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Trophic Ecology of *Sardinella gibbosa* (Pisces: Clupeidae) and *Atherinomorous lacunosus* (Pisces: Atherinidae) in Mtwapa Creek and Wasini Channel, Kenya

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Key words: trophic ecology, planktivorous fishes, habitat variability

Abstract—The food habits of two schooling planktivorous fishes, *Sardinella gibbosa* and *Atherinomorous lacunosus*, were investigated in Mtwapa creek and Wasini Channel of the Kenya coast. Spatial and temporal variations in their food and feeding habits were assessed using the percentage numerical abundance method, percentage frequency of occurrence, stomach fullness indices and the Tokeshi graphical method. This study established a clear spatial separation of Mtwapa creek from Wasini Channel in terms of the abiotic and biotic data. Highly significant differences (*t*-test, $P < 0.05$) were observed between the two study areas in temperature, salinity, transparency, conductivity, chlorophyll *a* and in zooplankton abundance and diversity. The diet of the two fish species showed clear spatial and temporal differences, which were dependent on habitat variability. The two species belong to the omnivorous trophic category. *Sardinella gibbosa* from both sites fed mostly on copepods during the two seasons. *Atherinomorous lacunosus* fed mostly on phytoplankton, copepods and nematodes during the NE Monsoon. However, its diet was dominated by nematodes during the SE Monsoon. Overall, both fish species exhibited generalised and opportunistic feeding habits. Their diet was influenced by changes in the quality and quantity of food in the environment and the fishes' migratory patterns.

INTRODUCTION

The study of fish stomach contents is a common way of investigating the food web in marine biological communities. Food is recognised as the main factor regulating growth, abundance and migration patterns of fish. However, few studies have been undertaken on the spatial and temporal variation in the food habits of the planktivorous fishes of the Western Indian Ocean. Several studies have been centered on the fish community structure and trophic organisation in Gazi Bay, Kenya: Kimani et al. (1996) studied the fish community in mangroves, De Troch et al. (1998) reported on the diets of abundant fishes from beach seine catches in seagrass beds and Wakwabi (1999) investigated the fish community structure and trophic organisation of the Bay. While most of these studies involve the trophic organisation of fish communities, there has been relatively little use of feeding habits as an indicator of habitat variability.

Fish feeding and food habits have been related to productivity of the marine ecosystem, which is determined by physical and chemical factors. These factors are derived from anthropogenic activities, e.g. release of raw sewage directly into the ecosystem and the reversing monsoon winds along the East African coast. This study therefore, investigates the effect of habitat complexity and

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variability on the trophic ecology of *Sardinella gibbosa* and *Atherinomorous lacunosus*. The major aim was to investigate the spatial and temporal variation in the feeding ecology of these two fish species in two ecologically distinct habitats along the Kenya coast.

MATERIALS AND METHODS

Study areas

The study was carried out in Mtwapa creek and Wasini Channel at the coast of Kenya (Fig. 1). Mtwapa creek is situated 25 km north of Mombasa

