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Influence of morphology and amphibious life-style on the feeding ecology of the mudskipper *Periophthalmus argentilineatus*

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The potential feeding advantages that are offered to the barred mudskipper *Periophthalmus argentilineatus* by its amphibious life-style were investigated. To this end the feeding ecology of these fish, the position they occupy in the mangrove food web and the importance of different morphological factors for their diet were studied. Analysis of gut contents showed that the major component of the barred mudskipper diet changes during growth from small crustaceans (*e.g.* copepods and amphipods) to polychaetes to mangrove crabs. This dietary shift was found to be facilitated through enlargement of the mouth, as well as elongation of the gut. The use of stable isotope analysis revealed that barred mudskippers had a similar trophic position as other zoobenthivore fish species, but that their diet did not appear to be affected by competition for food with other zoobenthivores. The amphibious habits of the barred mudskipper provide specific advantages to its feeding ecology, such as access to an abundant food source of mangrove crabs, which are mostly inaccessible for other fish species.

Key words: diet composition; food web; mudskipper; resource partitioning; stable isotopes; Tanzania.

INTRODUCTION

Feeding is an important aspect of ecology, influencing fitness, reproduction and longevity of individuals. The feeding efficiency of an individual depends on its morphology, biochemistry, physiology, behaviour and ecological relations with individuals of the same and other species (Wainwright & Richard, 1995; Piet, 1998).

Morphology plays a major role in determining the diet of a species because morphology can pose physical constraints on the minimum and maximum size of prey items which can be ingested and also influences the efficiency of prey

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capture and consumption (Wainwright & Richard, 1995). The most important morphological characteristic defining resource use is the gape, or maximal mouth dimensions, of a species (Piet, 1998). The gape puts restrictions on the dimensions of prey which can be ingested, while the morphology, physiology and biochemical characteristics of the gastrointestinal tract define the food sources which can or cannot be processed and digested after ingestion (German *et al.*, 2004). Thus, morphological properties define the feeding ability of an organism.

The characteristics which influence the use of resources in individual species are often subject to change during the ontogeny of a species (Werner & Gilliam, 1984). In fishes, growth is often accompanied by changes in morphology and ecology which enable them to use resources not previously utilized, and consequentially, enable them to shift their preference to food sources with a higher energy yield per unit effort (Wainwright & Richard, 1995).

The actual resource use is, however, also dependent on behaviour. Through behaviour a species can influence whether a potential niche contributes to the realized niche, which influences the availability of food resources to the species (Wainwright & Richard, 1995). Availability of resources is not only subject to the behaviour of individual species but is also indirectly influenced by competition and predation relationships which are caused by behaviour of other species within the community (Wainwright & Richard, 1995). Within communities where different species compete for the same food sources, partitioning of resources is an important ecological mechanism to optimize the use by the different competitors. Resource partitioning between species may occur in spatial and time dimensions (Ross, 1986; Piet, 1998), but in marine fish communities, partitioning mostly occurs in the trophic dimension (Ross, 1986; Sibbing & Nagelkerke, 2001).

In the mangrove forests of the Indo-Pacific region, fishes belonging to the mudskipper family Periophthalmidae occupy a specialized niche in the intertidal zone. The physiology and morphology of these fishes have been adapted to enable an amphibious existence in this zone with highly variable environmental conditions (Clayton, 1993). Their amphibious habits provide mudskippers with the possibility to dwell on exposed mudflats when other fish species are forced to retreat to deeper waters with outgoing tides. Mudskippers are thought to feed predominantly when they are out of the water during low tides (Colombini *et al.*, 1996; Nieder, 2001) and in this way probably partition resources with other fish species in space and time.

Periophthalmidae are generally considered to have a zoobenthivorous diet, but the contribution of different food items to the total diet differs between previous studies (Stebbins & Kalk, 1961; Clayton, 1993; Colombini *et al.*, 1996; Mhaisen & Al-Maliki, 1996; Udo, 2002). Insights into the diet, based on gut content analysis, may be skewed since food items may be unintentionally ingested or digested at different rates, and soft tissue food items may be indistinguishable for identification in the stomach.

The aim of the present study was to assess the influence of growth and subsequent morphological changes on the diet of the barred mudskipper *Periophthalmus argentilineatus* Valenciennes and to investigate the role of partitioning in space and time due to the amphibious behaviour of the barred mudskippers in competition with other zoobenthivorous fishes in the mangrove habitat.

MATERIALS AND METHODS

STUDY AREAS

This study was performed in the mangroves of Chwaka Bay and Mtoni, Tanzania (Fig. 1). These mangroves were selected because the difference in hydrology at both locations may be reflected in the diet of mudskippers and other zoobenthivorous fishes.

Chwaka Bay is a shallow bay of *c.* 35 km^2 at the east coast of Unguja Island, Zanzibar, which is located 30 km from the Tanzanian mainland. The bay opens to the Indian Ocean at the northern end where it is fringed by coral reefs. The southern end of Chwaka Bay consists of a fossil limestone reef that is intersected by deep channels and smaller creeks and is covered by large mangrove forests. The mangrove channels have a tidal amplitude of only 1 m due to the geomorphology of the bay and retain water during low tide (Richmond, 1997).

