

## Niche measures and feeding strategies of *Barbodes gonionotus* Bleeker and *Oreochromis* spp. from a ricefield in Bangladesh

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### Abstract

Intra- and interspecific virtual niche measures and feeding strategies of *Barbodes gonionotus* and *Oreochromis* spp. were studied from a ricefield in Bangladesh. Appropriateness and ease of interpretation of different indices were evaluated. Small sizes of both species had a relatively wider dietary breadth and used many of the resource categories available to them than the large size groups, though none were generalistic feeder. The dietary overlap of large *B. gonionotus* on the small was greater than the reverse, but biologically insignificant. While the dietary overlap of large *Oreochromis* spp. on the small was significantly greater. Interspecific dietary width was relatively broader for *B. gonionotus* than *Oreochromis* spp. and overlap of *B. gonionotus* on *Oreochromis* spp. was significantly greater than the reverse. Evidence of significant intraspecific dietary overlap between the two sizes of tilapia reflects strong competition and cautions for mixed-size stocking in rice-fish system. Besides, there seems fewer opportunities for habitat segregation between *B. gonionotus* and *Oreochromis* spp., due to the significant interspecific dietary overlap of the former on the latter in rice-fish system. Tilapia specialized on periphytic detrital aggregate while silver barb tended to consume aquatic macrophytes and molluscs. Small sizes of *B. gonionotus* should be preferred for rice-fish integration over the *Oreochromis* spp. due to their broader niche width and pronounced ontogenetic dietary shifts with the aging of the stock.

**Key words:** Silver barb & tilapia, Intra- & interspecific niche indices, Rice-fish system

### Introduction

Concurrent rice-fish farming is being practiced in most of southeast Asia, stocking one or many species of fishes with little or no knowledge of resource partitioning, foraging habits and strategy, dietary breadth and overlap. Therefore, fish yield is generally low.

Dietary overlap is affected by food availability, competition, and the size of the fish, among other factors. Though fish may broaden their dietary breadth when food resources are scarce, food items may remain sufficiently partitioned for competition to be avoided (Keast 1977, Keast and Fox 1990). Intraspecific niche overlap decreases with ontogenetic shifts in diet, i.e. differences in habitat utilization by young and adults and increasing disparity in size (Pen *et al.* 1993, Esteves and Galetti 1995).

The silver barb or tawes, *Barbodes gonionotus* Bleeker (formerly *P. javanicus*) and the tilapias [*Oreochromis mossambicus* (Peters) and *O. niloticus* (Linnaeus)] are widely stocked in the southeast Asian rice-fish systems (de la Cruz *et al.* 1992, Fernando 1993, Haroon *et al.* 1994). These two fishes are exotic in Bangladesh and are very popular because of their rapid growth and ability to thrive in seasonal waterbodies which are not suitable for the indigenous carps (Gupta and Rab 1994, Haroon *et al.* 1994, Kohinor *et al.* 1994, Miah *et al.* 1994, Wahab *et al.* 1995). No reports are available on their dietary breadth, overlap and feeding strategy in rice-fish systems be it Bangladesh or in other Asian countries.

The present study was undertaken to examine and compare the intra- and interspecific dietary breadth, the degree of diet similarity, overlap and feeding strategy of two size groups of *B. gonionotus* and *Oreochromis* spp. (*O. mossambicus* x *O. niloticus* natural hybrid) and a single size group of *B. gonionotus* and *Oreochromis* spp., stocked in ricefields. Different niche measures are compared and evaluated for appropriateness, ease of biologically significant interpretation and explanation. Similar comparative work on dietary breadth, degree of diet similarity, overlap and feeding strategy of two size groups of *B. gonionotus* and *Oreochromis* spp. were done earlier by Haroon and Pittman (1998b) in the pond environment.

### Materials and methods

The present work comprises three experiments carried out in an experimental ricefield at the Riverine Station, Chandpur of the Bangladesh Fisheries Research Institute. Two size categories (around 6 and 12 cm, total length) of *B. gonionotus*, were examined in the ricefield during April 1994 (Experiment I), similarly two size groups of *Oreochromis* spp. were investigated during July 1995 (Experiment II) and during September 1995 (Experiment III) a median size range (falling within 6 and 12 cm) of both *B. gonionotus* and *Oreochromis* spp. were examined in the ricefield. The fish and sub-surface plankton were sampled every 3 h for 48 h in the intraspecific trials and for 24 h in the interspecific study for gut contents and available resources analysis. We have categorized the fishes in size classes, simply because fish farmers look first for the fish size rather than the weight when selecting any stock.