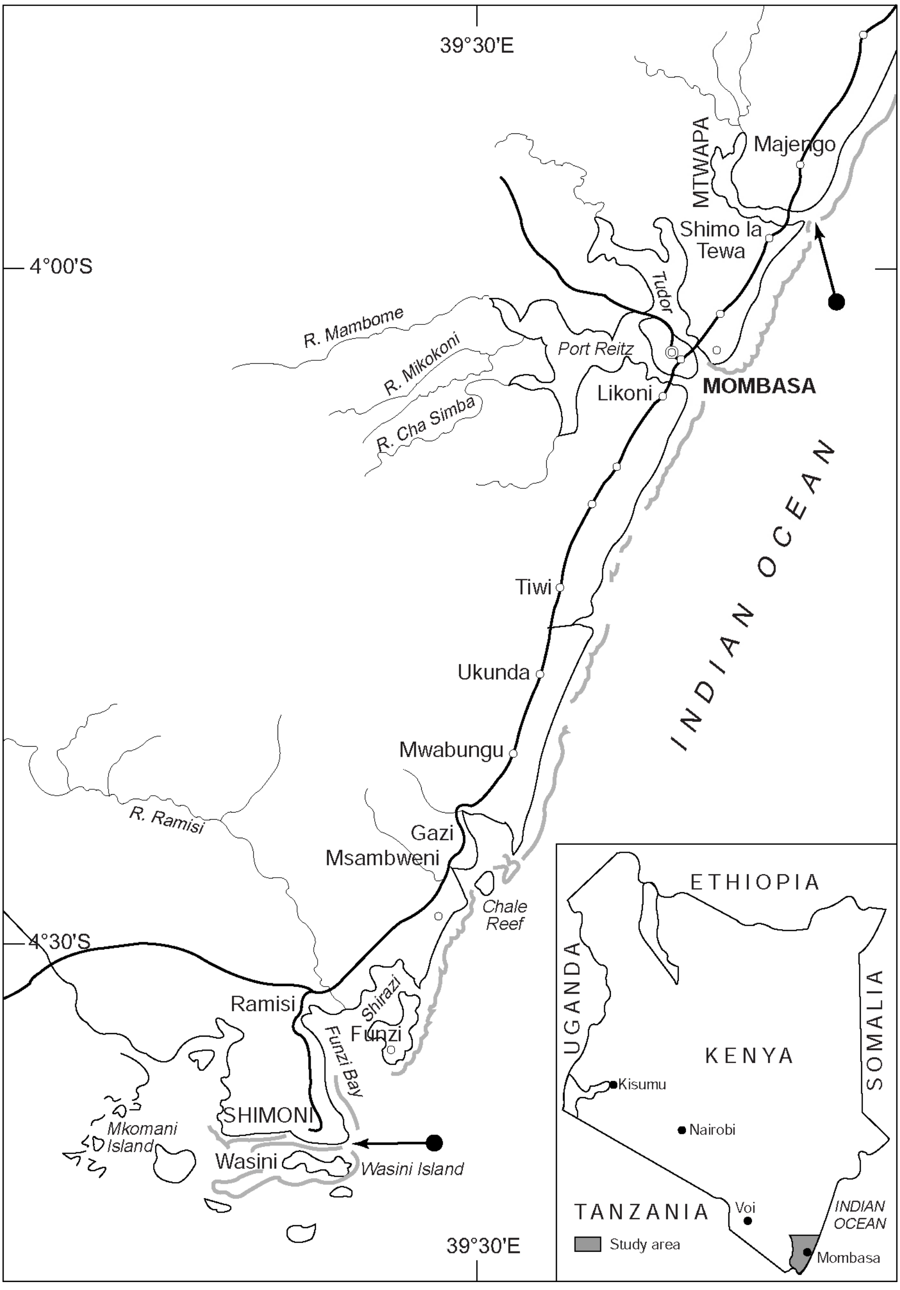

Fig. 1. Map of Kenyan coastline with positions of Mtwapa creek and Wasini channel indicated by arrows

(3° 55' S, 39° 45' E). It is a tidal creek lined by mangrove forests and extensive mudbanks. The creek receives fresh water input through a seasonal river. This creek is reported to be relatively eutrophic due to direct release of raw sewage into the creek at the vicinity of Shimo la Tewa government prison (Mwangi et al., 2001). Wasini Channel is situated 90 km south of Mombasa (4° 37' S, 39° 22' E). Very few scattered fringe mangroves cover the shoreline. There is no river input into the channel, which is sheltered from the Indian Ocean by Wasini Island. Climatic conditions in these two areas are determined by the reversing monsoon winds: the Northeast Monsoon (NEM) which occurs between November and March, and Southeast Monsoon (SEM) from May to October. The hot and dry period falls during the NEM while the cool, wet season occurs during the SEM (McClanahan, 1988).

Sampling and laboratory analysis

Monthly sampling was carried out in 2001 during both the NEM and SEM. Fish samples were caught from 3 sites in each study area, which represented the habitat conditions at each study area. The fish samples were collected during mid ebb tide using a cast net of 20-mm stretched mesh size. All fish were immediately preserved in a 10% formaldehyde–seawater solution. At each station, environmental variables were also determined. Temperature was measured using a mercury thermometer, salinity using a refractometer and pH on a digital pH meter. Transparency was measured using a Secchi disc. Dissolved oxygen was determined by the Winkler method while chlorophyll *a* was measured spectrophotometrically (Parsons et al., 1984).