The Mtoni mangroves are situated in the shallow estuary of the confluence of the Kizinga and Mzinga Rivers near the city of Dar es Salaam. These mangroves are

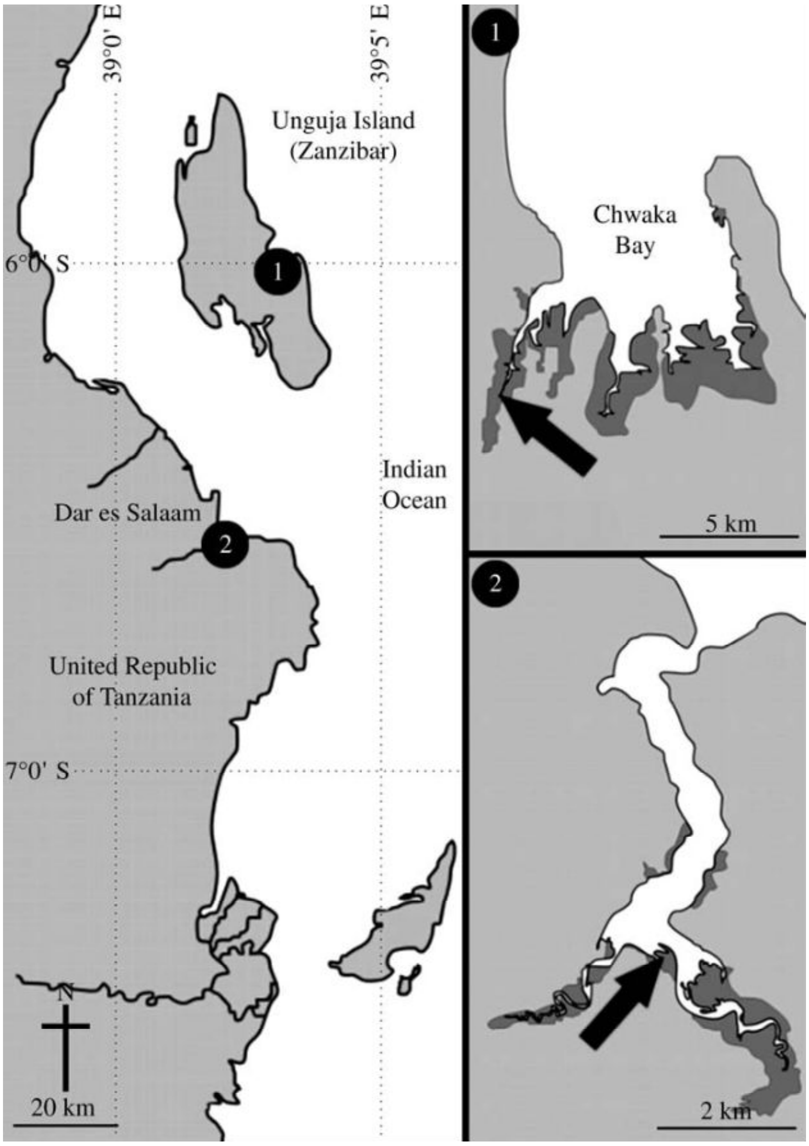

FIG. 1. Map of the coast of Tanzania with insets of (1) Chwaka Bay and (2) the Mtoni estuary. Shaded areas represent the mangrove stands. Collection sites are indicated with arrows.

subject to a tidal amplitude of 4 m (Tanzania Ports Authority, 2005) as a result of which all water is drained from the mangroves with the outgoing tides, while all water remaining in the habitat during low tide consists of small channels of surfacing ground water.

SAMPLE COLLECTION AND ANALYSIS

Barred mudskippers were collected at random with scoop nets on the exposed mudflats and in the creeks of Chwaka Bay and Mtoni estuary in January 2004. After collection, fish were placed in ice water to anaesthetize and to stop digestive activities in the gut. Body mass (to the nearest 0·1 g) and total body length (L_T; to the nearest mm) were measured for each specimen. Mouth width (maximum lateral measure of mouth gape), mouth height (maximum dorso-ventral measure of mouth gape) and gut length (from oesophagus to anus) were recorded to the nearest mm from dead specimens. The mouth dimensions and gut length were standardized to fish size by dividing these morphometric dimensions by the L_T of each individual fish. Complete guts were dissected and their contents stored in ethanol (70% v:v) until analysis.

Food items in the guts were identified with a stereomicroscope. The quantity of each food item was estimated as a percentage of its volume relative to the total volume of ingested food items in the gut. The food items from the digestive tract were classified to class level (Polychaeta, Bivalvia and Insecta) or order level (Isopoda, Amphipoda, Copepoda, Diptera, Tanaidacea, Arachnidae and Mysidacea), while fishes and detritus were classified as such. Ingested crabs and crab parts were identified to the lowest possible level (family, subfamily or species) and their carapace width and merus (the fourth segment of a crustacean pereopod) length were measured. The merus was used as a measure of crab size because this pereopod segment appeared to be most abundant in an undamaged state in the gut contents.