#### *Field preparation, fish stocking and sampling*

*Experiment I:* Rice (transplant Aman: *Paijam* - a local variety of *Oryza sativa*) was planted in an experimental field of 166 m<sup>2</sup> (having a refuge canal of 1.0 m breadth and 0.5 m depth, on one side of the plot) according to farmers traditional practice (Haroon *et al.* 1989). Once the tillers reached a height of 0.5 m and field conditions were as close as

possible to those of a natural wet-season ricefield (water depth 0.25 m in the paddy field and 0.7 m in the refuge), two sizes of *B. gonionotus* juveniles procured from the Riverine Station's hatchery were stocked at a total density of 7.0 juveniles m<sup>-2</sup> (581 individuals of each size). The small fishes were 4.5-5.52 cm (mean 4.85 cm) and 1.28-2.72 g (mean 1.72 g) and the large fishes were 11.54-13.4 cm (mean 12.64 cm) and 21.44-32.36 g (mean 27.81 g) at stocking. Prior to the experiment the fish had been fed a supplemental feed composed of 40% rice bran, 40% wheat bran and 20% fishmeal at 2-5% of body weight (bw) day<sup>-1</sup>. Before stocking in the experimental ricefield the fishes were kept in a flow-through system for 48 h to empty their gut contents. Two days after stocking, 10 fishes of each size were sampled every 3 h for a further 48 h with a knotless hapa net (3x2x1.5 m, mesh 0.5 cm). A total of 320 fishes (160 of each size) were collected.

*Experiment II:* Paddies were prepared in the following year in the same way in the same field, and conditions as close as possible to the natural wet-season ricefield were established. Two size categories of *Oreochromis* spp. juveniles procured from the Riverine Station's other nursery ponds were stocked in the ricefield at a total density of 7.0 juveniles m<sup>-2</sup> (581 individuals of each size). The small fishes were 4.9-8.0 cm (mean 6.82 cm) and 1.92-8.15 g (mean 5.02 g) and the large fishes were 10.3-13.8 cm (mean 12.0 cm) and 17.74-46.2 g (mean 27.84 g) at stocking. Prior to the experiment the fish had been fed a similar supplemental feed at the similar rates as for *B. gonionotus*. Stocked *Oreochromis* spp. had the same pre-treatment as *B. gonionotus* prior to release in the ricefield. A similar sampling regime was followed and a total of 320 fishes (160 of each size) were collected for gut analysis.

*Experiment III:* The same ricefield preparation and fish treatment was used in the final interspecific experiment when both species were stocked together. In this case a single size of both *B. gonionotus* and *Oreochromis* spp. were stocked at a total density of 7.0 juveniles m<sup>-2</sup> (581 individuals of each species). The silver barbs were 5.1-10.1 cm (mean 7.1 cm) and 2.5-14.39 g (mean 4.86 g) and the tilapias were 7.5-10.2 cm (mean 8.53 cm) and 8.11-16.66 g (mean 10.48 g). A similar sampling regime was followed and a total of 320 fishes (160 of each species) were collected for gut analysis.

### **Gut analysis**

Fishes were checked immediately after capture for regurgitation (if seen, the fish was replaced), and preserved in 10% buffered formalin until examined. Each fish was measured for total length (mm), and weighed ( $\pm$  0.001 g) within two weeks after collection and no correction factor for fixation was used.

As *B. gonionotus* lacks a well-defined stomach, only the anterior portion of the digestive tract lying between the esophagus and the first major curve of the small intestine was dissected out (Haroon and Pittman 1997) as digestion is less advanced in this portion and food items remain mostly identifiable. Silver barb have an intestine usually 2-3 times their body length (Sattar 1987). For *Oreochromis* spp. the anterior portion of the digestive tract lying between the esophagus and the first major bend of the small intestine, just after the stomach was dissected out (Haroon and Pittman 1998a). Tilapia have a relatively long and coiled intestine up to 14 times the body length

(Edwards 1987), although food digestion and assimilation is completed in the first half of the intestine (Bowen 1981).

Each gut or stomach was blotted uniformly with tissue paper, opened longitudinally and gut or stomach contents were transferred to a petridish or vial with a standard 10 ml of distilled water. Food items of animal origin were usually counted under a dissecting microscope, but in the case of tiny items and items of plant origin the gut or stomach contents were well mixed, one ml was sub-sampled by a digital Finn pipette to a Sedgwick-Rafter counting cell (1000 mm<sup>3</sup>, 50x20x1 mm) and 100 randomly chosen cells out of 1000 were examined under an inverted microscope. Three such sub-samples were enumerated per fish. All organisms were identified to the genus level (Prescott 1962, Ward and Whipple 1978) and percentage abundance was used for calculating the proportion of each food item in the gut or stomach (Windell and Bowen 1978, Bowen 1983). Only fishes with food in their gut or stomach were considered for calculation of the proportion of each food item.