Diet analysis

The diets of *Sardinella gibbosa* and *Atherinomorous lacunosus* were analysed for both Mtwapa Creek and Wasini Channel. For gut analysis, the fishes were dissected and their guts carefully severed from the oesophagus to the last portion of the intestine. Each gut was opened and the contents removed carefully and weighed to the nearest 0.01 g, after which they were emptied into 4 % ethanol in a Petri dish where they were examined under a binocular microscope. All items present in the gut were identified to the lowest possible taxa and counted. Some of the food items were sometimes in an advanced stage of digestion, and in those only the undigested portion of the organisms, usually the heads, were actually identified and counted. Various mathematical methods were applied to determine the food and feeding habits of these fishes. The intensity of feeding was studied by determining the degree of fullness of the stomach and expressed by the following formula defined by Hynes (1950).

$$FI = \frac{\text{Weight of ingested food}}{\text{Weight of fish}} \times 100\%$$

where FI = fullness index.

Diet composition was calculated as a percentage of each food item in the stomach contents and expressed as numerical abundance (% N). The number of guts having common food items were regrouped and the percentage frequency of occurrence (% F) of each food item in the stomach calculated. The feeding behaviour of each species was determined by Tokeshi analysis (Tokeshi, 1991). The mean individual feeding diversity (ID) was plotted against the population feeding diversity (PD) to indicate the feeding strategy of the species. ID and PD were determined using the following equations:

$$ID = \frac{(-P_{ij} \ln P_{ij})}{N}$$

$$PD = P_I \ln P_I$$

where N = the total number fish

P_{ij} = the proportion of prey type *i* in the *j*th fish.

P_I = the proportion of prey type *i* in the entire fish population.

The data for each species were analysed.

RESULTS

Environmental variables

There was a significant difference in temperature, salinity, Secchi depth transparency and conductivity between Mtwapa creek and Wasini Channel (*t*-test, $P < 0.05$). There was no significant difference in pH and dissolved oxygen readings of the two sites (*t*-test, $P > 0.05$).

Food composition and feeding strategies

Analysis of the diets of *S. gibbosa* and *A. lacunosus* with respect to mean number of prey items consumed using the χ^2 test for independence is presented in Table 1. It was observed that the stomachs of *S. gibbosa* and *A. lacunosus* from Mtwapa creek had a significantly ($P < 0.05$) greater number of prey items than those from Wasini (Table 1). For both *S. gibbosa* and *A. lacunosus,* the mean number of prey items consumed was higher during the NEM than in the SEM due to abundant food resources during the former season.

Table 1. Seasonal comparison of mean number of prey items in the stomach contents of *Sardinella gibbosa* and *Atherinomorous lacunosus.* N = mean number of prey; NEM, SEM = Northeast Monsoon, Southeast Monsoon respectively

	N			
Species/ Site	NEM	SEM	χ^2	P
S. gibbosa (Mtwapa)	142	16	4.86	0.03
S. gibbosa (Wasini)	21	7		
A. lacunosus (Mtwapa)	189	53	4.92	0.02
A. lacunosus (Wasini)	39	3		

The spatial and temporal variation in the diet composition of the species is presented in Table 2. Copepods were the most important prey items for *S. gibbosa* from both sites: Mtwapa creek during the NEM (37.1 %N) and SEM (24.8 %N), and in Wasini NEM (48.6 %N). Copepods were also important for *A. lacunosus* in Mtwapa creek during the NEM (63.4 %N) and SEM (33.2 %N). In addition to copepods, sergestids (19.1 %N) were

Table 2. The numerical composition (%N) of the major food items in the stomach contents of *Sardinella gibbosa* and *Atherinomorous lacunosus* from Mtwapa creek and Wasini Channel during the Northeast Monsoon (NEM) and Southwest Monsoon (SEM)

