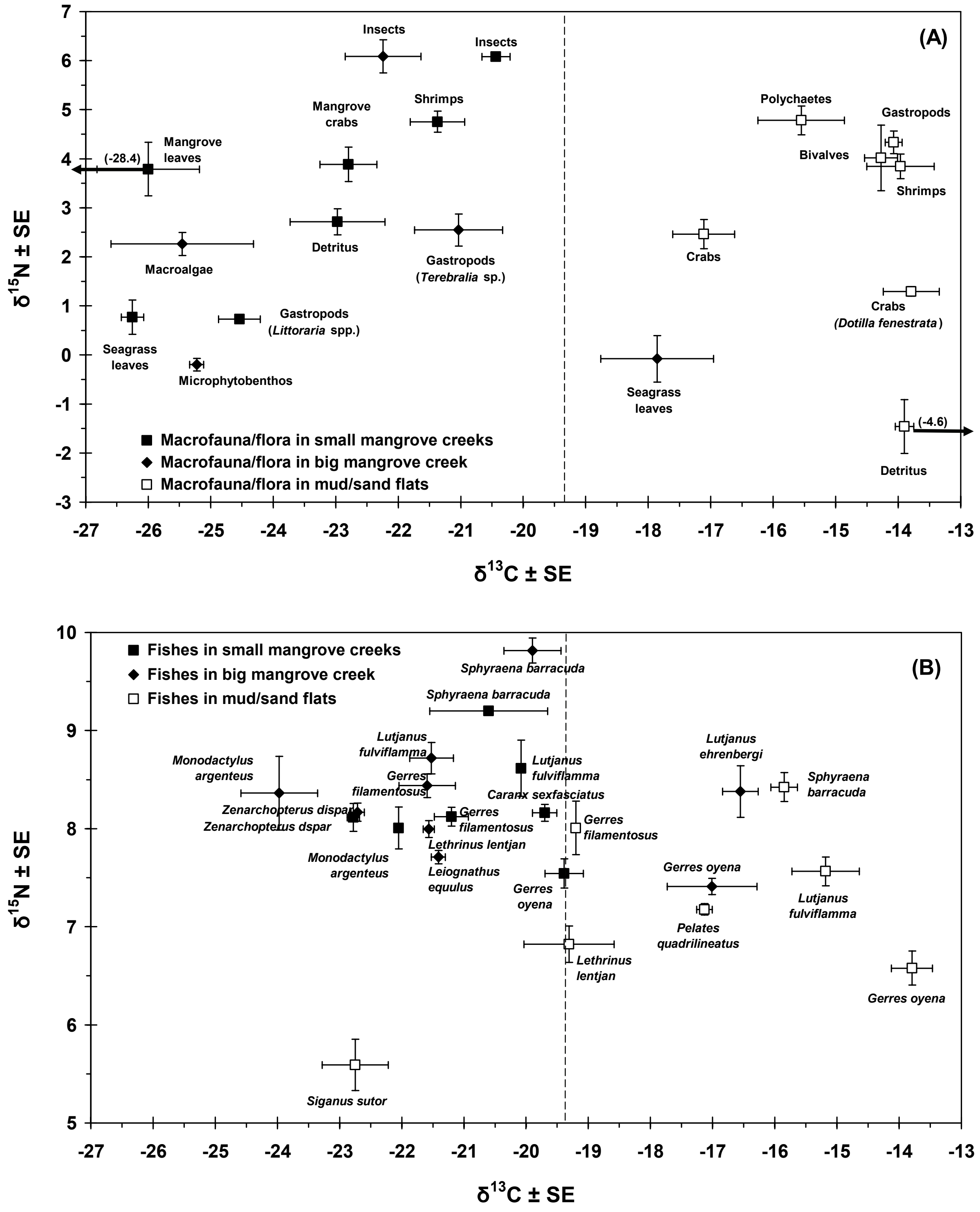
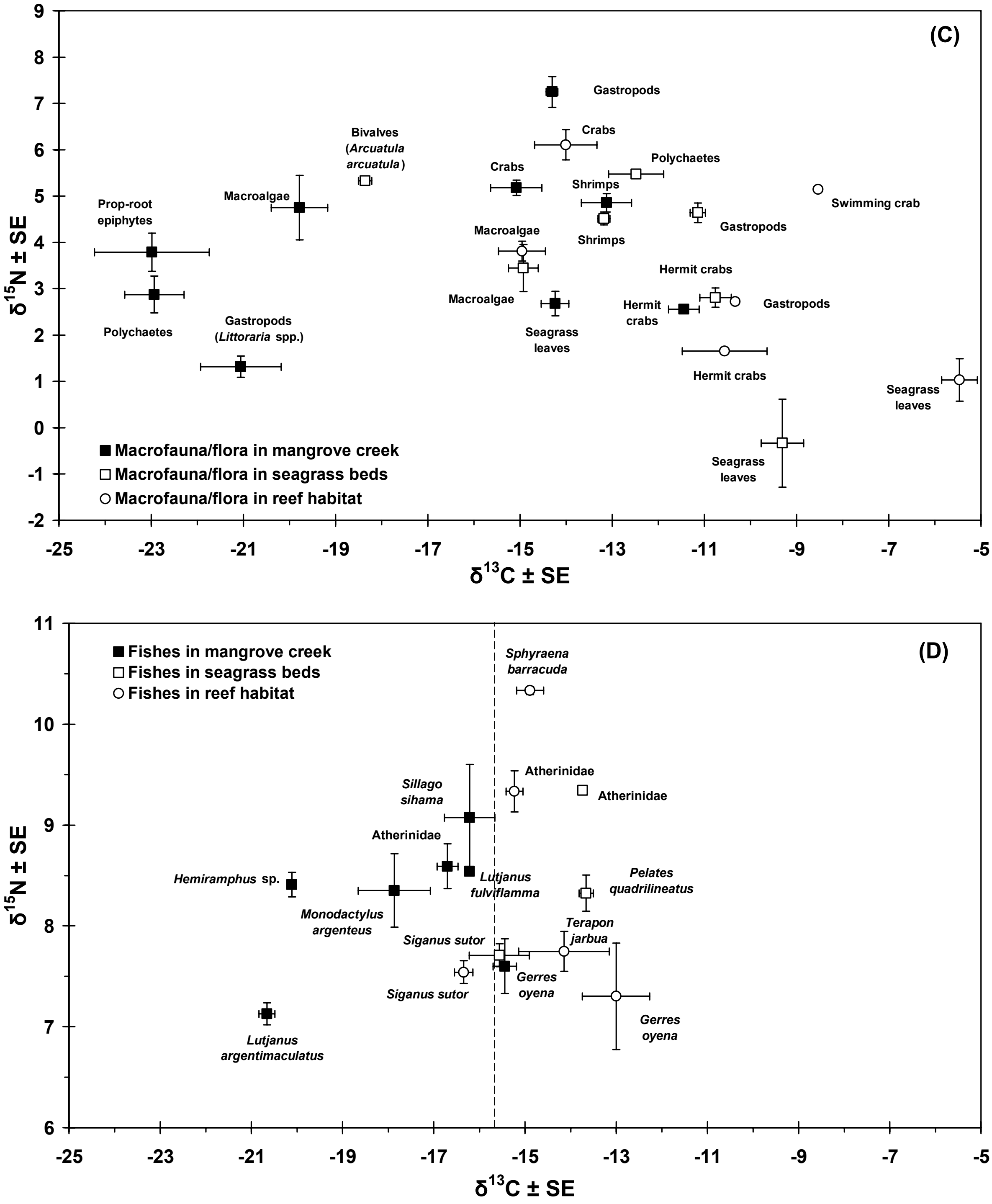


Fig. 2 Mean δ13C and δ15N values of macrofauna/flora and fishes from mangrove habitats and from adjacent habitats in continuously inundated Mapopwe creek (A-B) and Mbegani creek (C-D). The dotted lines indicate the main separation in δ13C values of between the mangrove and adjacent habitats.