### **Plankton**

Five 1-l samples of surface to sub-surface (0.02 m) water were taken from different areas of the ricefield (refuge canal, middle and extreme end of the field) every 3 h, prior to fish sampling, filtered through a 15 µm mesh plankton net, washed into plastic jars and made up to a standard 200 ml volume with 5% buffered formalin. Once well settled, plankton were concentrated in a standard 50 ml volume and preserved until examination. Three 1 ml sub-samples were examined from each plankton sample and the proportion and identification of each food item were done in the same way as for gut or stomach content.

### **Niche measures**

Diet breadth indices were calculated with Levin's modification of Simpson's diversity index  $B$  and  $B_n$  (Hurlbert 1978, Keast 1978, Easton *et al.* 1996).

$$B_x = 1/\sum (p_{xi}^2) \quad (1a)$$

$$B_y = 1/\sum (p_{yi}^2) \quad (1b)$$

where  $B_x$  and  $B_y$  are the dietary breadth (Shannon and Weaver information statistic) of  $x$  and  $y$  respectively (two different size classes or species),  $p_{xi}$  and  $p_{yi}$  are the proportions, out of all those resources used by  $x$  or  $y$ , that consists of food items in resource state  $i$ .  $B$  value varies from 1.0, when the population uses one resource state exclusively, to equal to  $R$ , when the population uses all resource categories in equal proportions.  $R$  is the number of food categories.

$$B_{nx} = 1/[R\sum p_{xi}^2] \quad (2a)$$

$$B_{ny} = 1/[R\sum p_{yi}^2] \quad (2b)$$

In Eq. 2a and 2b, the index (reciprocal of Simpson's diversity index) is normalized by  $R$ . Except for normalization other notations are the same as Eq. 1a and 1b. Conversely,  $B_n$  value ranges from  $1/R$ , when the population uses one resource state exclusively, to 1.0, when the population uses all resource states in equal proportions.

Feinsinger *et al.* (1981) stated that niche breadth, as defined by Levin (1968, cited in Keast 1978), Hurlbert (1978) and others, is simply a special case of sample similarity and proposed for using Czekanowski's *PS*, the proportional similarity index rather than Schoener's (1970) index.

$$PS_x = 1 - 0.5 \sum |p_{xi} - q_i| \quad (3a)$$

$$PS_y = 1 - 0.5 \sum |p_{yi} - q_i| \quad (3b)$$

where  $p_{xi}$  and  $p_{yi}$  are respectively the proportion of resource items in category  $i$  out of all items used by  $x$  or  $y$  and  $q_i$  is the proportion of  $i$  items in the resource base available to the population. Values for *PS* ranges from 1.0 for the broadest possible niche (when a population uses resources in proportion to their availability) to a minimum for the narrowest possible niche (when a population is specialized exclusively on the rarest resource state and consequently bypasses all other items).

Diet overlap indices were calculated with Levin's  $\alpha_{xy}$  and  $\alpha_{yx}$  (after Keast 1978, Wallace 1981) and Schoener's  $\alpha$  (Schoener 1970). The Levin's dietary overlap indices are represented by  $\alpha_{xy}$  (overlap of  $x$  on  $y$ ) and  $\alpha_{yx}$  (overlap of  $y$  on  $x$ ). Those are:

$$\alpha_{xy} = \sum (p_{xi} \cdot p_{yi}) / \sum p_{yi}^2 \quad (4a)$$

$$\alpha_{yx} = \sum (p_{xi} \cdot p_{yi}) / \sum p_{xi}^2 \quad (4b)$$

where  $p_{xi}$  and  $p_{yi}$  are similar as described for Eq. 2a and 2b. Values of  $\alpha_{xy}$  or  $\alpha_{yx}$  range from 0 to slightly over 1.0 and measures respectively the overlap of  $x$  on  $y$  or the reverse.

Schoener's overlap (1970) index is denoted by  $\alpha$ .

$$\alpha = 1 - 0.5 (\sum |p_{xi} - p_{yi}|) \quad (5)$$

where  $p_{xi}$  and  $p_{yi}$  are similar as described for Eq. 2a and 2b. Schoener's  $\alpha$  index varies from 0 representing no overlap to 1.0 reflecting complete overlap between the  $x$  and  $y$ . It is one of the least objectionable indices available (Wallace 1981, Martin 1984, Knight and Ross 1994) and widely used.