The most important food items of the barred mudskippers according to Colombini *et al.* (1996) were collected in the mangroves at both locations together with the barred mudskippers: crabs were collected from the subtidal mudflats, exposed intertidal mudflats and mangrove trees; amphipods and isopods were collected from the seagrasses on the intertidal mangrove flats; polychaetes were sieved from the sediment.

In addition to the barred mudskippers, zoobenthivores belonging to Gerridae, Lethrinidae and Lutjanidae, zoobenthivores and insectivores from the Hemiramphidae and omnivorous fishes from the Monodactylidae were sampled in Chwaka. In Mtoni, Albulidae, Callionymidae, Gerridae, Gobiidae, Leiognathidae, Lethrinidae, Teraponidae and Lutjanidae were sampled. Species belonging to these families were the most common species observed in or near the mangroves.

The diet of the barred mudskippers in Chwaka was compared with the diets of the fish species in the Chwaka mangroves that were reported by Lugendo *et al.* (2006). Lugendo *et al.* (2006) only collected fishes in the mangrove creeks during low tide. Fishes from the adjacent mangrove channel, however, could enter the creeks at high tide. As a result, barred mudskippers in the creeks potentially not only experienced competition for food from the zoobenthivorous fishes that were collected in the creek but also from fishes that were collected in the mangrove channel. Therefore, the diet of the barred mudskipper was tested for similarity with the diets of fishes from both the creek and the channel with a Bray-Curtis cluster analysis that was performed with BioDiversity Pro© version 2. In the cluster analysis, data on the gut contents were included for *Gerres filamentosus* Cuvier, *Gerres oyena* (Forsskål), *Lethrinus lentjan* (Lacepède), *Lutjanus fulviflamma* (Forsskål), *Monodactylus argenteus* (L.), *P. argentilineatus* and *Zenarchopterus dispar* (Valenciennes). The L_T classes of *P. argentilineatus* were clustered into three L_T ranges (2–5, 6–9 and 10–13 cm), and average gut contents were calculated for each of these L_T ranges for use in the cluster analysis. This could only be done for Chwaka since diet of the fish fauna of Mtoni was not determined (except for *P. argentilineatus*).

Muscle tissue from fishes, soft body tissues of crabs and complete samples of smaller food items were processed for stable isotope analysis. This technique provides a mean value of the diet over a period of weeks to months (Gearing, 1991). Samples for stable isotope analysis were dried at 70° C for 48 h and ground to a fine powder. The carbon and nitrogen stable isotopic composition was determined using a Carlo Erba NA 1500 element analyser coupled online *via* a Finnigan Conflo III, with a Thermo-Finnigan DeltaPlus mass-spectrophotometer. Carbon and nitrogen isotope signatures are expressed as ratios between the isotopes ^{12}C:^{13}C and ^{14}N:^{15}N, respectively, and are noted in the delta notation ($\delta^{13}C$, $\delta^{15}N$) in parts per thousand (‰) deviation from the isotopic ratios in the international standard reference samples Vienna PDB (Craig, 1957) and atmospheric nitrogen (Mariotti, 1983). Vienna PDB is the reference material of the IAEA that is replacing the original reference material (PDB) from a pulverized belemnite fossil from the Upper Cretaceous Pee Dee formation in South Carolina since the supply of the original reference material was exhausted.

To indicate potential food sources for the barred mudskippers on basis of the stable isotope results, the range of both isotope values was used by taking the minimal and maximal isotopic ratios as measured for barred mudskippers, and subtracting 1‰ carbon and 3‰ nitrogen to correct for enrichment as a result of increase in trophic level (Rau *et al.*, 1983; Minagawa & Wada, 1984). If the presence of only a single food source is assumed, the calculated range shows the signatures of potential food items.

STATISTICAL ANALYSIS

Pearson's correlations were used to study the correlation between L_T and morphological data. Data were tested for normality and homoscedasticity. One-way ANOVA, followed by a Tukey *post hoc* test, was used to test for differences between the stable isotopic signatures of the different barred mudskipper size classes and populations. All statistical analyses were performed with the software-package SPSS© 11.5 and statistical significance was accepted at $P \leq 0{\cdot}05$.

RESULTS

MORPHOMETRY

The barred mudskippers that were collected from Chwaka Bay ($n = 73$) ranged from 2·1 to 13·7 cm L_T with an average L_T of 8·4 cm, whereas the barred mudskippers collected in Mtoni ($n = 107$) had only a limited size range of 4·7 to 8·1 cm and an average L_T of 7·3. The length of the guts (from oesophagus to anus) found in barred mudskippers from Chwaka ($n = 58$) ranged from 1·2 to 26·5 cm with an average of 12·5 cm. In the barred mudskippers from Mtoni ($n = 46$), the gut length ranged from 3·7 to 10·9 cm, with an average of 7·2 cm.

The L_T of the barred mudskippers showed a strong correlation with mouth width, mouth height and gut length (Fig. 2; Pearson's correlations, $r^2 = 0{\cdot}925$, $n = 119$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}925$, $n = 119$, $P < 0{\cdot}001$ and $r^2 = 0{\cdot}895$, $n = 101$, $P < 0{\cdot}001$, respectively). The ratio between gut length and L_T ranged from 0·38 to a maximum value of 1·95, with a mean ± S.E. of 1·14 ± 0·03 ($n = 101$).