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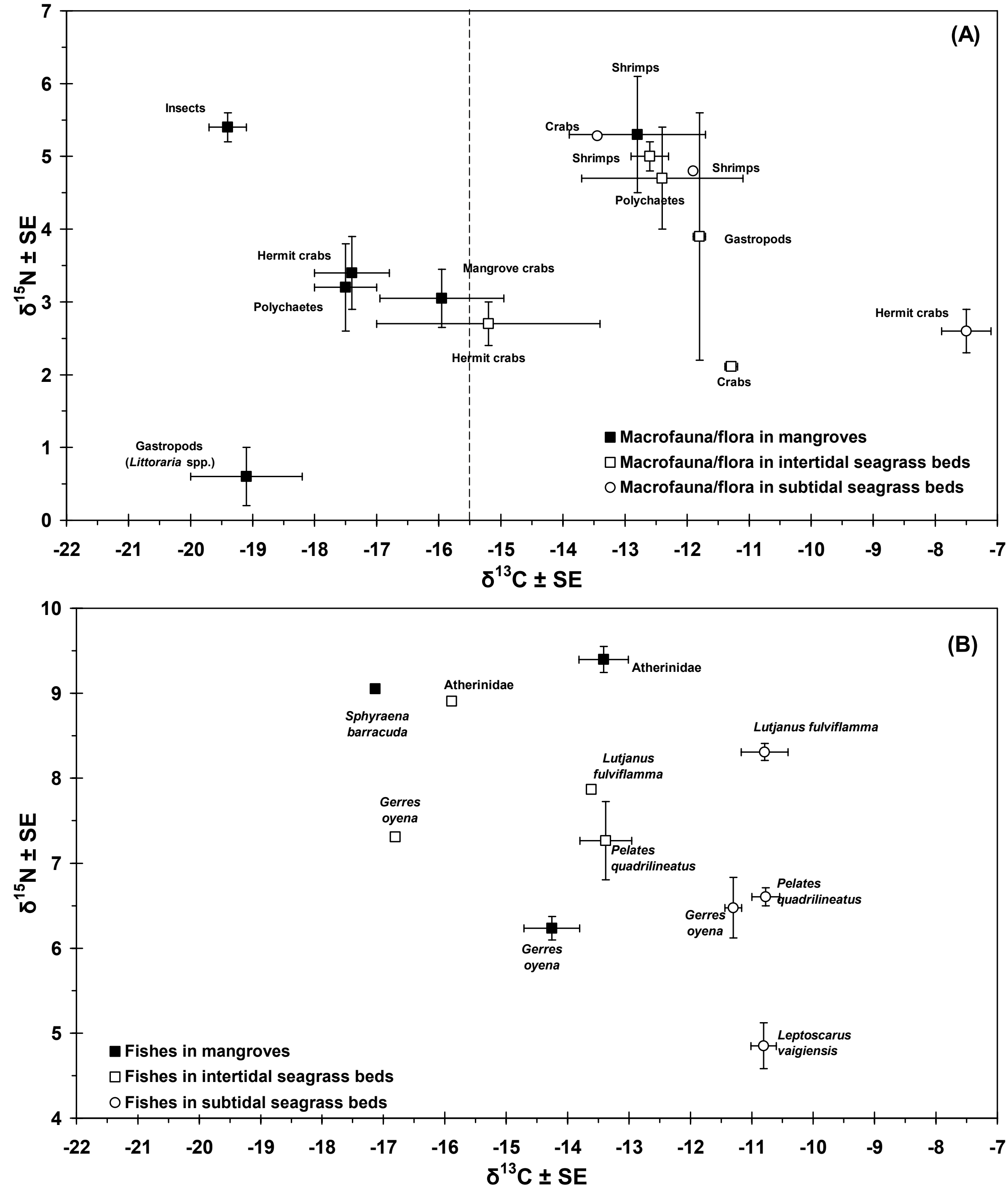
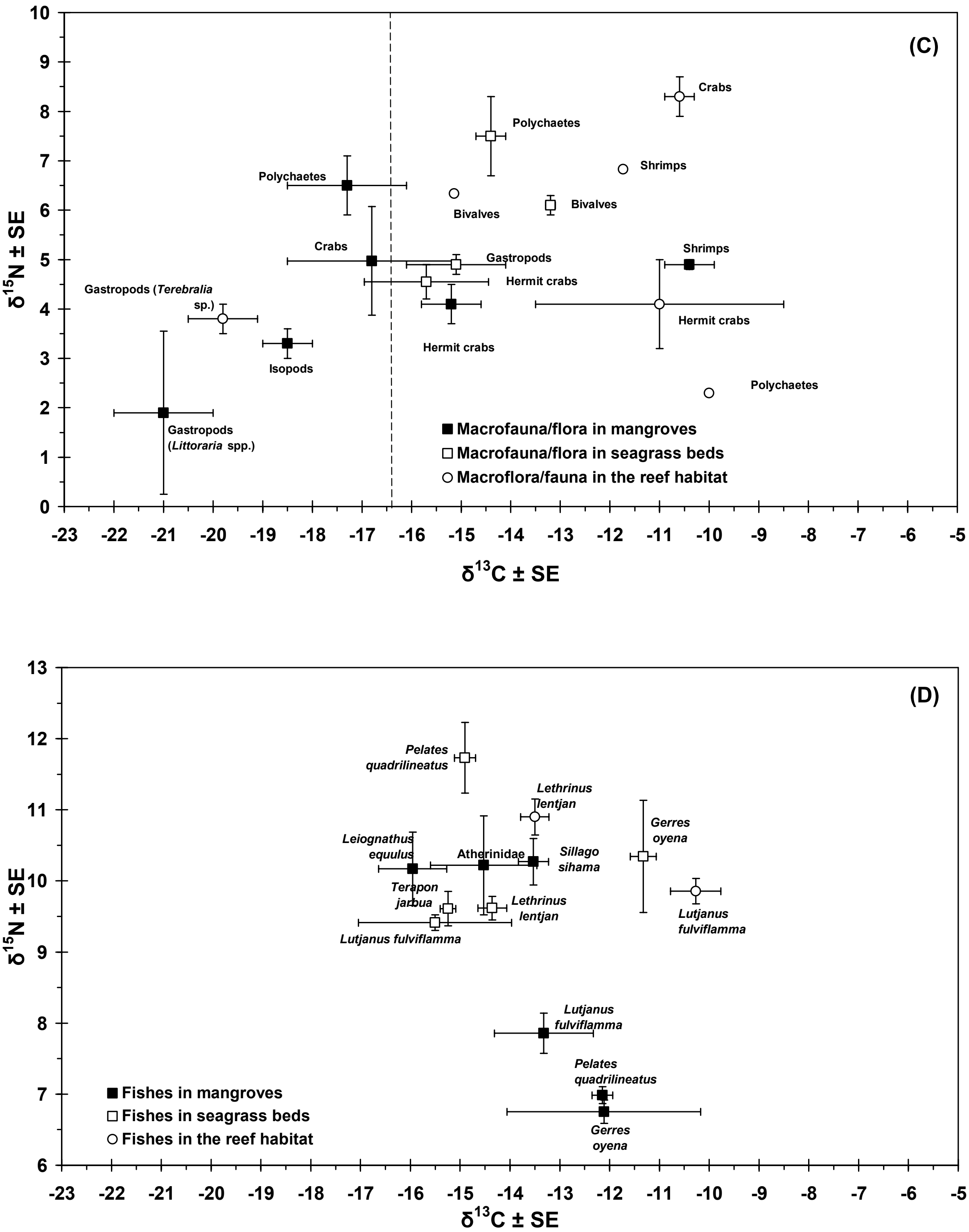