	Wasini				Mtwapa			
	S. gibbosa		*A. lacunosus*		*S. gibbosa*		*A. lacunosus*	
Prey categories	NEM	SEM	NEM	SEM	NEM	SEM	NEM	SEM
Copepods	48.60	10.77	10.91	16.37	37.12	24.83	63.41	33.00
Rotifera	15.06	–	–	5.26	–	–	–	–
Hyperrids	6.41	13.85	–	–	14.20	–	24.61	5.00
Nemerteans	5.39	–	7.82	–	–	–	–	–
Nematodes	4.70	35.38	8.85	36.26	–	5.13	–	5.00
Brachyuran megalopa	–	24.62	–	–	1.64	7.21	–	–
Sergestids	–	6.15	–	–	13.88	19.03	–	–
Carideans	–	–	–	–	8.76	–	–	–
Mysids	–	–	–	–	7.98	–	–	–
Cladocerans	–	–	–	–	4.79	–	–	–
Brachyuran larvae	–	–	–	–	–	11.75	–	16.00
Fish eggs	–	–	7.03	–	–	6.10	–	–
Lemellibranch larvae	–	–	22.63	–	–	6.02	–	24.00
Foraminifera	–	–	18.31	–	–	–	–	–
Ostracods	–	–	4.53	–	–	–	–	–
Flat worms	–	–	–	12.87	–	–	–	–
Polychaetes	–	–	–	5.85	–	–	–	–
Others	19.84	9.23	19.93	23.39	11.64	19.93	11.99	17.00

–, not found.

important prey for *S. gibbosa* (Mtwapa) during the SEM, while nematodes and brachyuran megalopas constituted the important food for *S. gibbosa* (Wasini, SEM) with 35.4 %N and 24.6 %N respectively. Lemellibranch larvae (22.6 %N) were the important prey for *A. lacunosus* (Wasini NEM) followed by foraminiferans (18.3 %N). During the SEM, *A. lacunosus* (Wasini) fed mainly on nematodes (36.26 %N) and copepods (16.4 %N).

Figure 2 shows the feeding strategies of *S. gibbosa* and *A. lacunosus* during the two monsoon periods. Both species exhibited generalist feeding behaviour. There were no spatial or temporal differences in their feeding strategies since all points in the Tokeshi's graph tended to cluster together.

Prey size

Further results on the variation in sizes of copepod and nematode prey are presented in Tables 3 & 4. The mean carapace length of copepods eaten by the two species ranged between 311 and 611 µm, and the mean carapace width varied from 135 mm to 294 µm (Table 3). Note that smaller copepods were taken by *A. lacunosus*, while *S. gibbosa* consumed larger-sized ones (ANOVA, $P < 0.05$, Tukey HSD, $P < 0.05$) (Table 3). *Atherinomorous lacunosus* ate slightly larger nematodes than *S. gibbosa*, though there was no significant difference in the body length of nematodes eaten by the two species (ANOVA, $P > 0.05$, Tukey HSD, $P > 0.05$) (Table 3).

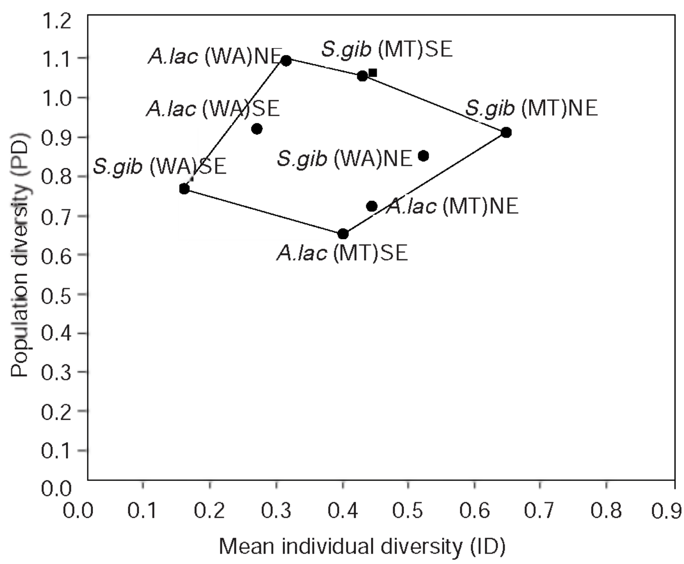

Fig. 2. Feeding strategies of *Sardinella gibbosa* and *Atherinomorous lacunosus* from Mtwapa creek (MT) and Wasini Channel (WA) during the NE and SE Monsoons as determined by Tokeshi graphical analysis