GUT CONTENT ANALYSIS

Analysis of the gut contents showed that *P. argentilineatus* is largely carnivorous. The diet of individuals from Chwaka Bay displayed a clear shift with body size, with their prey type increasing in size [Fig. 3(a)]. The small L_T classes

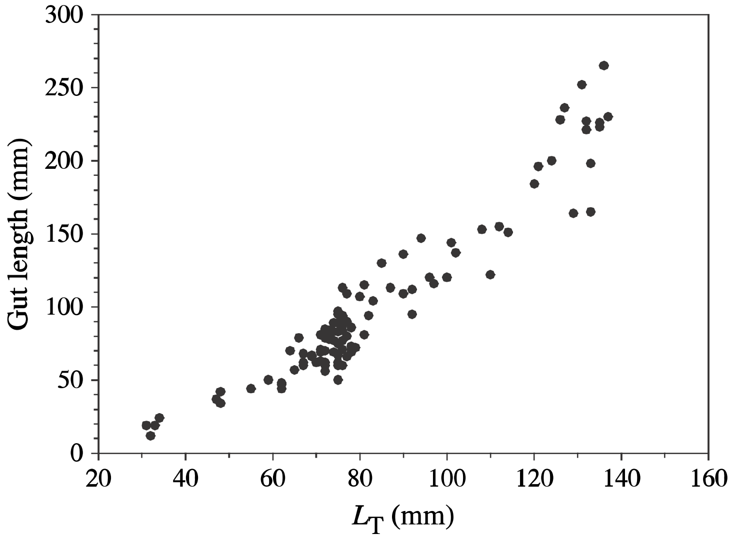

FIG. 2. Relative gut length of barred mudskippers as a function of total length (L_T). The relationship was significant ($r^2 = 0.895$, $P < 0.001$).

(20 to 50 mm) in Chwaka had a diet consisting mainly of copepods and amphipods, while copepods were not found in the guts of barred mudskippers >35 mm. Medium-sized fish (60 to 90 mm) had a diverse diet, with the contribution of amphipods decreasing and that of polychaetes and crabs increasing with L_T. In the largest L_T classes (100 to 130 mm), crabs were the principal component of the diet. Specimens of the genus *Uca* dominated the crabs found in guts of all fish size classes.

In Mtoni, polychaetes, amphipods, insects and fishes formed the main components of the diet of the barred mudskippers for the L_T classes of 40 to 70 mm [Fig. 3(b)]. Larger barred mudskippers were not present in the Mtoni mangroves due to decreased growth and life span (Kruitwagen *et al.*, 2006).

In the guts of barred mudskippers that had consumed crabs, crab leg parts (rather than complete crabs) were most abundant. The average number [Fig. 4(a)] as well as length [Fig. 4(b)] of ingested crab legs increased significantly with L_T, but also the range in values recorded for both variables increased with L_T.

Cluster analysis of the diet of the zoobenthivorous, insectivorous and omnivorous fishes in the channel and creek of the mangroves of Chwaka Bay on the basis of gut content analysis revealed that the diet of the barred mudskipper had little similarity ($\leq$23%) to the diets of other fish species (Fig. 5).

STABLE ISOTOPE ANALYSIS

The barred mudskippers at Chwaka Bay and Mtoni had a $\delta^{15}N$ signature that was similar to that of other zoobenthivorous fishes (Fig. 6). There was, however, a difference in $\delta^{13}C$ between the barred mudskippers and the other zoobenthivores, with the barred mudskippers from Chwaka Bay being significantly enriched in $\delta^{13}C$ by 1·9‰ ($P < 0.05$), and the barred mudskippers in Mtoni being significantly depleted by 3·6‰ ($P < 0.001$), relative to the other zoobenthivores. The $\delta^{13}C$ signatures of the barred mudskippers from Chwaka