Fig 3 Mean $\delta^{13}C$ and $\delta^{15}N$ values of macrofauna/flora and fishes from the mangrove habitats and from adjacent habitats, in Kaole (A-B), Nunge (C-D) and Mtoni (E-F). The fish species of Mtoni are represented by the following numbers, 1: *Leiognathus equulus*, 2: Gobiidae sp. 1, 3: *Terapon 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*, 13: *Lethrinus lentjan*, 14: *Arothron immaculatus* (Bloch & Schneider, 1801), 15: *Sardinella albella*, 16: *Leiognathus equulus*, 17: *Apogon* sp. 1, 18: *Apogon* sp. 2, 19: *Apogon* sp. 3, 20: *Terapon jarbua*, 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 & 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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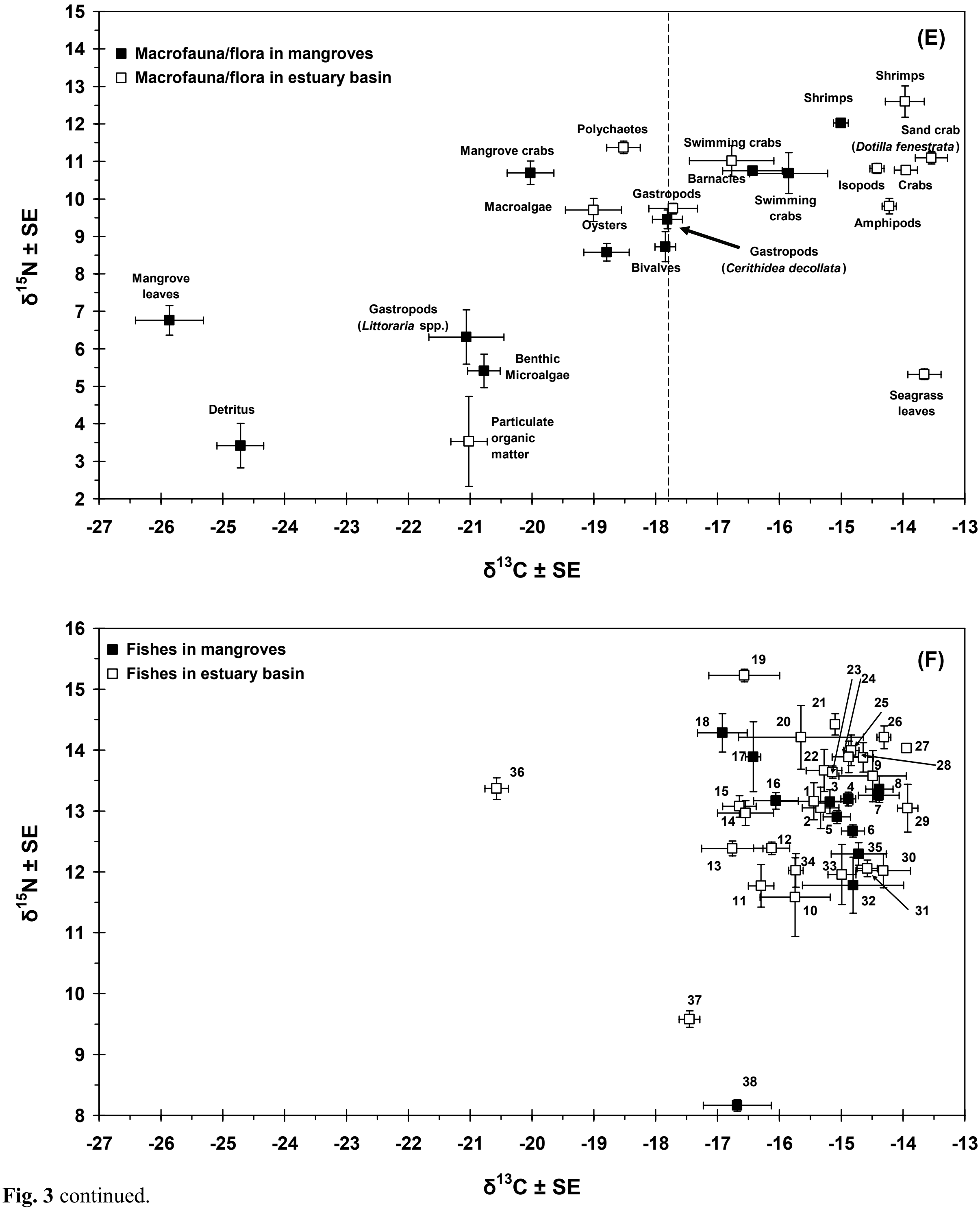

Fig. 3 continued.

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 mangrove 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 in close proximity 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. This is unlikely though, since food items from other habitats were always much 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 feed from all the studied habitats.

The above observations suggest that the utilisation 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 instead of 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 utilisation 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 & Gaimard, 1825), *G. filamentosus*, *G. oyena*, *Leiognathus equulus* (Forsskål, 1775), *Lutjanus argentimaculatus* (Forsskål, 1775), *L. fulviflamma*, *Lethrinus 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, supporting the fact that the fishes from the fringing mangroves probably obtain their food largely from the adjacent habitats. This observation is another indication that the degree of mangrove inundation is important in determining the extent to which a mangrove habitat is utilised as a feeding ground by fishes.

The size of the mangrove forest itself is believed to be another important factor that determines the importance of mangroves as major feeding grounds for fishes. Studies 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 utilised by fishes, as observed in the present study, supports our hypothesis that degree of mangrove inundation is a more important factor influencing the extent to which mangrove habitats are utilised as feeding grounds by fishes.

Although most fishes did not seem to use the fringing mangroves falling dry during low tide as major feeding habitats, some macrofauna did. Some macrofauna species were restricted to the mangrove habitats as suggested by the 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). This suggests that these species feed solely from the mangrove habitat. It was observed that they remained in the mangroves during low tide when these fall dry, which is possible due to various adaptive mechanisms that these animals posses. 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 presence of water and have to 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 (viz. shrimps, swimming crabs and hermit crabs) from the fringing mangroves, on the other hand, showed enriched δ^{13}C values (> 16.8‰) typical for macrofauna from the adjacent habitats, indicating an interaction or connectivity between the 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 fall dry during low tide they probably depend on food sources from the water layer brought in with the tides from the estuary during high tide. Furthermore, the δ^{13}C values of particulate organic matter from the estuary lay in-between those of seagrass and mangrove leaves, which could indicate 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 (δ^{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 (δ^{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 δ^{13}C value of the bivalve *Arcuatula arcuatula* from the seagrass habitat of Mbegani (mean δ^{13}C value of -18.4‰) suggests incorporation of a mixture of material from both the mangrove and seagrass habitats.

The questions that were posed at the beginning of this study can be answered as follows. 1) In almost all cases, food items from both mangroves settings could be discriminated in δ^{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. 2) Fishes from all habitats adjacent to mangroves, and those from the fringing mangroves showed a more enriched δ^{13}C signature, indicating that they probably obtained their food largely from the adjacent habitats. In contrast, the mangroves that allowed a more or less continuous utilisation of the mangrove habitats by fishes appeared to contribute to a larger degree to the food of fishes as compared to fringing mangroves that fall dry during low tide. This study has revealed that the potential of a mangrove habitat in functioning as a feeding area for fish can to be influenced by its configuration. Fringing mangrove habitats seem to contribute less to the food items of fishes as compared to continuously accessible mangrove-lined creeks. The observations in this study indicate that ecosystems showing more similarity in configuration function in a similar way despite geographical differences.

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Chapter 7

Synthesis and Conclusions

SYNTHESIS

Unlike in the Caribbean where mangroves and seagrass beds are widely acknowledged as important nursery habitats for juveniles of coral reef fishes (Nagelkerken *et al*. 2000; Cocheret de la Morinière *et al*. 2002; Nagelkerken *et al*. 2002; Mumby *et al*. 2004), the functioning of such habitats and especially that of mangroves within the Indo-Pacific region has become the subject of considerable research and debate. This is due to inconsistent information about the functioning of these ecosystems in different parts within the region (see for example Blaber 1980; Bell *et al*. 1984; Rodelli *et al*. 1984; Quinn & Kojis 1985; Little *et al*. 1988; Thollot & Kulbicki 1988; Blaber & Milton 1990; Chong *et al*. 1990; Thollot 1992; Tzeng & Wang 1992; Marguillier *et al*. 1997; Sheaves & Molony 2000; Chong *et al*. 2001; Bouillon *et al*. 2002a,b; Guest & Connolly 2004). Inadequate and confounded sampling procedures, improper data presentation/interpretation as well as the variations in sampled habitats are thought to be among the reasons for this discrepancy. Furthermore, world-wide there is plenty of knowledge about ecology of fishes residing in estuarine habitats containing mangroves and seagrass beds (Robertson & Duke 1987; Thayer *et al.* 1987; Bell *et al*. 1988; Little *et al.* 1988; Blaber *et al.* 1989; Blaber 1990; Blaber & Milton 1990; Laegdsgaard & Johnson 1995; van der Velde *et al.* 1995a,b; Kimani *et al.* 1996; Pinto & Punchihewa 1966; Ley *et al.* 1999; Barletta *et al.* 2000,2003,2005; Barletta-Bergan et al. 2002a,b; Ikejima *et al.* 2003; Martino & Able 2003). However, the information about the functioning of such habitats from non-estuarine habitats is limited and largely lacking from East Africa in particular. The inconsistent information on the functioning of these habitats within the Indo-Pacific region and the paucity of this knowledge from the non-estuarine habitats necessitate the evaluation of as many areas as possible within the region so as to reach a general consensus about the functioning of such habitats. This thesis contributes towards this important information gap and provides more understanding of the ecology of fishes in an area where this information is lacking. It describes the fish assemblages of such habitats from a non-estuarine embayment within the Indian Ocean; it also provides insight into the importance of these habitats as feeding grounds for fishes and the possible interrelation between these shallow-water habitats. This thesis goes further into investigating the possible reasons for the discrepancies in the functioning of mangroves as important feeding grounds for fishes. The knowledge gathered in this thesis is of paramount importance towards sound management and conservation of marine resources as a whole.