Table 3 . Interspecific differences in prey size eaten by *Sardinella gibbosa* and *Atherinomorous lacunosus* (± SE) (sample sizes in parentheses)

	Copepods		Nematodes	
	Carapace length (µm)	Carapace width (µm)	Body length (µm)	Body width (µm)
Species	P < 0.05	P < 0.05	P > 0.05	P < 0.05
S. gibbosa	665 ± 17 (587)	294 ± 9 (587)	391 ± 15 (250)	103 ±5 (250)
A. lacunosus	311 ± 40 (65)	135 ± 8 (65)	422 ± 25 (436)	1.37 ±5 (436)

There was no significant ontogenetic change in prey sizes eaten by either of the two fish species (Table 4). The mean copepod carapace length and width, and nematode body length were not significantly different between the size classes of *S. gibbosa* (ANOVA, P > 0.05, Tukey HSD, P > 0.05), but there was a difference in nematode body width (ANOVA, P < 0.05, Tukey HSD, P < 0.05). Neither did the prey sizes (copepod carapace length and width, and nematodes body width) eaten by *A. lacunosus* differ within the size classes (ANOVA, P > 0.05, Tukey HSD, P > 0.05) (Table 4). However, there existed a significant difference in the nematodes body width eaten by the different size classes (ANOVA, P < 0.05, Tukey HSD, P < 0.05). In all comparisons, copepod size and nematode body width contributed significantly to interspecific differences in size of prey eaten by the two species; while nematode body width contributed significantly only to ontogenetic differences in prey size.

Spatial difference in feeding intensity of *S. gibbosa* and *A. lacunosus*

The spatial and temporal variation in feeding intensities of *S. gibbosa* and *A. lacunosus* as measured using the stomach fullness indices are depicted in Fig. 3. The feeding intensities for *S. gibbosa* and *A. lacunosus* from Mtwapa creek were

Table 4. Ontogenetic changes in prey sizes eaten by *Sardinella gibbosa* and *Atherinomorous lacunosus* (± SE) (sample sizes in parentheses)

Size classes (mmSL)	Copepods		Nematodes	
	Carapace length (μm)	Carapace width (μm)	Body length (μm)	Body width (μm)
S. gibbosa	P > 0.05	P > 0.05	P > 0.05	P < 0.05
80 – 90	661 ± 27 (143)	311 ± 17 (143)	469 ±156 (94)	125 ± 31 (94)
91 – 100	697 ±126 (159)	359 ± 64 (159)	500 ± 66 (67)	164 ± 27 (67)
101 – 110	683 ± 23 (124)	289 ± 12 (124)	380 ± 16 (56)	98 ± 5 (56)
111 – 120	611 ± 34 (98)	273 ± 22 (98)	354 ± 28 (33)	94 ± 1 (33)
121 – 130	516 ± 92 (63)	164 ± 24 (63)	–	–
A. lacunosus	P > 0.05	P > 0.05	P > 0.05	P < 0.05
70 – 80	328 ± 43 (44)	138 ± 9 (44)	356 ± 18 (133)	135 ± 7 (133)
81 – 90	188 ± 1 (21)	109 ± 16 (21)	521 ± 85 (154)	167 ± 13 (154)
91 – 100	–	–	432 ± 33 (88)	130 ± 7 (88)
101 – 110	–	–	281 ± 1 (61)	109 ± 16 (61)

