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Trophic Ecology of Some Common Juvenile Fish Species in Mtwapa Creek, Kenya

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Abstract—The trophic status of common fish species in Mtwapa creek on the Kenyan coast was studied. Both the qualitative and quantitative spectra of the diets of these fish species were investigated. It was found that the eight most abundant fish species, *Sardinella gibbosa, Pellona ditchella, Spratelloides delicatilus, Atherinomorous lacunosus, Gerres oyena, Secutor insidiator* and *Leiognathus equula,* consumed principally copepods, while *Selar crumenophthalmus* fed mainly on fish scales. Polychaetes were an important diet for *Gerres oyena* and *Leiognathus equula. Spratelloides delicatilus* was a carnivore feeding only on zooplankton and zoobenthos, and had the lowest diet diversity (H' = 0.40). The rest were omnivorous. *Sardinella gibbosa, P. ditchella, L. equula, Sec. insidiator, G. oyena* and *Sel. crumenophthalmus* fed on phytoplankton, zooplankton, zoobenthos and detritus with a relatively higher diet diversity (H' = 0.68–0.96). *Atherinomorous lacunosus* did not take detritus in its diet and it had a lower diet diversity compared to the other omnivores (H' = 0.47).

The feeding niches of the examined species were highly overlapped. The Morisita feeding niche overlap values ranged between 0.84 and 1.00. Most of them were generalized opportunistic feeders except for *S. dilicatilus*, which exhibited a specialised feeding strategy. Overall, this study showed that the fishes had a flexible diet, which relied greatly on the prevailing biotic and abiotic conditions in their habitats.

INTRODUCTION

In the various studies aimed at understanding the feeding regimes, food preference, migrations, growth and breeding patterns of fish, diet has been found to be an important factor, especially in governing their growth, condition, fecundity and migration patterns (Rao, 1974).

Food habits of fish provide essential information for bionomic studies of single species, comparing related or coexisting species, describing assemblages and the analysis of ecosystem energetics and regulation (Sheldon & Meffe, 1993). The analysis of stomach contents in fish is a common method for investigating the diet of fish, and thus describing food chains and webs shared by different species. Such studies also reveal interactions among species i.e. among potential competitors and between predators and their prey (Rice, 1988). The composition of food items in the fish guts also provides information about the habitats in which the fish feed. The nature of this ingested food depends primarily on the mode of feeding, morphology of the feeding apparatus and the time of feeding. The composition and amounts taken also depend on selectivity and the availability of the prey (Pillay, 1952).

In studies on diets of fish along the Kenyan coast (Kimani et al., 1996; De Troch et al., 1998; Wakwabi, 1999), both micro- and macro-fauna

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were found to the principal diet items. The four trophic guilds identified were: omnivore, piscivore, zooplanktivore and benthic carnivore (Wakwabi, 1999). The omnivores had the lowest feeding niche while the zooplanktivores had the highest. In this paper, we describe the trophic ecology of some common fish species in Mtwapa Creek using analytical and graphical techniques that summarise broad patterns of feeding biology.

MATERIALS AND METHODS

Study area

This study was carried out in Mtwapa Creek (3° 55' S, 39° 45' E), situated 25 km north of Mombasa along the Kenyan coast (Fig. 1). Fish samples were collected from three sampling stations located within the creek. Shallow waters at the entrance and towards the inner parts characterize the creek. The middle section of the creek, especially near the bridge, is narrower and deeper. The creek receives freshwater from a seasonal river (River Mto Mkuu/ River Luadani) whose annual mean discharge is 0.3 m^3/s (Magori, 1997). A dense mangrove cover of mainly *Rhizophora mucronata* on extensive mud banks lines the edges of the creek. There is little obvious industrial development around Mtwapa creek except for the intensive boating activities. The creek is relatively eutrophic (Mwangi *et al.*, 2001) with evidence of seasonal water contamination attributed to river discharge, surface water runoff and raw sewage disposal, especially near Shimo la Tewa prison.