All these indices have been calculated from discrete counts, as animals choose resources item by item rather than joule by joule (Feinsinger *et al.* 1981), and compared to evaluate appropriateness and ease of biological interpretation. We have followed Zaret and Rand (1971), Wallace (1981), Martin (1984), Pen *et al.* (1993) in considering values of dietary overlap indices above the arbitrary level of 0.60 as representing a biologically significant overlap.

### **Feeding strategy**

Amundsen *et al.*'s (1996) modified approach of Costello's (1990) method was used for graphical analysis of feeding strategy. This is based on a two-dimensional representation where each data point represents the frequency of occurrence ( $F_i$ ) and the prey-specific abundance ( $\%P_i$ ) of a food category. Mathematically  $F_i$  and  $\%P_i$  can be described by the equations:

$$F_i = (N_i/N) \quad (6)$$

$$\%P_i = (\sum S_i / \sum S_{ii}) \times 100 \quad (7)$$

where  $N_i$  is the number of predators with prey type  $i$  in their stomach,  $N$  is the total number of predators with food in stomach,  $S_i$  is the stomach content comprised of prey type  $i$  (in number, weight or volume), and  $S_{ii}$  is the total stomach content in only those

predators with prey type *i* in their stomach. Only unidentifiable digested food items were excluded from the analysis.

## Results

### *Intraspecific niche measures*

*B. gonionotus*: Both sizes consumed relatively large amounts of macrophytes, 0.39 (proportion as fraction of 1.0) in small fish and 0.23 in large fish (Table 1). Zooplankton were more important to small than to large fish (0.26 vs. 0.02), as were insects (0.09 vs. 0.05). Of the microalgae, *Spirogyra* and *Oedogonium* (both filamentous green algae) were consumed in large amounts by small fish (>0.25). Large fish consumed only *Spirogyra* and *Cladophora* in small amounts. *Cypris* of the ostracods were consumed by both sizes. Molluscs were found only in the gut of large fish (0.60) as small bits of shell and muscle rather than the whole animal (Table 1).

**Table 1.** Resource availability and use by two sizes of *Barbodes gonionotus* (4.5-5.52 cm and 11.54-13.4 cm TL) during 26-28 April 1994, two sizes of *Oreochromis* spp. (4.9-8.0 cm and 10.3-13.8 cm TL) during 19-21 July 1995, and by a single size category of both *B. gonionotus* (5.1-10.1 cm TL) and *Oreochromis* spp. (7.5-10.2 cm TL) during 19-20 September 1995, in a ricefield from Bangladesh. (Unid.= unidentified; empty guts or stomachs were not included in the calculation)

Resource category	Intraspecific				Interspecific				
	Fraction available	<i>B. gonionotus</i> Fraction used by small <sup>1</sup> large <sup>2</sup>		Fraction available	<i>Oreochromis</i> spp. Fraction used by small <sup>3</sup> large <sup>4</sup>		Fraction available	Fraction used by <i>B. gon</i> <sup>5</sup> <i>O. sp.</i> <sup>6</sup>	
<b>Chlorophyceae</b>									
<i>Ankistrodesmus</i>			0.0487						
<i>Closterium</i>	0.0024	0.0007		0.0012		0.0144	0.0003	0.0044	
<i>Pleurotaenium</i>	0.0045	0.0008				0.0348	0.0028		
<i>Pediastrum</i>	0.0041		0.0084		0.0002				
<i>Scenedesmus</i>	0.2305		0.0374	0.0001					
<i>Sphaerocystis</i>	0.2461								
<i>Volvox</i>						0.1208	0.13	0.0029	
<i>Oedogonium</i>	0.0021	0.1295							
<i>Ulothrix</i>	0.001								
<i>Spirogyra</i>	0.0045	0.1261	0.0184	0.0014					
<i>Cladophora</i>		0.0063	0.0208						
<i>Pithophora</i>				0.0345					
<i>Rhizoclonium</i>				0.0721	0.0003		0.0032		
<b>Cyanophyceae</b>									
<i>Anabaena</i>			0.0026	0.0005	0.1084	0.0208			
<i>Merismopedia</i>	0.193		0.1464						