Community structure of fishes of Chwaka Bay

Although shallow water habitats containing mangroves and seagrass beds are of considerable importance for Tanzania's fisheries and conservation, information on the fish community species inventory and functioning of these ecosystems is scarce. **Chapters 2-4** of this thesis describe the fish assemblage of shallow water habitats including mangroves and seagrass beds from Chwaka Bay, Zanzibar. All these habitats were sampled using a similar fishing method so as to make the data from the different habitats comparable. As shown in **Chapters 2-4** these habitats are dominated by juvenile fishes of both ecological and economic importance. The high abundance and diversity of juvenile fishes found in these habitats is not surprising and is generally associated with advantages that are thought to be offered by these habitats as compared to coral reef areas. These advantages include high food abundance and reduced predation risks. The high juvenile abundance observed in these habitats reveal that the mangrove and seagrass ecosystems which are found within the non-estuarine habitats are important juvenile habitats similar to those found within estuaries (Blaber 1980; Bell *et al.* 1984; Robertson & Duke 1987; Thayer *et al.* 1987; Little *et al.* 1988; Morton 1990; Robertson & Blaber 1992; van der Velde *et al.* 1995a; Kimani *et al.* 1996; Barletta *et al.* 2000, Blaber 2000, Barletta *et al.* 2003). Furthermore, like estuarine fish communities (Robertson & Duke 1990; Barletta *et al.* 2000, 2003, Blaber 2000, Barletta-Bergan *et al.* 2002b; Ikejima *et al.* 2003; Strydom 2003; Jaureguizar *et al.* 2004), the non-estuarine fish assemblage of Chwaka Bay was shown not to be static; there occurred variations in the fish community both in space and time (**Chapters 2-4**). Spatial variations were recorded in fish diversity, size-related distribution patterns and densities in different bay habitats. Comparing the mangroves and seagrass beds the following trends were observed; while the seagrass beds in proximity to mangroves were found to harbour the most diverse assemblage of juvenile fishes, the mangrove creeks harboured less diverse but the highest densities of juvenile fishes. As regards the fish size-related distribution patterns, mangroves harbour small sized juveniles as compared to individuals of the same species that were found in the seagrass beds. These variations were attributed to differences in habitat characteristics, location (nature of adjacent habitat), habitat preferences, and possibly ontogenetic migration. On a temporal basis, it was observed that the mangrove habitats were the most susceptible to surface freshwater runoff especially during the period of heavy rains which resulted into the decline in the fish community structure (density, biomass and diversity) in these habitats, while the fish communities of the seagrass beds were hardly affected. The observed temporal variations in the fish community structure were attributed to the decline in salinity within the mangrove habitats (**Chapter 3**). This observation of a drastic decline in a fish community as a result of a decline in salinity is characteristic for this marine bay and contrary to estuarine fish communities which appear to be somewhat stable at times of low salinities (Barletta *et al.* 2003; Barletta *et al.* 2000).

Habitat preference

The fish community of Chwaka Bay showed some degree of habitat preference; while some fishes were found in multiple habitats, others were restricted to a single habitat type. It is important to note here that the seagrass beds in proximity to mangroves appear the most preferred habitat as they harboured the most diverse fish assemblage (**Chapters 2** and **4**). As shown in **Chapter 4**, juveniles of *Gerres oyena*, *Lethrinus lentjan*, *Lutjanus fulviflamma* and *Sphyraena barracuda* were generalists (found in all studied embayment habitats). In contrast, juveniles of *Cheilio inermis*, *Hipposcarus* *harid*, *Leptoscarus vaigiensis*, and *Scolopsis ghanam* inhabited seagrass beds only while those of *Gerres filamentosus* and *Monodactylus argenteus* were mainly found in the mangrove habitats. It is important to note that as shown by the PCA graph (**Chapter 3**) some species, i.e. *G. filamentosus* and *M. argenteus*, were restricted to the mangrove habitats even during the rainy season, although with a reduced density.

Interestingly, during heavy rains (i.e., during April-May) when salinity and water clarity declined, most species disappeared from the mangroves. This is an indication that in non-estuarine habitats like those of Chwaka Bay where marine fish species form the major part of the fish community, habitat preference is probably subject to stable marine conditions for most fish species, whereas under unfavourable conditions habitat preference becomes a less important factor.

Interaction between bay habitats

Fish assemblages that are found in shallow water habitats exhibit interactions between bay habitats as a result of migration, be it tidal (due to a big tidal range found in the Indo-Pacific), feeding, shelter or ontogenetic (Cocheret de la Morinière *et al*. 2003). Assessing connectivity/interaction between these shallow water habitats is particularly critical considering that the connectivity may be negatively affected due to the extensive habitat loss and degradation that has occurred in these shallow water habitats during the last decades (Chambers 1992; Kennish 2002). It also emphasizes the need to conserve these habitats not in isolation but as a single system, for a sound management outcome. As pointed out by Mumby (2006) conservation strategies should protect connected corridors of habitats and facilitate the natural migration of species among habitats. The stable isotope study (**Chapter 5**) revealed that mangrove and seagrass ecosystems do not exist in isolation; there is a degree of connectivity between these habitats. The habitat connectivity revealed by the stable carbon isotopes of individual fish species (**Chapter 5)** in different bay habitats demonstrated a possible early ontogenetic migration and/or tidal migration. However, as shown by similarity in fish assemblages between habitats (**Chapter 2**) and by connectivity between habitats through feeding (**Chapter 5**), there is an interaction between nearby habitats, but a limited interaction between those which are far apart. The possible reason could be the distance between habitats. Nøttestad *et al*. (1999) pointed out that the distance to be covered during (tida/feeding) migration 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.

As shown in **Chapter 4** there is a gradual increase in size of fish species with increasing distance away from the mangroves. Species such as *Lethrinus lentjan*, *L. variegatus*, *P. quadrilineatus*, *Siganus sutor* and *Sphyraena barracuda* were found as small-sized individuals in shallow and turbid mangrove areas, whereas large-sized individuals were observed in deeper and less turbid seagrass beds. The habitat connectivity that was revealed from the isotope study (**Chapter 5**) gives some clue on the possible occurrence of a step-wise ontogenetic migration in the above mentioned fish species.

In contrast, juveniles of some fish species were found mainly in the mangroves (e.g. *Gerres filamentosus* and *Monodactylus argenteus*) and were never found in the seagrass beds. The question which arises here is 'if the mangroves are (potential) nursery habitats, then how do such fish species from the mangroves migrate to the coral reefs?' Most likely (and probably the only possibility), such fishes migrate to coral reef habitats through direct ontogenetic migration rather than step-wise ontogenetic migration. The abundance of juveniles of fish species such as *G. filamentosus* and *M. argenteus* in the mangroves, and their complete absence from the seagrass beds, as well as their complete absence as adults in the mangroves and in the seagrass beds supports this.

Evaluation of mangroves and seagrass beds of Chwaka Bay as potential nursery habitats

As shown in **Chapters 2** and **3**, juveniles form a major proportion of the fish assemblage of Chwaka Bay. Many fish species that are assumed to utilise these nearshore habitats as nurseries (Dorenbosch *et al.* 2005; Froese & Pauly 2005), were found throughout the bay, sometimes in relatively high densities. These included *Lutjanus fulviflamma*, *Hipposcarus harid*, *Monodactylus argenteus*, *Scolopsis ghanam*, *Siganus sutor* and *Sphyraena barracuda*, suggesting that Chwaka Bay is a potential nursery habitat. However, according to Beck *et al.* (2001) and Heck *et al.* (2003) this observation is not sufficient to qualify Chwaka Bay as a "nursery habitat". For a habitat to be qualified as a "nursery habitat" it should contribute disproportionately more individuals than other shallow water habitats to spatially separate adult populations on an areal basis. This information gap necessitates considerable research within this region. As shown in **Chapter 2**, the mangrove creeks harbour the highest density of juveniles than any other bay habitat. Furthermore, as shown in **Chapter 3**, individuals of the fish species that were found in mangrove areas were smaller in size as compared to individuals of the same species that were found in the seagrass beds. This suggests a possible ontogenetic migration occurring in these bay habitats. Although the present study did not focus on the adult life stages, the almost total absence of adults in the studied bay habitats suggests that large fishes must be present elsewhere, possibly in the deeper parts of the bay or on the adjacent coral reef. A study by Dorenbosch *et al.* (2005) on the fish community of coral reef adjacent to Chwaka Bay provides some evidence on the likely dependence of some coral reef fish species on the presence of seagrass beds and mangroves.