Fish sampling

Fish were caught using a simple, 20-m-long, 2-m-wide beach seine-net with a 20-mm stretched mesh size. With the help of an outboard powered boat, the net was laid perpendicular to the shore starting from the shoreline into the waters. It was then

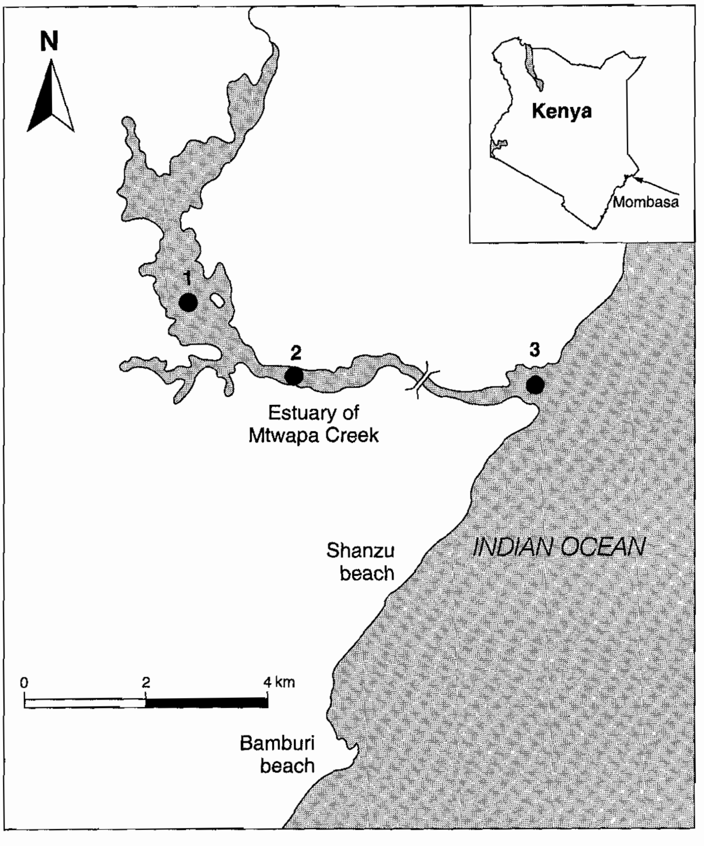

Fig. 1. The location of three sampling sites in Mtwapa Creek, Kenya

dragged in a semi-circular manner shoreward and hauled onto the beach. Three tows were made at each station. The catches from the three tows at each study area were pooled to constitute the fish community at the station. The fish samples were sorted and identified to species level using identification keys from Brock (1978), Fischer & Bianchi (1984) and Smith (1986). Fishing schools of *Atherinomorus lacunosus* and *Sardinella gibbosa* were often found close to each other. Standard body length was measured to the nearest millimetre. All fish caught were immediately fixed in 10% formaldehyde and later preserved in 70% ethanol.

Diet analysis

The eight commonest fish species were selected for stomach content analysis. These included three clupeids: *Sardinella gibbossa*, *Pellona ditchella* and *Spratelloides delicatulus*; one atherinid: *Atherinomorous lacunosus*; two leiognathids: *Secutor insidiator* and *Leiognathus equulus*; one gerreid: *Gerres oyena* and one carangid: *Selar crumenopthalmus.*

The fish caught were randomly subsampled and all were juveniles (Table 1). Fish for stomach content analyses were weighed and later dissected to open the viscera. Fish stomachs were carefully severed from the oesophagus to the last portion of the intestine. Each stomach was opened and its contents carefully removed and weighed to the nearest 0.0001g. Stomach contents were fixed in 4% buffered formaldehyde and preserved in 70% ethanol before further analysis. During analysis the contents were emptied into a Petri dish and examined under a binocular microscope. They were sorted through and identified as much as possible to the lowest taxonomic levels and counted. In order to minimise the underestimation of small and soft prey, utmost care was given to the identification of small fragments. For partially digested food items, only the undigested portion of the organisms, usually the head, was used for identification and counts. All the identified prey items were counted and used for subsequent dietary analysis.

Various indices described below were applied to the weights and counts data to determine the food habits of these fishes. Fish stomach fullness index (FI) as a measure of feeding intensity (Hureau, 1969) was obtained as

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

The percentage frequency of occurrence of each dietary category in the stomach of all fish (%F) and the relative contribution of each dietary category to the numbers (%N) of the total food items in the stomach of each fish were calculated (Berge, 1979) as

$$\% F = (n_{fi} / N_f) \times 100$$

where n_{fi} = number of fish with prey item *i* in the stomach contents and N_f = total number of fish examined, and

$$\% N = (n_i / N_{tot}) \times 100$$

where n_i = number of individuals of prey item *i*, found in the stomach contents of each species, and N_{tot} = total number of prey items encountered in the stomach contents of each species.