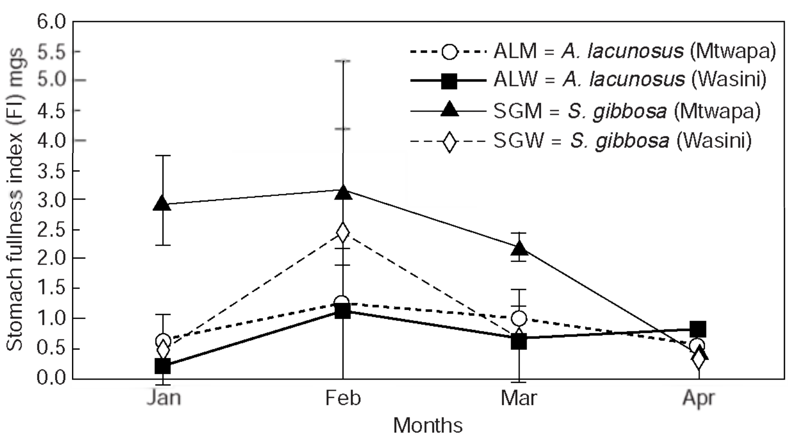

Fig. 3. Spatial variation in stomach fullness indices (mean ± SE) for *A. lacunosus* and *S. gibbosa* from Mtwapa creek and Wasini Channel

higher compared to those of Wasini Channel. There was a significant difference between the feeding intensity of *S. gibbosa* from Mtwapa creek and those from Wasini Channel (ANOVA, $P < 0.05$). However, no significant differences were present in the feeding intensity of *A. lacunosus* between the two study sites (ANOVA, $P > 0.05$).

DISCUSSION

Environmental variables

There was a clear distinction in the conductivity, salinity, temperature and Secchi depth transparency of stations located in Mtwapa creek and those in Wasini Channel. Physical removal from each other (80 km) and differences in vegetation structure and benthic environment may have contributed this variation. Increased nutrient input in Mtwapa creek from sewage effluents from the adjacent Shimo la Tewa prison, may also have caused the observed differences (Mwangi et al., 2001).

Food composition and feeding strategies of *S. gibbosa* and *A. lacunosus* during the Northeast and Southeast Monsoon

Temporal and spatial separation in the diet composition of *S. gibbosa* and *A. lacunosus* was observed. The diets of the two species were separated during the two monsoon periods based on prey availability. The overall dominance of copepods in the stomach contents of *S. gibbosa* and *A. lacunosus* during the NEM than in the SEM was attributed to the relative abundance of copepods in the environment. This period was also associated with high water transparency that made it easier for both species, which are mainly visual feeders (Major, 1977), to locate their prey. During the SE monsoon when transparency was lowered due to increased turbidity as a result of increased turbulence and river / runoff inputs from terrestrial environment, there was relatively low visibility for the two fish species thus restraining their feeding activity in this season. This resulted in low feeding intensity and lower percentage composition of copepods in their diet during the SE monsoon season.

Any attempt at generalising the feeding ecology of fish confronts the problem posed by the trophic flexibility—including ontogenetic, seasonal and diel changes in diet that many species show (Wootton, 1990). Fish may also change their feeding behaviour depending on food availability and prevailing environmental conditions. *Sardinella gibbosa* and *A. lacunosus* from Mtwapa creek and Wasini exhibited a generalised feeding strategy during both the NE and SE monsoons. From the foregoing, both species responded to seasonal changes in food availability, since they reflected an opportunistic behaviour and trophic adaptability.

Tropical fish in coastal water are acknowledged to be generalists, as they have to cope with a seasonally changing environment (Lowe-McConnell, 1991). The reversing monsoons along the East African coast is for example the main overriding feature affecting the local climate in this area (Richmond, 1997). These monsoon winds, together with the changes in the major coastal and oceanic currents in the region, control many ecological processes (McClanahan, 1988).

Clupeids have long been recognised as opportunistic foragers that feed on suitable food as encountered (Koslow, 1981; James, 1988). This habit results in flexible feeding cycles that depend on local conditions. Laboratory and field data indicate that intermediate microphages (*S. gibbosa* and *A. lacunosus*) display a high degree of opportunism in fulfilling their dietary requirements (Koslow, 1981). They are energy maximisers, capable of alternating their feeding strategies to use the available trophic spectrum efficiently. It has been commonly recognised that the diets of these fish reflect the composition of the ambient plankton communities (King & Macleod, 1976; Koslow, 1981; James, 1987). From the foregoing, can be concluded that the two species are generalist and opportunistic feeders.