On the contrary, the mangrove creeks contained a higher proportion of zoobenthivores/piscivores (which could be potential predators on small juvenile fishes) than any other bay habitat (**Chapter 2**). This proportion was made up of mangrove resident species (large juveniles/sub-adults and adults). This relatively high proportion of potential piscivores within the mangrove creeks raises a question on the suitability of the mangrove creeks as potential nursery habitats. Sheaves (2001) argued for the use of "abundance of piscivores" in shallow waters as a criterion for considering a habitat as a potential nursery ground. Additionally, the susceptibility of the mangrove habitats to changes in environmental factors during the rainy season as reported in **Chapter**

3 and the subsequent decline in fish populations in this habitat during this season presents doubts on the potential of the mangroves as nursery habitats. On the other hand, the high diversity of juvenile fishes in Chwaka seagrass beds, relatively low proportions of piscivores, and the stable environmental conditions even during rainy period suggest a higher potential of the seagrass beds as a nursery habitat over the mangroves. It should be noted that, this evaluation is being done on the basis of the data collected during the low tide; the situation during the high tide is likely to be different. The access of large predators coming in with the tide could increase predator densities within the mangroves and could also bring in a potential number of predators over the seagrass beds.

Shallow water habitats as feeding grounds for fishes

As shown in **Chapter 5**, the different bay habitats were all used as feeding grounds by different fish species. Gut content and stable carbon isotope analyses showed evidence that the studied fish species generally relied on algae (herbivores) and/or macro-invertebrates (omnivores and zoobenthivores) as a food source, with crustaceans (crabs, shrimps and copepods) playing a major role. Although the stable isotope signatures showed evidence for food dependence of the studied fish species on mangrove and seagrass ecosystems, the direct consumption of either mangrove or seagrass leaves seemed to be absent or very low. 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 substrate 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 the mangroves and seagrass beds (Laegdsgaard & Johnson 2001; Cocheret de la Morinière *et al*. 2004; Nakamura & Sano 2005; Verweij *et al*. 2006).

Mangrove habitats as feeding grounds for fishes

The importance of mangroves as feeding grounds for fish and other macrozoobenthos in the Indian Ocean and elsewhere has been a subject of debate. In **Chapter 6** of this thesis we propose that one of the reasons for the discrepancies in the role of mangroves as feeding habitats could be due to the fact that studies that report on the functioning of mangroves have been conducted in mangrove systems that differed in their settings (landscape). Stable isotope analysis of carbon and nitrogen was used to investigate whether mangrove landscape configuration could influence the functioning of mangroves as an important feeding area. The two mangrove settings were: mangrove-lined creeks which retain water during low tides and fringing mangroves that drain completely during low tides. **Chapter 6** reveals that the utilisation of mangrove habitats as feeding grounds for fishes seems to be different in different mangrove systems. 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.

It has been shown from **Chapters 5** and **6** that only mangroves which are more or less permanently inundated can serve as important feeding grounds, only for fishes that are living within the mangrove habitats, and that the fishes found in adjacent habitats do not use these habitats as important feeding grounds. Two important questions arise here. 1. If fishes (from the fringing mangroves and those from adjacent habitats in all different settings of mangroves) do not feed significantly from the mangroves, why do they visit the mangroves? 2. What is the primary importance of mangroves to these fishes? Is it provision of food or shelter/refuge? The answer to question 1 could be: the likely reason why these fishes would move into mangroves during high tide is protection against predation by using the structural complexity of mangrove aerial roots. As observed in other studies, structural complexity in relation to predation risk is an important factor in determining distribution of juvenile fishes (Laegdsgaard and Johnson 2001; Cocheret de la Morinière *et al*. 2004; Verweij *et al*. 2006). The answer to question 2 is that, the primary function/importance of mangroves to fishes, especially from the studied mangroves, appears to be shelter/refuge. Most fishes move into the mangrove ecosystems in search for safe habitats against predation; however, if conditions allow (such as degree and duration of inundation) these fishes would also feed from these habitats. Being able to feed within the mangroves especially at a juvenile stage is likely to have a double advantage: a juvenile fish may benefit by feeding from a rich invertebrate fauna of mangrove forests (Sheridan 1997) and also obtain the protection afforded by the structural complexity found in these habitats.

CONCLUSIONS

This thesis aimed at answering the following question: ‘Do the mangroves and seagrass beds along the Tanzanian coast serve as important habitats for juvenile fishes?’ It was also aimed at showing how a non-estuarine (marine) bay compares with estuaries as well as other marine bays in other regions. This thesis shows that shallow water habitats (including mangroves and seagrass beds) from a non-estuarine (marine) bay of Tanzania are important juvenile habitats for both resident and transient fish species many of which are of commercial importance (**Chapters 2-4**). It was also shown that a marine embayment can experience a seasonal influx of freshwater just during heavy rains which can result into changes in environmental conditions similar to those that occur in estuarine habitats. However, unlike the fish communities occurring in estuarine habitats which are more or less adapted to decline in salinity, the fish communities of marine bays are not stable as was revealed by the marked decline in fish densities, biomasses and diversity during the rainy period (**Chapter 3**). This thesis has also shown that the fish community of this non-estuarine bay shows a spatial size-related distribution patterns with small juveniles in the turbid mangrove habitats and large juveniles on the more clear-water seagrass beds towards the coral reef and deeper parts of the bay (**Chapter 4**); this pattern suggests the possible existence of ontogenetic migration. This thesis also shows that shallow water habitats including mangroves and seagrass beds do not occur in isolation. These habitats are interlinked through fish movements (be it tidal, feeding or ontogenetic migration). Shallow water habitats including mangroves and seagrass beds can constitute an important feeding ground for fishes (**Chapters 5** and **6**); however, the setting of a mangrove ecosystem is an important factor that influences its usage as a feeding ground for fishes. This thesis has revealed that mangroves ecosystems from the same region but differing in landscape configuration function differently and that other factors (such as duration of inundation) could be equally important or even more important than the geographical position of a mangrove ecosystem.

RECOMMENDATIONS FOR FURTHER RESEARCH

Generally, this thesis has shown that mangroves and seagrass beds of Tanzania are important juvenile habitats to fishes many of which are of commercial importance. Although some of these fishes can be categorized as reef fishes, it is still not clear if these reef fishes that are found as juveniles in the mangroves and seagrass beds later migrate to the reef. Futhermore, according to Beck *et al*. (2001) and Heck *et al*. (2003) the presence of juveniles in mangroves and seagrass beds is not sufficient to qualify them as a "nursery habitat". For a habitat to be qualified as a "nursery habitat" it should contribute disproportionately more individuals to spatially separate adult populations per unit of surface area than other habitats. This information gap necessitates the carrying out of considerable research within this region. While the findings of the present thesis can be used as a baseline for further research on shallow water habitats containing mangroves and seagrass beds as potential nursery habitats for fishes, techniques such as mark and recapture, the use of otolith micro-chemistry and the involvement of the entire mangrove-seagrass-reef continuum could help to substantiate the contribution of these shallow water habitats to reef populations and hence confirm the nursery role hypothesis.

Stable isotope data of fishes in the Tanzanian shallow water habitats are scarce. It is however, known that the movements of fishes between habitats can be traced using stable isotopes of carbon and nitrogen, given the differential isotopic signatures of the respective food webs. Stable isotope studies on the fish communities of shallow water habitats including mangrove-seagrass-coral reef continuum could be used to trace fish movements and this would add more knowledge of the functioning of these ecosystems as nursery areas in East Africa and in the Indian Ocean as a whole.

The present thesis has shown that the shallow water habitats including mangroves and seagrass beds can serve as important feeding grounds for fishes. It has also shown that mangrove setting (duration of inundation) is an important factor influencing the functioning of a mangrove ecosystem as a feeding ground. However, feeding from these shallow water habitats is just one important function that these shallow water habitats can offer to fishes. Other functions such as shelter and refuge to fishes cannot be underestimated. The mangrove ecosystem that proved not to be an important feeding ground for fishes could form an important habitat that provides shelter and refuge to fishes. The importance of shallow water habitats in the provision of shelter to fishes needs to be studied in different shallow water habitats and in particular in different settings of mangroves so as to establish how different mangrove ecosystems function in as far as shelter/refuge function is concerned.