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<b>Bacillariophyceae</b>									
<i>Coscinodiscus</i>	0.0019								
<i>Cyclotella</i>	0.0079								
<i>Gomphonema</i>	0.0005								
<i>Melosira</i>				0.0185	0.0019	0.0012			
<i>Surirella</i>	0.001								
<i>Synedra</i>	0.001								
<b>Euglenophyceae</b>									
<i>Phacus</i>	0.004			0.0037					
Unid.		0.392	0.227				0.2845	0.0049	
Macrophytes									
<b>Ciliata</b>									
<i>Vorticella</i>	0.0001								
<b>Rotifera</b>									
<i>Brachionus</i>							0.0074	0.0004	0.0012
<i>Euchlanis</i>	0.001								
<i>Keratella</i>				0.0037					
<i>Lecene</i>	0.0002	0.0011					0.0078		
<i>Monostyla</i>	0.002								
<i>Platyias</i>							0.1005		
<i>Polyarthra</i>	0.0033			0.0156			0.0639		
<b>Crustacea</b>									
<i>Alona</i>				0.0089					
<i>Bosmina</i>				0.0031	0.0033				
<i>Cyclops</i>	0.1350	0.236	0.0181	0.0344	0.0005		0.1011	0.0371	
<i>Daphnia</i>				0.00778	0.0002				
<i>Diaptomus</i>	0.0180	0.0069	0.0045	0.4292			0.1527		
<i>Diphanosoma</i>				0.0057			0.0066		
<i>Moina</i>	0.0052	0.0054		0.0052	0.0007		0.0139	0.0111	
<i>Polyphemus</i>	0.0026						0.0420	0.0017	
Unid. egg					0.0069				
Unid. nauplii	0.1272	0.0067		0.205	0.0082	0.0047	0.2136	0.0127	0.0041
Unid. <i>Mysis</i> larv							0.0045		
<b>Ostracoda</b>									
<i>Cypris</i>	0.0001	0.0002		0.0157	0.0014	0.0012	0.0078	0.0238	0.0006
Unid. insects		0.0883	0.0568		0.0339		0.1222	0.0051	
remain									
Unid. molluscs			0.5977				0.0116		
remain									
Detrital aggrega					0.837	0.9917	0.3380	0.9768	
Silt and sand			0.0566						
Total	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

<sup>1</sup>n = 108, <sup>2</sup>n = 74, <sup>3</sup>n = 90, <sup>4</sup>n = 39, <sup>5</sup>n = 55 and <sup>6</sup>n = 35; only fishes with food in the stomachs were considered.

Dietary breadth values were a little wider in the small sizes ( $B = 3.99$ ,  $B_n = 0.12$ ) than the larger (Table 2). PS indices also reflect that both sizes of *B. gonionotus*. are using some

resource items exclusively, though small ones have relatively broader selection of prey items, about 5 times greater niche width ( $PS = 0.155$ ) than the larger ones (Table 2).

Intraspecific dietary overlap of large fish on small ( $\alpha_{yx} = 0.41$ ) was much greater than the reverse ( $\alpha_{xy} = 0.24$ ), but biologically insignificant in both ways. Schoener's index ( $\alpha = 0.33$ ) also supports this trend of biologically insignificant intraspecific dietary overlap (Table 2).

**Table 2.** Intraspecific virtual diet breadth and overlap indices\* of two sizes of *Barbodes gonionotus* (4.5-5.52 cm and 11.54-13.4 cm TL) during 26-28 April 1994 and two sizes of *Oreochromis* spp. (4.9-8.0 cm and 10.3-13.8 cm TL) during 19-21 July 1995 in a ricefield from Bangladesh ( $x$  = small size,  $y$  = large size;  $B_x$  and  $B_y$  = dietary breadths of  $x$  and  $y$ ;  $B_{nx}$  and  $B_{ny}$  = dietary breadths of  $x$  and  $y$ ;  $PS_x$  and  $PS_y$  = proportional similarity index of  $x$  and  $y$  respectively;  $\alpha_{xy}$  = overlap of  $x$  on  $y$ ,  $\alpha_{yx}$  = overlap of  $y$  on  $x$  and  $\alpha$  = Schoener's overlap index)

Fish species	Niche indices								
	Czekanowski's		Levin's				Schoener's		
	$PS_x$	$PS_y$	$B_x$	$B_y$	$B_{nx}$	$B_{ny}$	$\alpha_{xy}$	$\alpha_{yx}$	$\alpha$
<i>B. gonionotus</i>	0.155	0.03	3.99	3.37	0.12	0.07	0.24	0.41	0.33
<i>Oreochromis</i> spp	0.02	0.015	1.42	1.02	0.05	0.04	0.84	1.18	0.85

\* diet overlap values  $>0.60$  are shown in bold and are considered to be biologically significant, Zaret and Rand 1971.

*Oreochromis* spp.: Both sizes of tilapia fed mainly on the periphytic detrital aggregate (PDA), 0.84 in small and 0.99 in large (Table 1) and showed an overall avoidance for zooplankton, microalgae and consumed no aquatic macrophytes. Of the zooplankton, small fish preferred crustacean eggs and nauplii, and randomly consumed *Bosmina*. Large fish avoided all adult crustaceans and their eggs but consumed a few nauplii. Rotifers were avoided by both sizes while *Cypris* of ostracods were consumed by both sizes. Insects were consumed (0.03) by the small fish only (Table 1).