Copepods were the most important prey item for both *S. gibbosa* and *A. lacunosus* in Mtwapa creek during the NE monsoon. However, nematodes were more important in their diets during the SE monsoon. This demonstrates a switching from one type of prey to another as the relative abundance of the prey changes. The above observations clearly show that habitat variability can affect predator behaviour as well as prey availability, resulting in habitat specific foraging strategies. Both *S. gibbosa* and *A. lacunosus* exhibited flexible feeding strategies that could be contributing to their success in this seasonal environment. The observed results clearly indicate the effects of habitat variability which in turn affects the trophic ecology of the planktivorous fishes inhabiting these ecosystems.

Prey size

Visual predators pursue the prey item that appears largest at the start of the search (O' Brien et al., 1976). *Sardinella gibbosa* consistently ate larger individuals of copepods than *A. lacunosus*. This could suggest that it is a mainly visual predator. The high proportion of phytoplankton and small-sized copepods in the diet of *A. lacunosus* suggests that in addition to visual feeding (Major, 1977), *A. lacunosus* is also a filter feeder. The difference in copepod sizes eaten by these two co-existing species is probably a strategy to reduce interspecific competition for this prey. From this study, the prey sizes (copepods) did not differ significantly with increase in size of the fish. However, other studies have shown that the range of prey size increased with increase in fish body size (Morato et al., 2000). Similarly, larger predators were found to utilise all food resources ranging from smaller prey items to larger ones, thus giving them a competitive advantage (Brooks & Dobson, 1965).

Spatial differences in the feeding intensities of *S. gibbosa* and *A. lacunosus*

The spatial differences observed in feeding intensities of *S. gibbosa* and *A. lacunosus* is a result of spatial niche differences between Mtwapa creek and Wasini Channel. The stomach fullness index closely reflects these spatial differences. Differences in productivity and food availability between habitats as a result of presence or absence of mangrove vegetation influences the distribution and feeding activities of fish (Robertson & Duke, 1987). Extensive mangrove vegetation and mud banks surround Mtwapa creek creating micro-habitats that support dense populations of micro- and macrofauna at both benthic (Ruwa, 1990) and planktonic levels (Osore, 1994). Mtwapa creeks also have evidence of eutrophication due to raw sewage continuously flowing into the creek from Shimo la Tewa prison. This results in increased nutrient content in the creek and hence high productivity levels (Mwangi et al., 2001). One notable attribute of mangroves is their high net primary productivity compared to other aquatic ecosystems. This production results in high leaf and litter fall that forms the basis for the detritus food web for microbes, molluscs, crabs and fish. They also bind roots and sediments creating a stable habitat for burrowing organisms. In this regard, Mtwapa creek is therefore considered rich in planktonic and benthic food supply. *Sardinella gibbosa* and *A. lacunosus* are both planktivores and benthivores, hence they were able to utilise the available food resource adequately resulting in very high fullness indices in the creek ecosystem as compared to Wasini Channel.

Although primary production in the form of chlorophyll *a* and zooplankton production was higher in Wasini Channel than Mtwapa creek, the benthic zone in Wasini Channel seems to have supported a very low population of micro- and macrofauna. Production in Wasini Channel seems to rely mainly on photosynthetic processes unlike Mtwapa creek where detritus also plays a major role in energy flow. Hence, the low stomach fullness indices that were observed in *S. gibbosa* and *A. lacunosus* from Wasini Channel indicate an inadequate food resource in the benthic zone. In addition, benthic organisms tend to be larger in size than planktonic organisms. Fish feeding on a larger proportion of benthic organisms tend to have a higher fullness index than those feeding mostly on planktonic organisms.

CONCLUSIONS

Although *S. gibbosa* and *A. lacunosus* shared common nearshore microhabitats and most of the times foraged together, they utilised the spatial and nutritional resources of the environment variably. The utilisation of detritus as dietary component for *S. gibbosa* allowed it to take advantage of an abundant food resource in the benthic zone while minimising competition with *A. lacunosus* which did not feed on detritus.

Both *S. gibbosa* and *A. lacunosus* use two key microhabitats as foraging grounds: the pelagic and benthic zones of the sea. They forage on holoplankton and meroplankton in the pelagic zones and on zoobenthos from near the seabed. In all the habitats, feeding strategies for the two species remained the same. Spatial and temporal differences in the prey items consumed, shows how habitat variability, and therefore food availability, affects the food types consumed by the fish.

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