Most of the data presented in this thesis give a general picture of what occurs in Chwaka Bay during low spring tides and especially in the shallow habitats which could be accessed with the sampling gear (net) used and also during the day-time. Future sampling should include day and night samplings, encompass the whole tidal range and all moon phases, and much deeper areas and the adjacent coral reef.

As stated in this thesis, the mesh size (1.8 mm) used in the present study was not adequate for catching larvae and small juveniles. It is recommended that future studies should also include other techniques that will sample the whole size range of fishes. This will generate information on the recruitment of fishes, e.g. the size at which larval fishes settle in these habitats.

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SUMMARY

The importance of mangroves and seagrass beds as important habitats for fishes has been a subject of debate and considerable research. While the importance of both seagrass beds and mangroves as a juvenile habitat for coral reef fishes is well demonstrated in the Caribbean region, the functioning of these shallow water habitats and particularly the mangroves within the Indo-Pacific region is doubtful. Furthermore, there is scarcity of knowledge on the functioning of non-estuarine bays within the Indo-Pacific region and the coast of east Africa in particular, since most of research has been done within estuaries. This thesis gives an insight into the potential of mangroves and seagrass beds of Tanzania as important habitats for juvenile fishes.

Chapters 2-4 of this thesis describe the fish community of the non-estuarine embayment (Chwaka Bay) both in terms of spatial and temporal variations. As reported in **Chapter 2**, the fish community of Chwaka Bay is dominated by small juveniles many of which are of commercial fishery importance. This observation is an indication that mangroves and seagrass beds situated within a marine (non-estuarine) embayment can serve as important habitats for juvenile fishes. However, as shown in **Chapters 2-4**, the distribution of species and size-related distribution patterns, as well as the abundance was not similar throughout bay habitats or even throughout the year. As regards the species composition and abundance, neighbouring bay habitats contained more similar fish assemblages than bay habitats that were far apart (i.e. mangrove creeks vs. Marumbi seagrass beds). Proximity to mangroves and/or coral reefs and habitat type are thought to influence the fish assemblages and hence the differences in fish species overlap observed.

Fish populations are not stable; they always vary in space and time. Being a non-estuarine embayment, the environmental variables as well as the fish community structure in each habitat remained relatively constant for most part of the year; however, a marked decline (in density, biomass and species richness and in salinity in particular) was observed during the rainy period with larger changes in the mangroves and mud/sand flats habitats than in the seagrass beds (**Chapter 3**). A drastic change in salinity coupled with changes in other environmental variables was proposed to be the cause for the decline in the fish community, especially within the mangroves and mud/sand flats. Moreover, the results indicate that although mangroves were the preferred settling habitats for *Gerres filamentosus*, *Gerres oyena*, *Lethrinus lentjan* and *Monodactylus argenteus*, there was a degree of timing during favourable conditions for settlement especially during the dry season (December – February period) and not during the rainy season (April-May) when the environmental conditions and especially salinity declines.

In connection with the nursery hypothesis, most fishes found within mangrove and seagrass ecosystems as juveniles at a certain stage probably outgrow the protection of these habitats and likely migrate permanently from their nursery habitats to deeper water, such as adjacent coral reefs. They probably do so through direct or step-wise ontogenetic migration. By using seine net, thirteen

commercially important fish species were investigated to see if they exhibit an ontogenetic migration (**Chapter 4**). Five of the 13 studied species (*Lethrinus lentjan*, *L. variegatus*, *Pelates quadrilineatus*, *Siganus sutor* and *Sphyraena barracuda*) were found as small-sized individuals in shallow and turbid mangrove areas, whereas large-sized individuals were observed in deeper and less turbid seagrass beds. A possible explanation for this pattern could be an ontogenetic shift in habitat utilisation, as established by stable isotope results (**Chapter 5**). As regards the species richness of different bay habitats, the seagrass beds near to mangroves (Chwaka seagrass beds) showed the most diverse fish assemblage of all habitats, possibly because it functions as a corridor between the mangroves and deeper parts of the embayment. Mud/sand flats had the least diverse fish assemblage (**Chapter 2** and **4**). This thesis shows that Chwaka Bay contains a large number (around 150) of fish species, however, only a few species dominate in terms of both density and biomass (**Chapter 2**). It also shows that some fish species exhibit habitat preferences while others are ubiquitous (**Chapter 2** and **4**).

The relative importance of bay habitats, consisting of mangrove creeks and channel, seagrass beds, and mud/sand flats, as feeding grounds for a number of fish species was studied in Chwaka Bay, using gut content analysis and stable isotope analysis of carbon and nitrogen (**Chapter 5**). The mean δ^{13}C values of fishes and food items from the different bay habitats studied showed that all bay habitats were significant feeding grounds for fishes. The mean δ^{13}C values fishes and food items from the mangroves were the most depleted ($\leq$ -19‰) and those from the seagrass beds the most enriched ($\geq$ -14‰). Similar to other studies done in different geographical locations, the importance of mangrove and seagrasses themselves as a primary source of carbon to higher trophic levels was limited. This thesis also revealed connectivity with respect to feeding between different habitats which could be a result of either daily tidal migrations or recent ontogenetic migration (**Chapter 5**).

The importance of different mangrove ecosystems as feeding grounds for fishes and other macrozoobenthos is presented in **Chapter 6**. By using stable isotope analysis of carbon and nitrogen, we investigated two different settings of mangrove ecosystems along the Tanzanian coast, to establish if the topography of a mangrove ecosystem influences the use of this habitat as a potential feeding ground by fishes. The δ^{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 δ^{13}C of some food items from the fringing mangroves with those from adjacent habitats, and the more enriched δ^{13}C signatures of fishes from the fringing mangroves with respect to most typical food items from the mangroves 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.

In summary, this thesis reveals that shallow water habitats (including mangroves and seagrass beds) from a non-estuarine (marine) bay of Tanzania are important juvenile habitats for both resident and transient fish species, many of which are of commercial importance. This thesis also shows that shallow water habitats including mangroves and seagrass beds are not isolated from each other. These habitats are interlinked through fish movements (be it tidal, feeding or ontogenetic migration). Shallow water habitats including mangroves and seagrass beds can constitute an important feeding ground for fishes; however, the setting of a mangrove ecosystem is an important factor that influences its utilisation as a feeding ground for fishes. This thesis has revealed that mangroves ecosystems from the same region but differing in landscape configuration function differently and that other factors (such as duration of inundation) could be equally important or even more important than the geographical position of a mangrove ecosystem. The findings of this thesis can be use to design strategies for sustainable utilisation and management of shallow-water habitats and resources.

SAMENVATTING

De waarde van mangroves en zeegrasvelden als habitat voor vis is het onderwerp van een voortdurende discussie en vele studies. Terwijl er veel bewijs is voor de waarde van de mangroves en zeegrasvelden in het Caribische gebied als habitat voor vis, bestaat er twijfel over de waarde van deze habitats voor vis in het gebied van de Indische en Stille oceanen. Aangezien het onderzoek in baaien in dit gebied en langs de Oost Afrikaanse kust vooral gericht is op estuaria, is er bovendien weinig bekend over het functioneren van niet-estuariene baaien. In dit proefschrift is onderzocht welke waarde de mangroves en zeegrasvelden langs de kust van Tanzania voor juveniele vis hebben.

In de hoofdstukken 2 tot en met 4 wordt de samenstelling van de visgemeenschappen van de baai van Chwaka, een niet-estuariene baai, in de tijd en ruimte onderzocht. Zoals beschreven in hoofdstuk 2 bestaat de visgemeenschap van de baai van Chwaka voornamelijk uit juvenielen, waarvan velen soorten die van belang zijn voor de visserij. Deze waarneming suggereert dat mangroves en zeegrasvelden in niet-estuariene baaien als waardevolle habitats voor juveniele vis kunnen dienen. De abundantie en verspreiding van zowel soorten als lengteklassen vertoonden echter variatie in de tijd en tussen de habitats in de baai. De visgemeenschappen van direct naast elkaar gelegen habitats vertoonden meer overeenkomsten in soortensamenstelling en abundantie dan verder uit elkaar gelegen habitats (zoals de mangrove kreken en de zeegrasvelden voor Marumbi). Het type habitat en de nabijheid van mangroves of koraalriffen worden gedacht van invloed te zijn op de samenstelling van visgemeenschappen.