The Shannon–Weiner diversity index (H) (Washington, 1984) was calculated to determine fish diet diversity:

$$H = n \log n - \hat{A} (Ø \log Ø) / N$$

where n = number of species in a sample, Ø = number of individuals in a species, and N = total number of individuals in a sample.

One step towards an understanding of community organization is to measure the overlap in resource use among the different species. The most common resources measured in order to calculate overlap are food and space (or microhabitat). The simplified Morisita index proposed by Horn (1966) as a similarity index was used to measure the feeding niche overlap between the eight fish species that were selected for diet analysis in this study, i.e.

$$C_H = 2 \hat{A} P_{ij} P_{ik} / \hat{A} P^2_{ij} + \hat{A} P^2_{ik}$$

where

C_H = Simplified Morisita index of overlap between species *j* and species *k*.; P_{ij} P_{ik} = proportions of resource *i* of the total resources used by the two species (*i*= 1, 2 … n), and n = total number of resource states.

The feeding strategy of each species was determined by Tokeshi analysis (Tokeshi, 1991). Mean individual feeding diversity (ID) and population feeding diversity (PD) were determined using the following equations.

$$ID = (- \sum P_{ij} \ln P_{ij}) / N$$
$$PD = \sum P_i \ln P_i$$

where N = the total number fish examined.
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 ID was plotted against PD to indicate the feeding strategy of the species.

RESULTS

Diet composition

The dietary status of eight most common fish species is summarized in Table 1 and Fig. 2. All prey items which accounted for less than 5 % N in the diet of each of the fish species were grouped together and categorised as "others". Comparison of the dietary distribution of the prey across all the eight species by Friedman's ANOVA showed a significant difference among all species in the proportions of each eaten prey (P<0.05). The frequencies of occurrence of each prey type were all significantly different among the eight species (P<0.05). There was a positive correlation between the frequency of occurrence (%F) and the percentage abundance (%N) contributed by each prey item eaten by all the eight species (r = 0.57, P<0.05).

Spratelloides delicatilus

An average of 20 prey categories were identified in the stomach contents (Table 1). Copepods (51.8% N) and brachyuran larvae (44.2% N) were the dominant dietary items (Fig. 2). Copepods, brachyuran larvae and gastropod larvae were encountered in 100, 100 and 87.2 %F respectively of all examined stomachs for this species. The absence of phytoplankton and detritus in the diet of this species is noted.

Sardinella gibbosa

Average of 26 prey categories were present in the stomach contents of *Sardinella gibbosa* (Table 1). Numerically, copepods were the most important prey item (41.6%N). Other important prey items were the hyperrids, mysids and cladocerans that accounted for 33.5%N, 10.3%N and 5.3%N respectively (Fig. 2). The prey items with the highest frequency of occurrence (%F) were the phytoplankton, detritus, copepods, mysids, and brachyuran megalopas, which occurred in 100, 100, 100, 73.3, and 63.3 % respectively in the examined stomachs.

Table 1. Summary of the dietary data from stomach contents analysis of eight fish species caught from Mtwapa creek. * Denotes absence of phytoplankton and ** denotes absence of detritus in the stomach contents. N_T = total number of fish caught, N = sample size, S_{mmSL} = size class, Lmax =maximum length, N_P = Mean no. of preys, H= diet diversity, F.I =Mean stomach fullness index.

Fish species	N_T	N	S_{mmSL}	$Lmax_{mmSL}$	N_P	H	F.I ± SE	Feeding strategy
S. delicatilus */**	206	78	38 - 55	70	20	0.40	0.84 ± 0.20	Specialist
S. gibbosa	431	123	57 - 94	170	26	0.68	4.96 ± 1.24	Generalist
P. ditchella	243	102	55 - 130	160	25	0.97	2.18 ± 0.46	Generalist
A. lacunosus **	372	95	49 - 71	150	9	0.47	1.26 ± 0.51	Generalist
G. oyena	96	35	43 - 73	300	22	0.88	4.50 ± 0.10	Generalist
S. crumenophthalmus	63	38	120 - 150	600	20	0.74	0.50 ± 0.09	Generalist
S. insidiator	193	64	45 - 55	113	18	0.74	2.50 ± 0.36	Generalist
L. equula	120	44	48 - 90	280	16	0.92	4.77 ± 0.24	Generalist