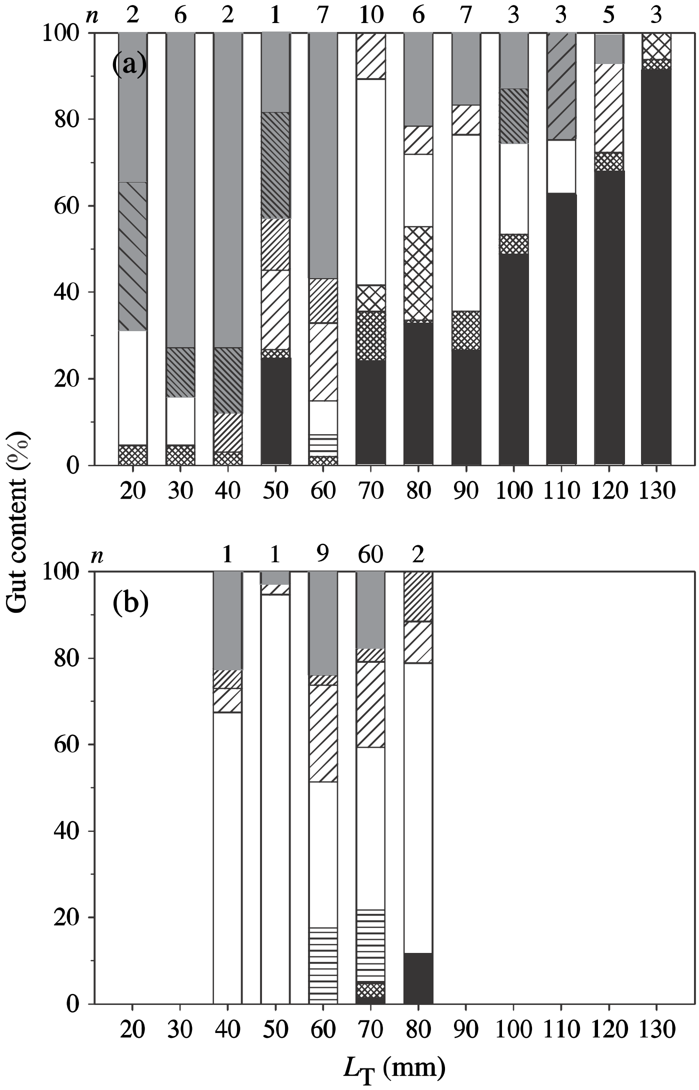

FIG. 3. Food items ingested by barred mudskippers from (a) Chwaka and (b) Mtoni. Major dietary categories: ◼, amphipods; ◾, copepods; ▧, mysid shrimps; ◩, isopods; ▨, dipteran larvae; ⧄, insects; □, polychaetes; ▤, fishes; ⊠, detritus; ▦, miscellaneous food items; ■, crabs in relation to total length (L_T). *n*, the number of fish per L_T class. Food items that comprised <5% of the gut contents of a L_T class were grouped as miscellaneous food items.

and Mtoni did not differ significantly ($P \geq 0{\cdot}05$). Stable nitrogen isotope ratios of mudskippers were *c.* 5‰ lower in Chwaka Bay than in Mtoni (Fig. 6).

The relatively large variation in stable carbon isotopic signatures of individual barred mudskippers from Chwaka Bay resulted in a large range for the signature of potential food items [Fig. 6(a)]. The predicted range showed an overlap with the isotopic signatures of crabs, insects and shrimps. In Mtoni, the predicted range in stable isotopic values of potential food items showed an overlap with the signatures of polychaetes and *Uca* crabs [Fig. 6(b)].

The δ^{15}N signatures of barred mudskippers showed a significant increase with L_T in Chwaka Bay (Fig. 7; Pearson's correlation, $r^2 = 0{\cdot}442$, $n = 29$, $P < 0{\cdot}001$). In the population of Mtoni, there was no significant relationship between L_T and δ^{15}N signatures (Pearson's correlation, $r^2 = 0{\cdot}202$, $n = 15$,

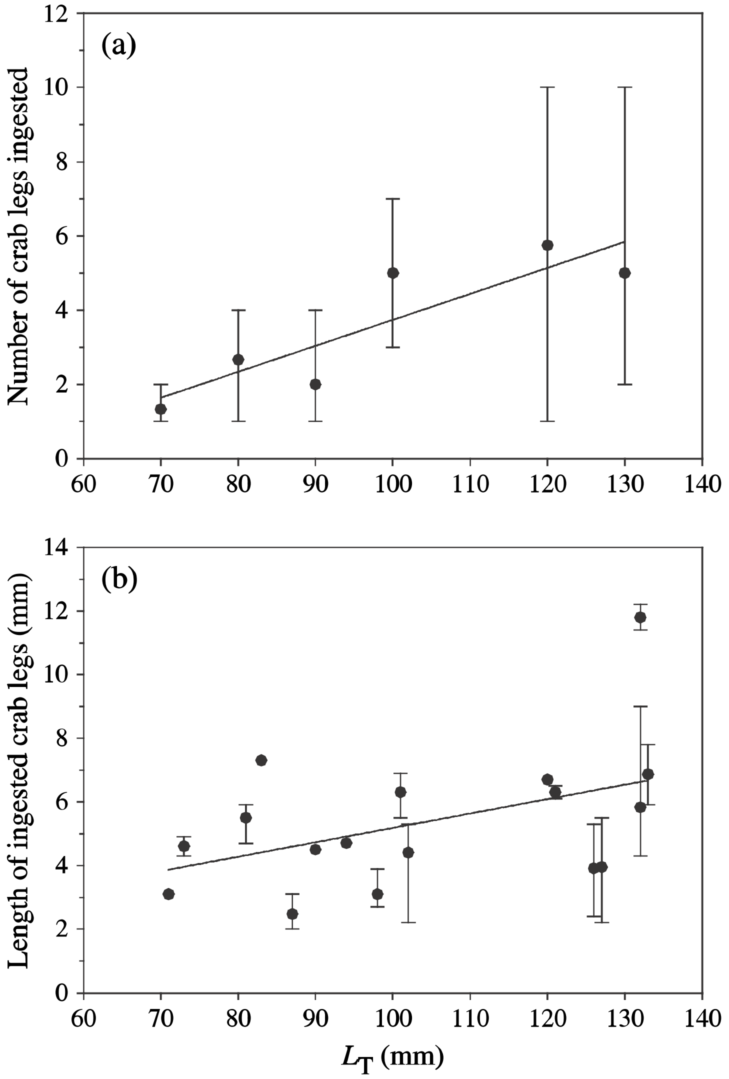

FIG. 4. (a) Mean ± range number of crab legs (meri) ingested and (b) average length of the merus of ingested crab legs as a function of the total length of the barred mudskipper. The curves were fitted by (a) $y = -3{\cdot}44 + 0{\cdot}71x$ ($r^2 = 0{\cdot}235$, $P < 0{\cdot}05$) and (b) $y = 1{\cdot}77 + 0{\cdot}27x$ ($r^2 = 0{\cdot}075$, $P < 0{\cdot}05$).