Niche width values were marginally broader in the small fish ( $B = 1.42$ ,  $B_n = 0.05$ ) than in the large fish ( $B = 1.02$ ,  $B_n = 0.04$ ) (Table 2). Czekanowski's PS indices also confirm this trend of dependence on single or few selective food items ( $PS = 0.02$  in the small,  $PS = 0.015$  in the large), discriminating others. Dietary breadth of *Oreochromis* spp. is relatively narrower than that of *B. gonionotus*.

Dietary overlap indices revealed that both sizes of tilapia had biologically significant intraspecific overlap ( $\alpha_{xy} = 0.84$ ,  $\alpha_{yx} = 1.18$ ) to each other, exclusively for the PDA. The overlap strength of large sizes on the smalls was about 1.4 times greater than the reverse. Schoener's index ( $\alpha = 0.85$ ) also revealed biologically significant intraspecific dietary overlap between the sizes (Table 2).

### Interspecific niche measures

*B. gonionotus* fed on the PDA but in lesser proportion (0.34) than the *Oreochromis* spp. as well as feeding on aquatic macrophytes (0.28), *Volvox* (0.13) of the green algae and insects (0.12). *Oreochromis* spp. fed exclusively on the PDA (0.98) avoiding blue-green algae, most of the green algae, adult crustaceans and molluscs (Table 1).



Interspecific dietary width (Table 3) was little higher for *B. gonionotus* ( $B= 4.35$ ,  $B_n= 0.21$  and  $PS= 0.21$ ) than *Oreochromis* spp. ( $B= 1.05$ ,  $B_n= 0.05$  and  $PS= 0.02$ ). *Oreochromis* spp. display exclusive specialization for PDA while *B. gonionotus* have many alternative preferences in addition to PDA.

**Table 3.** Interspecific virtual diet breadth and overlap indices\* of a single size category of both *Barbodes gonionotus* (5.1-10.1 cm TL) and *Oreochromis* spp. (7.5-10.2 cm TL) during 19-20 September 1995, in a ricefield from Bangladesh ( $x = B. gonionotus$  and  $y = Oreochromis$  spp)

Fish species	Niche indices					
	Czekanowski's		Levin's			Schoene
	PS	B	$B_n$	$\alpha_{xy}$	$\alpha_{yx}$	$\alpha$
<i>B. gonionotus</i>	0.21	4.35	0.21	1.46		0.36
<i>Oreochromis</i> spp.	0.02	1.05	0.05		0.35	

\* diet overlap values  $>0.60$  are shown in bold and are considered to be biologically significant, Zaret and Rand 1971.

Interspecific dietary overlap of *B. gonionotus* on *Oreochromis* spp. ( $\alpha_{xy}= 1.46$ ) was more than 4 times greater and biologically significant than the reverse ( $\alpha_{yx}= 0.35$ ). Schoener's index ( $\alpha= 0.36$ ) indicated that the interspecific dietary overlap between this size range of *B. gonionotus* and *Oreochromis* spp. was biologically insignificant (Table 3).

#### *Intraspecific feeding strategy*

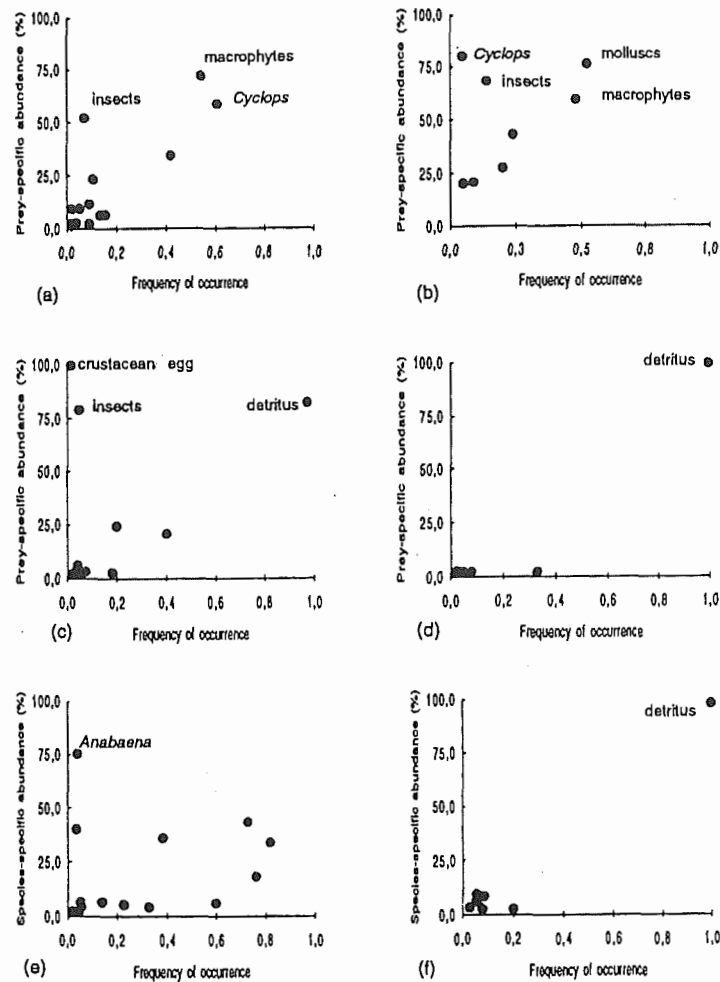
Most of the small individuals of *B. gonionotus* consumed moderately dominant food items, occasionally including items with low specific abundance and low occurrence reflecting mixed feeding strategy. Nonetheless, some individuals showed moderate specialization (individual level) for aquatic insects while others showed moderate population specialization for aquatic macrophytes and *Cyclops* of the crustaceans (Fig. 1a). Most of the large individuals of *B. gonionotus* consumed dominant food items as well as rare food items have been consumed occasionally by some individuals (Fig. 1b). However, some large ones showed individual specialization on *Cyclops* (crustaceans) and aquatic insects while others showed population specialization for molluscs and aquatic macrophytes.