De samenstelling van visgemeenschappen is niet stabiel, maar is onderhevig aan veranderingen in plaats en tijd. In de niet-estuariene baai van Chwaka bleken zowel de omgevingsfactoren als de structuur van de visgemeenschap relatief constant tijdens het grootste deel van het jaar. In het regenseizoen werd echter een drastische afname in visdichtheid, visbiomassa, soortenrijkdom en zoutgehalte waargenomen. Deze veranderingen waren groter in de mangroves en op de modder- en zandplaten dan in de zeegrasvelden (hoofdstuk 3). Een sterke verandering in zoutgehalte in combinatie met veranderingen in andere omgevingsfactoren werd gezien als de oorzaak voor de veranderingen in de visgemeenschap. Hoewel de voorkeur van *Gerres filamentosus*, *Gerres oyena*, *Lethrinus lentjan* en *Monodactylus argenteus* uitging naar vestiging in de mangroves, bleek de vestiging in deze habitat tijdgebonden: vissen vestigden zich in deze habitat tijdens het droge seizoen waarin de condities gunstig waren, en niet in het regenseizoen waarin verschillende omgevingsfactoren minder gunstig waren en het zoutgehalte lager is.

Volgens de kinderkamer hypothese zullen de meeste vissen die zich tijdens juveniele stadia ophouden in mangroves en zeegrasvelden de bescherming die deze habitats bieden op een zeker moment ontgroeien. De vissen zullen zich vervolgens middels directe migratie of stapsgewijze ontogenetische migratie verplaatsen naar habitats met grotere waterdiepte, zoals koraalriffen. In hoofdstuk 4 is met behulp van zegenvisserij onderzocht of 13 commercieel belangrijke soorten

ontogenetische migratie vertonen. Van vijf van deze soorten, te weten *Lethrinus lentjan*, *L. variegatus*, *Pelates quadrilineatus*, *Siganus sutor* en *Sphyraena barracuda*, werden kleine individuen in de ondiepe en troebele wateren van de mangroves gevonden, terwijl grote individuen in diepere en heldere wateren van zeegrasvelden werden waargenomen. Deze verspreiding kan verklaard worden door een ontogenetische aanpassing in habitat gebruik, zoals blijkt uit analyse van de stabiele isotopen signaturen. De visgemeenschap van een zeegrasveld in de nabijheid van mangroves (de zeegrasvelden bij het dorp Chwaka) bleek de hoogste soortenrijkdom te hebben van de onderzochte habitats, wellicht door de functie als corridor tussen de mangroves en de diepere delen van de baai. De visgemeenschappen van de modder- en zandplaten hadden de laagste soortenrijkdom. Dit proefschrift laat zien dat ongeveer 152 vissoorten in de baai van Chwaka aanwezig zijn, maar dat slechts enkele soorten de visgemeenschap in aantal en biomassa domineren (hoofdstuk 2). Verder blijkt dat sommige van de aanwezige soorten duidelijke habitatvoorkeuren hebben, terwijl andere soorten geen voorkeur lijken te hebben (hoofdstukken 2 en 4).

In de hoofdstukken 5 en 6 worden resultaten gepresenteerd die verder inzicht geven in het functioneren van de ondiepe habitats. De waarde van de habitats in baaien (mangrove kreken, mangrove kanalen, zeegrasvelden, modder- en zandbanken) als foerageergebied voor vissen is onderzocht in de baai van Chwaka met behulp van analyse van de maaginhoud en stabiele koolstof en stikstof isotopen (hoofdstuk 5). Uit de analyse van de δ^{13}C-waarden van vissen en voedselbronnen in de verschillende habitats bleek dat alle habitats een significante waarde als foerageergebied voor vissen hadden. De gemiddelde δ^{13}C-waarden voor vissen en voedselbronnen was het laagst in de mangroves (≤-19‰) en het hoogst in zeegrasvelden (≥-14‰). Net als in studies die elders zijn uitgevoerd, bleek ook in deze studie dat de waarde van mangroves en zeegrasvelden als primaire bron van koolstof voor de hogere trofische niveaus gering was. Bovendien werd in hoofdstuk 5 aangetoond dat er een hoge mate van connectiviteit tussen de verschillende habitats was door de uitwisseling van voedingsstoffen, hetgeen kan wijzen op dagelijkse tij-gestuurde migratie of recente ontogenetische migratie.

De waarde van de verschillende mangrove habitats als foerageergebied voor vissen en ander macrozoobenthos is onderzocht in hoofdstuk 6. Met behulp van de analyse van stabiele koolstof en stikstof isotopen is onderzoek gedaan naar de invloed van geomorfologie van mangroves op de waarde van de mangroves als foerageergebied voor vis. Hierbij zijn twee mangrove typen die langs de kust van Tanzania voorkomen onderzocht. In mangroves waar kreken aanwezig zijn, is de koolstof signatuur van de meeste vissen vergelijkbaar met de voedselbronnen in de mangroves, waaruit blijkt dat de vissen in de mangrovehabitat foerageren. In baaien waar de mangroves slechts een smalle oeverstrook innemen, zogenaamde “fringing mangroves”, blijkt dat de vissen een hogere koolstof signatuur hebben dan de typische voedselbronnen in de mangroves. Hieruit blijkt dat de vissen zowel binnen als buiten de mangroves foerageren, waarbij de bijdrage van de mangroves klein is. Deze resultaten laten zien dat de mangrovekreken een grotere rol als foerageergebied hebben dan de mangroves die slechts een smalle oeverstrook innemen. Dit hangt waarschijnlijk samen met de mate waarin de mangroves bij vloed onder water staan. De vrijwel ononderbroken toegankelijkheid van de kreken biedt vissen meer verblijf- en foerageermogelijkheden dan de smalle mangrovestroken die enkel tijdens vloed toegankelijk zijn en bij afgaand tij weer verlaten moeten worden.

Samenvattend toont dit proefschrift aan dat ondiepe habitats in baaien langs de kust van Tanzania, waaronder mangroves en zeegrasvelden, waardevolle habitats vormen voor zowel residente als doortrekkende vissoorten, waaronder commercieel belangrijke soorten. Verder wordt in dit proefschrift aangetoond dat ondiepe habitats niet op zichzelf staand, maar in grote mate verbonden zijn door de verplaatsingen van vis (getijde migratie, ontogenetische migratie en foerageermigratie). De ondiepe habitats vormen potentieel waardevolle foerageergebieden voor vis, maar de geomorfologie van de mangroves blijkt een factor te zijn die bepalend is voor het gebruik van de habitat als foerageergebied door vissen. In dit proefschrift is aangetoond dat mangroves die in dezelfde geografische regio gelegen zijn maar die verschillen in geomorfologie verschillend functioneren. Andere factoren zoals de duur van inundatie tijdens vloed kunnen een even grote of zelfs grotere invloed op het functioneren van een habitat hebben dan de geografische ligging. De inzichten die dit proefschrift verschaft kunnen van grote waarde zijn bij het opstellen van strategieën voor duurzaam gebruik en beheer van ondiepe kusthabitats en de grondstoffen die deze habitats voortbrengen.

MUHTASARI

Umuhimu wa mikoko na nyasi za baharini kama makazi ya samaki umekuwa mada kubwa ya mjadala na utafiti. Wakati umuhimu wa nyasi za baharini na mikoko, kama makazi muhimu ya samaki wa mwamba tumbawe umethibitishwa katika eneo la Karibiani, utendaji kazi wa makazi haya katika maji yenye kina kifupi na hasa jamii ya mikoko ya eneo la Kipasifiki si dhahiri. Pia, kuna uhaba wa uelewa juu ya utendaji kazi wa ghuba zisizo na milango ya mito katika eneo la Pasifiki, hususan, Pwani ya Afrika Mashariki. Hii ni kwa sababu tafiti nyingi hapa Afrika Mashariki zimefanyika katika ghuba zenge milango ya mito. Tasnifu hii inatoa mwanga wa kumaizi uwezekano wa mikoko na nyasi za baharini zinazopatikana katika ghuba zisizokuwa na milango ya mito, kuwa makazi muhimu kwa samaki wadogo katika pwani ya Tanzania.