$P > 0{\cdot}05$), which was probably the result of the small L_T range of fish at this location. No relationship was found between $\delta^{13}C$ and fish L_T in Chwaka Bay or Mtoni (Pearson's correlation, $r^2 = 0{\cdot}183$, $n = 29$, $P > 0{\cdot}05$ and $r^2 = 0{\cdot}017$, $n = 15$, $P > 0{\cdot}05$, respectively).

DISCUSSION

The analysis of the morphometry of the barred mudskipper shows that mouth height, mouth width and gut length increase with body growth. Whereas increase in mouth dimensions is a common feature during the ontogeny of all fishes (Luczkovich *et al.*, 1995; Wainwright & Richard, 1995), the relative gut length generally differs between feeding guilds. The general pattern found in the gut lengths of fishes is that the highest relative gut lengths occur in herbivores, lowest relative lengths in carnivores and intermediate relative

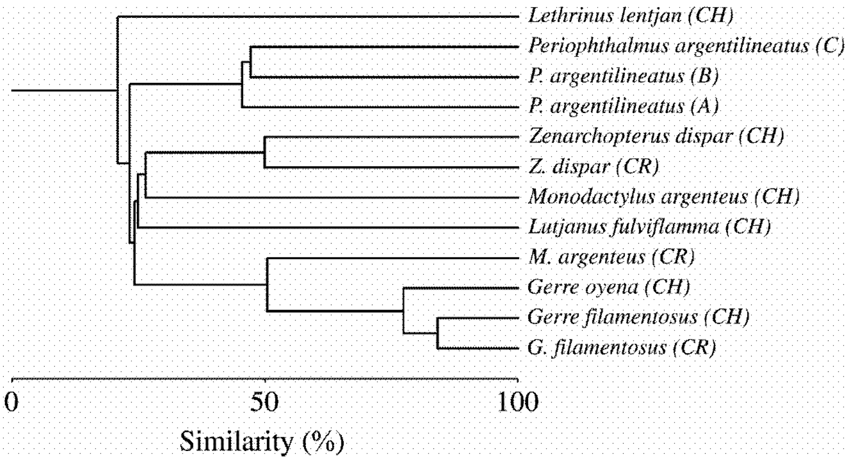

FIG. 5. Similarity among diets of fishes from the Chwaka Bay mangroves [fishes were from the mangrove channel (CH) or the mangrove creek (CR)]. Barred mudskippers were only collected in the creeks. For the barred mudskippers three total length ranges have been defined: A, 20–59; B, 60–99 and C, 100–139 mm.

lengths in omnivores because the digestion of plant materials takes more time than digestion of animal tissues. Shifts to a more herbivorous diet result in elongation of the gut, while a carnivorous diet results in a shorter gut (Piet, 1998; Drewe *et al.*, 2004). Thus, changes in relative gut length may occur when the diet shifts during growth, or in species that are dependent on energy-poor food resources (Piet, 1998; Gutowska *et al.*, 2004). In addition, diet-induced elongations can be accompanied by changes in the activities and levels of different groups of digestive enzymes (Drewe *et al.*, 2004; German *et al.*, 2004).

The data show that the barred mudskipper diets shift from small zooplankton towards large decapod crabs during body growth of the fish. During the life stages when barred mudskippers prey on decapod crabs, the range of crab sizes which are targeted increases and larger crabs are included in the diet. Small decapod crabs continue to be part of the diet, presumably due to the limited size range of *Uca* crabs (Litulo, 2005). Simultaneous with the shift in diet the relative gut length increases. The manifestation of both changes in the barred mudskipper contradicts the general guild-based pattern of gut lengths (Piet, 1998), while changes in other gobiid fishes are consistent with the pattern (Geevarghese, 1983; Clayton & Snowden, 2000; Yang *et al.* 2003).

The dietary shift in the present study towards larger crustaceans also means a shift to consumption of crustaceans having exoskeletons with higher chitin content, which are more difficult to degrade and require more chitinolytic (*i.e.* chitin digesting) activities than the exoskeletons which are ingested by juvenile barred mudskippers. The chitinolytic enzymes in fishes comprise chitinases for initial break down of chitin skeletons into chitobiose dimers and chitobiases for further breakdown (Fänge *et al.*, 1979). It has been found that fishes with short guts have high stomach chitinase activities to disrupt the exoskeletons in order to gain access to the nutrient-rich inner tissues of crabs, while fishes with longer guts have both chitinase and high chitobiase activities to degrade the exoskeletons completely and use of the exoskeletons themselves as a source of nutrients (Gutowska *et al.*, 2004). Although no enzyme activities were