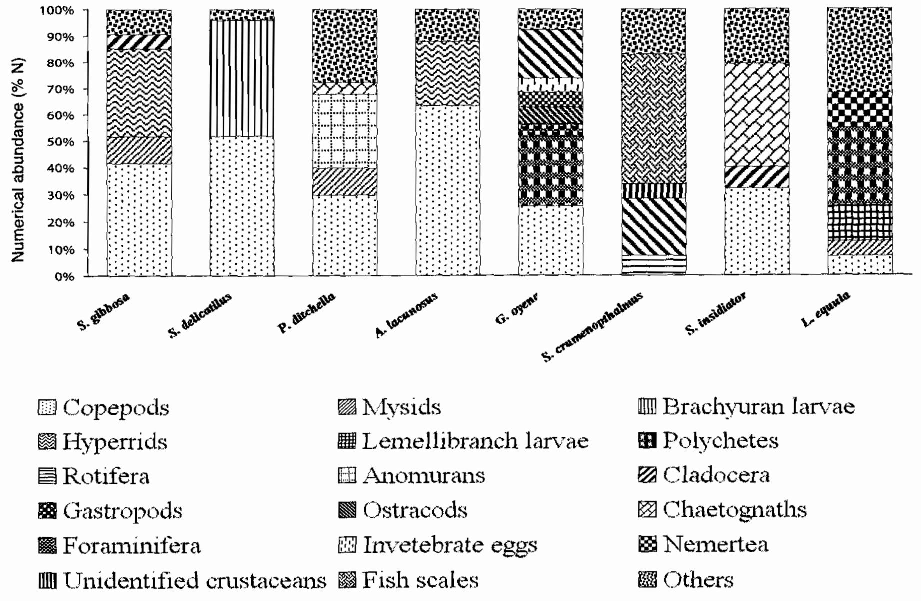

Fig 2. The numerical composition (%N) of most common prey items, in the stomach contents of fish species

Pellona ditchella

An average of 25 prey categories were identified (Table 1). Copepods (29.7%N), anomuran larvae (28%N), and mysids (10%N) were the most important prey items (Fig 2). Detritus, phytoplankton and copepods occurred in 100% of the examined stomachs while mysids occurred in 85%.

Atherinomorous lacunosus

Nine prey categories were identified (Table 1) where copepods (63.4% N) and hyperrids (24.6% N) dominated the diet (Fig. 2). Phytoplankton, copepods and hyperrids had the highest frequency of occurrence, i.e. 100, 100 and 85.7 %F respectively.

Gerres oyena

Twenty-two prey categories were identified for *G. oyena* (Table 1). Numerically, copepods (25.8%N), polychaete larvae (25.8%N), nematodes (18.4%N), ostracods (6.4%N), foraminifera (5.7%N) and invertebrate eggs (5.5%N) were the important prey in that order (Fig. 2). Detritus, phytoplankton and copepods occurred in 100% of the examined stomachs; polychaete larvae and nematodes occurred in 77.8%.

Selar crumenophthalmus

An average of 20 prey categories were encountered (Table 1). This species mainly fed on fish scales (49.3%N), nematodes (21.1%N) and rotifers (7.3%N) (Fig. 2). Other prey items were eaten but in very low quantities. Detritus, phytoplankton and fish scales occurred in 100% of the examined stomachs while rotifers occurred in 55.5%.

Secutor insidiator

Secutor insidiator had 18 prey categories (Table 1). Chaetognaths (39.3%N) and copepods (32.2%N) were the important prey in their diet (Fig. 22). Items taken with the highest frequency of occurrence were phytoplankton, detritus, copepods (each 100%F), rotifers and cladocerans (each 46.7%F).

Leiognathus equula

An average of 16 prey categories were identified (Table 1). The important prey items were polychaete larvae (28.7% N), foraminifera (15.2% N), nemertea and lemellibranch larvae (each 13.5% N), copepods (7.2% N) and mysids (5.5% N) (Fig. 2). Phytoplankton and detritus occurred in 100% of the examined stomachs, while polychaete larvae, copepods and nemerteans occurred in 92.4%, 84.6% and 76.9% of the stomachs respectively.