Katika tasnifu hii Sura ya 2 na ya 4 zinaelezea juu ya jamii ya samaki katika ghuba isiyo na milango ya mito (Ghuba ya Chwaka). Kama ilivyoripitiwa katika Sura ya 2, jamii ya samaki wa ghuba ya Chwaka imetawaliwa na samaki wadogo ambao ni muhimu kwa biashara katika sekta ya uvuvi. Uchunguzi huu ni dalili kwamba mikoko na nyasi za baharini katika ghuba isiyo na milango ya mito vinaweza kutumika kama makazi muhimu ya samaki wadogo. Hata hivyo, kama ilivyooneshwa katika Sura 2 - 4, mgawanyiko wa spishi na mpangilio kulingana na ukubwa wa samaki pamoja na wingi haukuwa sawa katika maeneo yote ya ghuba na hata pia katika kipindi chote cha mwaka. Kuhusu mgawanyiko wa spishi na wingi wake, makazi ya samaki yaliyo jirani yalisheheni mkusanyiko wa samaki ulioshabihiana zaidi kuliko makazi yasiyo jirani. Aina ya makazi ya samaki pamoja na ujirani wa makazi hayo na maeneo ya mikoko na/au miamba tumbawe unadhaniwa kuchangia kuathiri mkusanyiko wa samaki na mpishano wa spishi za samaki ulioonekana.

Wingi wa samaki hubadilika kutegemeana na mahali na wakati. Kwa kuwa Chwaka ni ghuba isiyokuwa na milango ya mito, mazingira ya makazi ya samaki pamoja na muundo wa jamii ya samaki ndani ya ghuba kwa kiasi fulani hubaki thabiti kwa sehemu kubwa ya mwaka. Hata hivyo, kushuka kulikogundulika (kwa wingi wa samaki, wingi wa spishi na uchumvi katika eneo la ghuba) kulidhihirika zaidi wakati wa kipindi cha mvua za masika; mabadiliko makubwa yakitokea kwenye maeneo ya mikoko na kwenye upwa-tope kuliko kwenye nyasi za baharini (Sura ya 3). Badiliko kubwa katika uchumvi pamoja na mabadiliko ya viashiria vingine vya mazingira lilitajwa kuwa chanzo cha kupungua kwa upatikanaji wa jamii nyingi za samaki, hasa katika maeneo ya mikoko na kwenye upwa-tope. Aidha, matokeo yanaonesha kuwa japokuwa mikoko ndiyo makazi yaliyopendelewa na baadhi ya samaki wadogo, kulikuwa na kiasi cha mpangilio wa muda na wakati husika wa ukazi, hasa wakati wa kiangazi (Desemba-Februari) na si kipindi cha mvua (Aprili-Mei) muda ambao hali za mazingira na hasa uchumvi huzorota.

Kwa muktadha wa nadharia tete inayohusu maeneo ya makuzi ya samaki, samaki wachanga wanaopatikana katika maeneo ya mikoko na katika mfumo wa ikolojia wa nyasi za baharini, yumkini, hufikia hatua fulani ya ukuaji ambapo huyahama makazi haya. Samaki hawa huenda kwenye makazi

ya kudumu hususan kwenye kina kirefu cha maji kama vile kwenye miamba tumbawe. Hufanya hivyo kwa kuhama kwa mara moja au kwa hatua. Kwa kutumia wavu wa juya, spishi kumi na tatu, muhimu katika biashara ya uvuvi, zilichunguzwa kuona kama zinaonesha kuhama kwa samaki (Sura ya 4). Tano kati ya hizo zilionesha samaki wadogo wakiwa kwenye maeneo ya mikoko na upwa-tope, na samaki wakubwa wakiwa kwenye nyasi za baharini zilizo katika kina kirefu. Ufafanuzi sahihi wa mlolongo huu ulioonekana unaweza kuwa ni kubadilika kwa mahitaji katika matumizi ya makazi, kama ilivyothibitishwa na matokeo ya uchanganuzi wa atomi imara aina ya isotopu (Sura ya 5). Kuhusu wingi wa spishi katika makazi mbalimbali ya ghuba; nyasi za baharini zilizo karibu na mikoko zilionesha mkusanyiko anuwai mkubwa wa samaki kuliko makazi mengine. Hii huenda ni kwa sababu ya kuwepo kwa eno hili kati ya maeneo ya mikoko na maeneo ya mwamba tumbawe na hivyo kuweza kutumika kama korido kwa samaki kati ya maeneo hayo. Aghalabu, eneo la upwa-tope lilikuwa na mkusanyiko anuwai mdogo wa samaki (Sura ya 2 na 4). Tasnifu hii inaonesha kwamba ghuba ya Chwaka ina idadi kubwa ya spishi ya samaki (takriban 150 hivi), hata hivyo, ni aina chache ya spishi imetawala (Sura ya 2). Pia imedhihirika kuwa baadhi ya spishi hupendelea baadhi ya makazi wakati spishi nyingine huenea kila mahali (Sura ya 2 na 4).

Umuhimu unaohusiana na makazi ya ghuba, kama mikoko hori, nyasi za baharini na upwa-tope, kama malisho ya spishi za samaki ulichunguzwa katika ghuba ya Chwaka, kwa kutumia mchanganuo wa kadiri wa utumbo na mchanganuo wa atomi imara aina ya isotopu ya kaboni na naitrojeni (Sura ya 5). Utafiti huu umeonesha kwamba makazi yote ya ghuba yalikuwa sehemu muhimu za malisho ya samaki. Sawa na tafiti nyingine zilizofanywa katika sehemu tofauti za kijiografia, majani ya mikoko pamoja na nyasi za baharini vyenyewe havikuwa chakula kikuu kwa samaki na wanyama wengine waliohusishwa katika utafiti huu. Tasnifu hii pia imedhihirisha kufungamana kwa makazi mbalimbali ya malisho ambayo yanaweza kuwa ni matokeo ya ama maji kupwa na kujaa, au kuhama kwa samaki (Sura ya 5).

Umuhimu wa mifumo tofauti ya ikolojia ya mikoko kama malisho ya samaki na viumbe wengine umewasilishwa katika Sura ya 6. Kwa kutumia mchanganuo wa atomi imara ya isotopu ya kaboni na naitrojeni, tulichunguza muktadha mbili tofauti za mifumo ya ikolojia ya mikoko katika pwani ya Tanzania, kuelezea kama mandhari ya mifumo ya ikolojia ya mikoko huathiri matumizi ya makazi haya kama malisho ya kuwafaa samaki. Utafiti huu umeonesha kuwa samaki wengi kutoka kwenye mikoko hori (yenye vijito vinavyotuamisha maji wakati wa maji kupwa) wameonesha utumiaji mkubwa wa vyakula vyenye viasili vitokavyo katika mifumo ya ikolojia ya mikoko. Hata hivyo, jamii ya samaki wanaotoka katika maeneo ya mikoko isiyohori walionesha utumiaji finyu wa vyakula vyenye viasili vipatikanavyo katika mikoko ya aina hiyo. Matokeo haya yanapendekeza kwamba maeneo ya mikoko isiyohori yameonesha umuhimu mdogo kama malisho ya kuwafaa samaki ukilinganisha na mikoko hori; yumkini, ni kwa sababu za tofauti ya “kiwango cha muda” wa kuishi ndani ya mikoko. Uwezekano wa kuishi muda mrefu zaidi ndani ya mikoko hori huweza kutoa muda zaidi kwa samaki kubaki na kula katika mikoko hiyo ikilinganishwa na mikoko isiyohori ambayo

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CURRICULUM VITAE

Blandina R. Lugendo was born on 15th March 1970 in Korogwe, Tanga, Tanzania. She obtained her secondary education at Usagara Secondary School from January 1985 to November 1988 (ordinary level) and at Korogwe Girls' Secondary School from July 1989 to May 1991 (advanced level). From September 1992 to June 1995 she pursued a Bachelor of Science degree course in Marine Biology and Microbiology at the University of Dar es Salaam, Tanzania. She then pursued a Masters Degree course (by thesis) in Marine Biology at the same University and finished in February 2000. During her Master of Science degree program she attended several courses in line with her career including FRONTIER-TANZANIA Course on Marine Survey and Monitoring Techniques, and UoN/VUB/KMFRI/IOC/BADC Postgraduate Course in Tropical Coastal Ecology Management and Conservation. In August 2000 she was employed by the University of Dar es Salaam as an assistant lecturer in the then department of Zoology and Marine Biology of the Faculty of Science, University of Dar es Salaam. In January 2003 she was transferred to the newly established Faculty of Aquatic Sciences and Technology of the University of Dar es Salaam, under the department of Aquatic Environment and Conservation. She started her PhD program in June 2001. In March 2004, she was awarded a UNESCO-LOREAL for Women in Science Fellowship which she used to extend her PhD research to Bagamoyo, Tanzania mainland. After successful defense of her PhD thesis, she will continue to work with the department of Aquatic Environment and Conservation, Faculty of Aquatic of Sciences and Technology, University of Dar es Salaam, Tanzania. Currently she is a member of West Indian Ocean Marine Scientists Association (WIOMSA), and Marine Action Conservation of Tanzania (MACT).