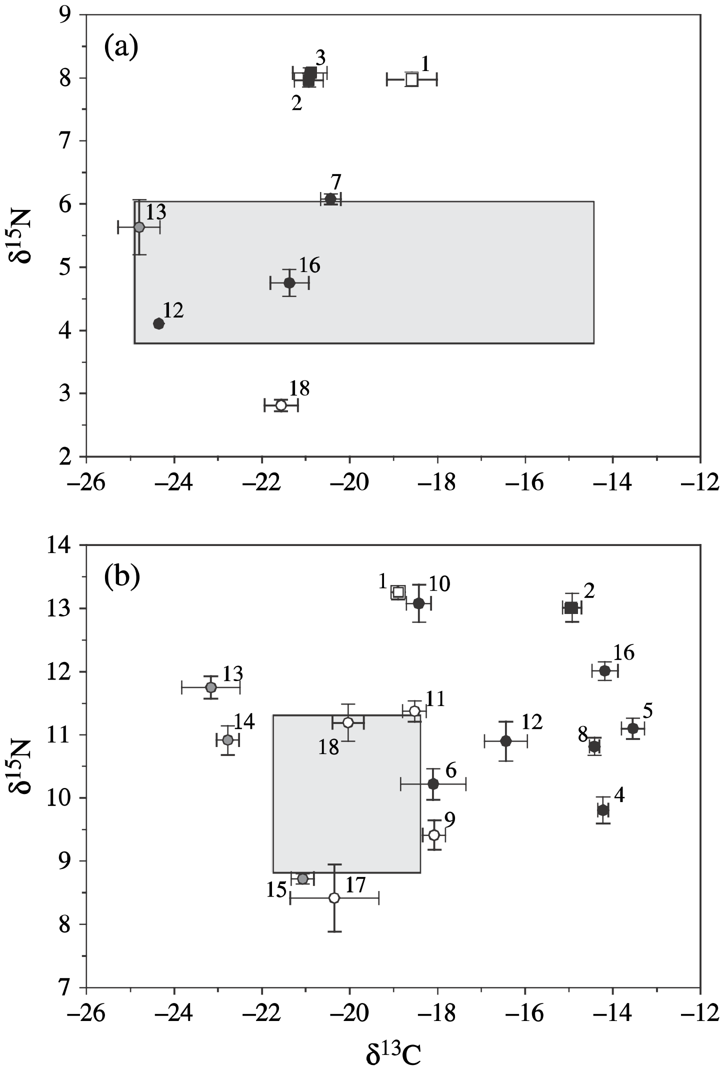

FIG. 6. Stable carbon and nitrogen isotope values (mean ± S.E.) of macrofauna and zoobenthivorous fishes in (a) Chwaka and (b) Mtoni. The species were collected from the subtidal mudflats (■), intertidal mudflats (□) or mangrove trees (▨). The shaded box shows the isotopic range of potential food items for the barred mudskippers (based on 100% consumption of a single food source) for both sites: 1, barred mudskipper; 2, zoobenthivorous fishes (creek); 3, zoobenthivorous fishes (channel); 4, amphipods; 5, *Dotilla fenestrate*; 6, hermit crabs; 7, insects; 8, isopods; 9, *Macrophthalmus* sp.; 10, *Metopograpsus* sp.; 11, polychaetes; 12, portunid crabs; 13, *Sesarma guttatum*; 14, *Sesarma* sp. 1; 15, *Sesarma* sp. 2; 16, shrimps; 17, *Uca dussumieri*; 18, *Uca* sp.

actually analysed in the present study, the data on the barred mudskipper morphology and diet reveal that elongation of the barred mudskipper gut coincides with an increase in chitin content of the diet and suggest that the elongation facilitates digestion by prolongation of gut evacuation times.

The changes in morphometry of the barred mudskipper appear to be closely connected to changes in the diet. While the mouth dimensions define the maximum size of prey that can be handled during early life stages, the length and possibly the biochemistry of the gastrointestinal tract define the type of prey, which can be digested. Consequentially, dietary changes in growing barred mudskippers appear to be controlled by both ingestion and digestive capacities.

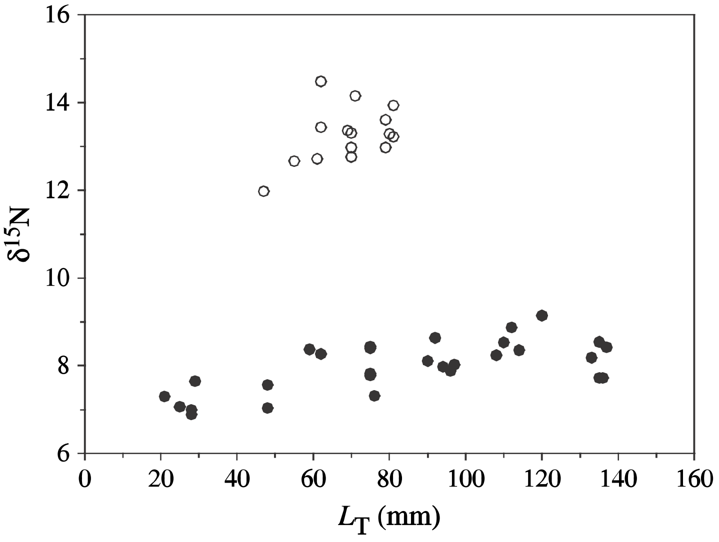

FIG. 7. Stable nitrogen isotope values of barred mudskippers in Chwaka (●) and Mtoni (○) in relation to total length. The relationship was significant for Chwaka ($r^2 = 0{\cdot}442$, $P < 0{\cdot}001$) but not for Mtoni ($r^2 = 0{\cdot}202$, $P > 0{\cdot}05$).