Diet diversity and feeding niche overlap

Pellona ditchella was found to have the most diverse diet (H = 0.97), followed by *L. equula* (H = 0.92) and *G. oyena* (H = 0.88) (Table 1). These fish fed mostly on hyper-benthos: hyperrids, mysids, polychaetes, nematodes and gastropod larvae. The next group with intermediate diet diversity was *Sel. crumenopthalmus* (H = 0.74), *Sec. insidiator* (H = 0.74) and *Sar. gibbosa* (H = 0.68). This group fed mainly on holoplanktonic copepods and chaetognaths except *Sel. crumenopthalmus*, which ate more fish scales and nematodes. Species with the lowest feeding niche breadth (i.e. with lowest diet diversity) were, *A. lacunosus* (H = 0.47) and *Spr. delicatilus* (H = 0.40). Their diets were characterized by the absence of detritus in the stomach contents of *A. lacunosus* and absence of both phytoplankton and detritus in *Spr. delicatilus* (Table 1). Differences in feeding intensity among the species were assessed by comparing the mean stomach fullness indices. Species that did not include detritus in their diet had much lower fullness indices than those that took detritus, planktonic and benthic organisms. Consequently, the diet diversity of those with a low FI was lower, as observed in *Spr. delicatilus* and *A. lacunosus* (Table 1).

The results on feeding niche overlap between the eight fish species are shown in Table 2. There were considerably high values of feeding niche overlap between the eight investigated species. The highest values were recorded between *A. lacunosus/Spr. delicatilus*, *Sel. crumenophthalmus/Sar. gibbosa*, *Sec. insidiator/Sar. gibbosa* and finally *Sec. insidiator/Sel. crumenophthalmus*. On the other hand, the lowest values were recorded between *G. oyena* and *Spr. delicatilus*, *G. oyena* and *A. lacunosus*, *L. equula* and *Spr. delicatilus* and between *L. equula* and *A. lacunosus*.

Table 2. Morisita feeding niche overlap among fish species in Mtwapa creek. Highest feeding niche overlap values are marked (**) while lowest values are marked (*).

Fish species	*Sar. gib.*	*Spr. del.*	*P. dit.*	*A. lac.*	*G. oye*	*Sel. cru.*	*Sec. ins.*	*L. equ.*
Sar. gibbosa	1.000							
Spr. delicatilus	0.986	1.000						
P. ditchella	0.972	0.902	1.000					
A. lacunosus	0.977	1.000**	0.904	1.000				
G. oyena	0.968	0.897*	0.999**	0.837*	1.000			
Sel. crumenopthalmus	1.000**	0.977	0.972	0.977	0.968	1.000		
Sec. insidiator	1.000**	0.965	0.983	0.966	0.980	1.000**	1.000	
L. equula	0.950	0.868*	0.996	0.853*	0.997**	0.949	0.964	1.000

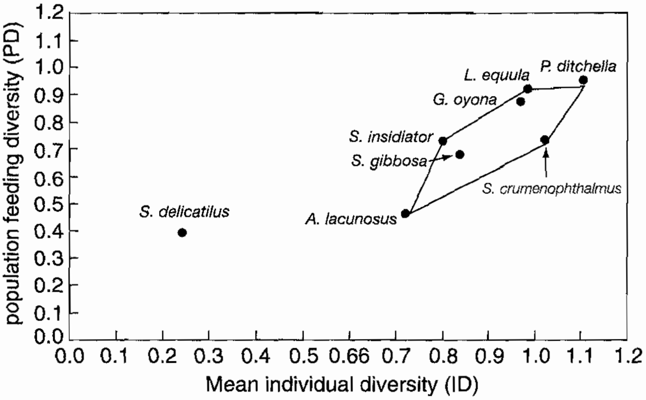

Fig. 3. The feeding stategies of eight fish species from Mtwapa creek as determined by Tokeshi graphical analysis (Tokeshi, 1991)

Feeding strategies

Using the Tokeshi graphical analysis method on feeding strategies, *Spr. delicatilus* was clearly separated from the other seven species (Fig. 3). It was noted that for *Spr. delicatilus*, both individual and population feeding diversities were low, indicating a specialised feeding strategy. The other seven species were characterised by high individual (ID) and population feeding diversities (PD), suggesting a more generalist and opportunistic feeding strategy. Species with low ID and PD are specialised feeders (Tokeshi, 1991), while those with high ID and low PD are generalists. Species with high ID and high PD are generalists with a homogeneous feeding pattern.