All small *Oreochromis* spp. had been feeding on PDA, but small proportions of other food types were also included occasionally. A few showed individual specialization on certain food items like, crustacean eggs and aquatic insects (Fig. 1c). Similarly, all large *Oreochromis* spp. were found feeding on PDA but small proportions of other food items were also consumed occasionally by some individuals (Fig. 1d).

#### *Interspecific feeding strategy*

In case of *B. gonionotus* (interspecific study) most of the prey were of rare occurrences (Fig. 1e). The most important food items were consumed by more than half of the fish, but their average contribution to the gut contents of these fishes was low. In addition,

some individuals showed specialization for *Anabaena*, a blue-green algae (Fig. 1e). In contrast, *Oreochromis* spp. was found feeding exclusively on PDA but a few individuals also consumed other food items in small proportions (Fig. 1f).



**Fig.1.** The feeding strategy diagram: prey-specific abundance plotted against frequency of occurrence of different food items in the diet of two sizes of *Barbodes gonionotus* (4.5-5.52 and 11.54-13.4 cm TL) during 26-28 April 1994, two sizes of *Oreochromis* spp. (4.9-8.0 and 10.3-13.8 cm TL) during 19-21 July 1995, and by a single size category of both *B. gonionotus* (5.1-10.1 cm TL) and *Oreochromis* spp. (7.5-10.2 cm TL) during 19-20 September 1995, in a ricefield from Bangladesh (Amundsen *et al.*'s 1996 modified approach to Costello's 1990 method). (a) *B. gonionotus*, 4.5-5.52 cm TL ( $n = 108$ ); (b) *B. gonionotus*, 11.54-13.4 cm TL ( $n = 42$ ); (c) *Oreochromis* spp., 4.9-8.0 cm TL ( $n = 90$ ); (d) *Oreochromis* spp., 10.3-13.4 cm TL ( $n = 39$ ); (e) *B. gonionotus*, 5.1-10.1 cm TL ( $n = 55$ ) and (f) *Oreochromis* spp., 7.5-10.2 cm TL ( $n = 35$ ). The black dots represent different food items (only the important items are labeled on the figures).

### Discussion

The small size groups of both species had a wider dietary niche than the large individuals. Large fish increased their specialization on certain food items (on aquatic macrophytes by *B. gonionotus* and on PDA by *Oreochromis* spp.) and narrowed down their niche width with increasing size and competitive ability (Haroon and Pittman 1997,

1998a and 1998b). The interspecific dietary niche was wider for the silver barbs than the tilapias, indicating greater specialization and less pronounced ontogenetic dietary shifts in tilapia.

Insignificant intraspecific dietary overlap between the two sizes of barbs reflects a resource partitioning according to size or ontogenetic shift in diet. Resource partitioning may also occur in time, since small barbs are feeding most actively around midday while large barbs are more active near dusk and after dawn (Haroon and Pittman 1997). By contrast, both sizes of tilapia display peak feeding activity around midday (Haroon and Pittman 1998a), suggesting that temporal, spatial and habitat overlap will affect the resource utilization and the growth of tilapia in mixed-size rearing.