The nitrogen isotopic signatures show that the barred mudskippers belong to the trophic level of the secondary consumers in both ecosystems. The $\delta^{15}N$ of the barred mudskippers in Chwaka Bay further show a slight enrichment with fish growth which indicates that the barred mudskippers shift their diet to species from higher trophic levels, which is supported by the observation of a dietary shift in the gut contents. Overall elevated $\delta^{15}N$ values in Mtoni relative to Chwaka result from high input of foreign nutrients into the Mtoni estuary (Mashauri & Mayo, 1989) but do not result in changes in foodweb structure (Kruitwagen *et al.*, 2006).

The combination of $\delta^{13}C$ and $\delta^{15}N$ values shows that the barred mudskippers in both Chwaka and Mtoni mostly prey on species related to the mangroves, while the origin of the resources for the other zoobenthivore fishes differs between the two sites. In Mtoni, the zoobenthivores were much more enriched in carbon than the barred mudskippers, which shows that the zoobenthivores have a higher dependency on bay habitats, other than mangroves, for food. In contrast, the zoobenthivore fishes in Chwaka are slightly depleted relative to the barred mudskippers, which indicates that the zoobenthivores have a higher dependency on food from the mangroves than the barred mudskippers. Since the barred mudskippers had full access to the mangroves at both sites in this study at all times, accessibility did not affect the carbon signatures of these fish. The accessibility of the mangroves for other zoobenthivorous fishes was subject to the tidal amplitude and was thus translated to differences in carbon isotopic signatures: only fishes with continuous mangrove access (Chwaka) could utilize resources from the habitat to a high degree, whereas fishes with temporal access to mangroves (Mtoni) could take less food from these areas. The influence of tidal regime on the value of the mangroves as a feeding habitat was also found in a study by Nagelkerken & van der Velde (2004), in which only mangrove residents were found to feed inside the mangroves.

During their juvenile stage, the barred mudskippers used food resources (*e.g.* copepods and amphipods), which are commonly used as food items by other zoobenthivorous fishes in tropical coastal habitats (Nagelkerken *et al.*, 2000; Kamukuru & Mgaya, 2004). Minimization of competition pressure through temporal resource partitioning, which is provided by the amphibious habits of the barred mudskippers in combination with the tidal regime, may facilitate the use of the same food sources by juvenile barred mudskippers and other zoobenthivores when assuming that food is limiting.

During later life stages, however, the fish shift to a diet of mangrove crabs which are largely unavailable to other zoobenthivores because these crabs shelter at high tide when the other zoobenthivorous fishes feed in this habitat. This dietary shift could theoretically be driven by competition with other zoobenthivore fishes. Comparison of the diet of different size ranges of barred mudskippers with the diet of other zoobenthivorous fishes in Chwaka, however, revealed little similarity between the diets. This shows that there is little interspecific competition for the food sources that are used by the barred mudskipper at this site. The cluster analysis also revealed that the dietary shift that is observed in the barred mudskipper diet does not result in differences in similarity between the diets barred mudskippers and other fish species; thus, the dietary shift does not decrease competition pressure and is therefore unlikely to be the driving factor behind the shift in the diet of the barred mudskipper. The comparison of the diet of the barred mudskipper with the diets of other zoobenthivorous fishes could only be made for Chwaka, but since no indications of interspecific competition or predation as driving forces behind the observed dietary changes were found, the changes in diet can also be expected to occur in other barred mudskipper populations.

Diet changes were probably driven by the increasing energetic needs and mechanical capabilities of growing barred mudskippers which were limited to available food resources in the intertidal mangrove habitat (Kathiresan & Bingham, 2001). Feeding in the subtidal waters to supplement the increasing demands is not considered to be an option for the barred mudskippers because they are thought to have poor eyesight during submergence due to adaptations for aerial vision (Stebbins & Kalk, 1961; Colombini *et al.*, 1996; Nieder, 2001). Hence, barred mudskippers may have adapted to food sources (*i.e.* crustaceans) which may be difficult to digest and require special digestive adaptations but which are readily available in the intertidal habitat. As a result, the feeding behaviour of the amphibious barred mudskipper results in a spatial and temporal resource partitioning from other zoobenthivores.

The combination of morphological data, gut content and stable isotope analysis indicates that the amphibious habits of the barred mudskippers provide them with specific advantages over other zoobenthivore fishes. The data show that despite some overlap in the diet, competition with other zoobenthivores can possibly be minimized during juvenile life stages through temporal resource partitioning. Morphological changes in combination with the amphibious lifestyle subsequently facilitate a dietary shift to food sources (*i.e.* mangrove crabs), which are generally unavailable for potentially competing zoobenthivore fishes, indicating also a spatial resource partitioning.

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