DISCUSSION

In this study, two trophic categories were identified among the eight species of fish that were examined. *Spr. delicatilus* was exclusively carnivorous, feeding mainly on zooplankton and zoobenthos. It was characterised by a very low diet diversity / feeding niche breadth of H = 0.40 and low fullness index (F.I = 0.84), while *Sar. gibbosa*, *P. ditchella*, *L. equula*, *Sec. insidiator*, *G. oyena* and *Sel. crumenopthalmus* belonged to the omnivorous category. This latter group fed on phytoplankton, zooplankton, detritus and zoobenthos with a relatively higher feeding niche breadth ranging between H = 0.68 for *Sar. gibbosa* and H = 0.96 for *P. ditchella*. Except *Sel. crumenophthalmus*, this group also had higher stomach fullness indices. A third group which consisted of *A. lacunosus* was found to feed on phytoplankton, zooplankton and zoobenthos only, and had a lower feeding niche (H = 0.47) as compared to the other omnivores. In De Troch et al. (1998) and Wakwabi (1999), it was noted that low stomach fullness index and very low diet diversity are characteristic of planktivorous species, while benthivores tend to have intermediate fullness indices with very diverse diets.

James (1988) reviewed the diet of some commercially important clupeids and found that most of them were omnivorous microphagists that derived the bulk of their energy from zooplankton. Their feeding modes have also been described from laboratory and field studies (Blaxter & Holliday, 1958). In addition to filter and particulate feeding, some species are capable of capturing floating prey (James, 1987). Many filter-feeders display tendencies towards detritivory, utilizing the high detrital loads and large biomass of unicellular benthic algae present in the shallow coastal and estuarine waters they inhabit (Darnell, 1958). The diets of *Sar. gibbosa* and *P. dichella* examined in this study support this view. Flexibility in the feeding behaviour of these species enables them to efficiently utilise the available food.

The diet diversity of omnivorous fishes was high compared to that of the carnivorous fish. This was because the omnivores fed on a wider range of food items than the carnivore (*Spr. delicatilus*). Note that the fish species classified as carnivorous mostly fed on zooplankton and zoobenthos. *Atherinomorous lacunosus,* which did not feed on detritus, also had relatively low diet diversity. The high diversity of prey items found in the diets of the omnivorous group suggests that they are more generalist predators.

This study also shows that the investigated fish species foraged on a wide variety of prey organisms with a high level of interspecific dietary overlap. The examined fish species were caught from the same habitat. Therefore, selection of common habitats resulted in high dietary overlap and possible interspecific competition for available food resource. Similarly, high dietary overlap may also indicate low competition, if resources are not limited or carrying capacities are not reached (Tokeshi, 1999), since the ratio of demand to supply is of vital concern in the relationship between ecological overlap and competition (Pianka, 1994). Hence, the low diet niche overlap values present in *G. oyena*/*Spr. delicatilus*, *G. oyena*/*A. lacunosus, L. equula*/*Spr. delicatilus* and *L. equula*/*A. lacunosus* occurred because *G. oyena* and *L. equula* utilised more diverse food resources including endobenthos, which *A. lacunosus* and *Spr. delicatilus* did not ingest.

Seven of the examined fish species exhibited a generalist feeding strategy. *Spratelloides delicatilus*, which had a diet specialised on copepods and brachyuran larvae was the only specialist. The species had the lowest mean individual and population diet diversity as shown by Tokeshi's method. *Atherinomorous lacunosus*, although exhibiting a generalist feeding strategy, had a relatively low individual and population diet diversity compared to the other generalists, because unlike the other species, it did not take detritus in its diet. The high feeding niche overlap between *Spr. delicatilus* and *A. lacunosus* observed in this study may also be attributed to utilisation of the same food resource.

CONCLUSIONS

Although *Sar. gibbosa* and *A. lacunosus* shared common near-shore microhabitats and most of the time foraged together, they utilised its spatial and nutritional resources of the environment differentially by differentiating their feeding niche breadth and selecting different preys. *Sardinella gibbosa* had a higher diet breadth than *A. lacunosus*, since it utilised detritus as a dietary component.

Site-specific features of particular habitats and their associated predator and prey assemblages determine feeding patterns in fish. The choice of prey by the examined fish species seemed to depend upon food availability, and hence they can also be referred to as opportunistic feeders. Fish species with a generalised and flexible feeding behaviour are less vulnerable to changes in abundance or availability of particular prey categories, giving them a competitive advantage over specialised feeders.

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