There was neither a high within-phenotype (generalization) nor high between-phenotype (specialization) contribution to the niche width for the silver barbs. Small silver barbs showed a mixed feeding strategy, with varying degrees of specialization and generalization for different food items. The population of silver barbs indicated specialization for certain food items and the dietary width was relatively narrow ( $PS = 0.16$ ). Large silver barbs also showed a mixed feeding strategy with some individuals specializing on certain food types and a population specialization on other food types, and the niche width was narrower than that of small ( $PS = 0.03$ ). When reared with tilapia, the silver barb showed a relatively high within-phenotype contribution to the increased niche width ( $PS = 0.21$ ), indicating more generalized feeding strategy.

Small tilapia demonstrated individual specialization for crustacean eggs and aquatic insects in addition to population specialization for PDA, giving a narrow niche breadth ( $PS = 0.02$ ). At the population level, large tilapia specialized exclusively on PDA and hence the niche width was narrowest ( $PS = 0.015$ ). When reared with barbs, tilapia displayed a similar feeding strategy and narrow niche breadth.

Our results suggest that an ontogenetic shift in diet occurs more strongly in silver barb (Haroon and Pittman 1997) than in tilapia (Haroon and Pittman 1998a). The various sizes of a single species may occupy several trophic units depending on their ontogenetic progression in diet (Eggold and Motta 1992), suggesting that optimal stocking strategies for *B. gonionotus* should consider a changing resource utilization with the aging of the stock.

$B_n$  is more useful than  $B$  as the former incorporates the number of food categories available while the latter does not. The use of Czekanowski's  $PS$  reveals more information about the ecological determinants of dietary breadth as it simultaneously incorporates the availability and use of the particular resource category. For example, the values of 0.16 and 0.03 for  $PS$  indices of small and large silver barb respectively, 0.02 and 0.015 for  $PS$  indices of small and large tilapia respectively and 0.21 and 0.02 for  $PS$  indices of silver barb and tilapia respectively are easily interpreted - of all the food categories available  $1/6.45$  (0.16) and  $1/33.3$  (0.03) part of foods were obtained respectively by the small and large silver barb, while  $1/50$  (0.02) and  $1/66.7$  (0.015) part of foods were obtained respectively by the small and large tilapia. Similarly,  $1/4.8$  (0.21) and  $1/50$  (0.02) part of the food items were obtained by the silver barb and tilapia, respectively.

PS measures most accurately the actual area of intersection between two frequency distributions and is therefore more robust than Levin's  $B$  or  $B_n$  and Ivlev's (1961) electivity indices. It has often been used to measure niche overlap (Colwell and Futuyma 1971). Feinsinger *et al.* (1981) concluded that PS is more appropriate than Schoener's (1970) index for measuring the degree to which an animal's diet is specialized for testing hypotheses on foraging tactics. PS values will either change as the resource spectrum changes if the particular species or size being considered discriminates against resource items in other categories, or maintain a similar value if the same selectivity over time is found regardless of changes in resource states (Hurlbert 1978, Petraitis 1979, Feinsinger *et al.* 1981). Another consideration is that, niche breadth measures the variability in resource use while the conceptual basis for variation in niche breadth is resource selectivity by the individuals (Petraitis 1979).

In investigating the available resources, we sampled only plankton, which contained mostly minute forms. Had we taken benthos and macrovegetation into account, the dietary breadth indices with PS would have been more robust and different. However, because of the use of absolute differences between the resource use and availability in Equations 3a and 3b, there is a PS value for a certain resource item even though that particular food item was not ingested by the species or sizes concerned.

The interspecific dietary overlap between the silver barb and the tilapia was biologically insignificant with Schoener's index. However, Levin's overlap indices revealed that the dietary overlap of the silver barb on the tilapia is much greater and biologically significant while the reverse is not significant. Here lies the significance in the use of Levin's dietary overlap indices over the Schoener's.

For future work on niche measures, the appropriate index would seem to be Czekanowski's PS (Eqns. 3a and 3b) for the niche breadth and Levin's  $\alpha_{xy}$  (Eq. 4a) and  $\alpha_{yx}$  (Eq. 4b) for the niche overlaps. Although Schoener's index is widely used, we agree with Wallace (1981) and Martin (1984) that it is the least objectionable of the indices only when resource availability data are not present.

In general, an observed biologically significant dietary overlap ( $>0.60$ ) is considered indicative of competition, which may not always be the case. The existence and intensity of competition can only be ascertained by comparing actual to virtual dietary overlap of the competitors. The existence of competition would be certain if virtual overlap exceeds the actual overlap value (Colwell and Futuyma 1971). Niche breadth and overlap, when measured under natural conditions, are called 'actual' metrics, while 'virtual' niche breadth and overlap are the corresponding values measured in the absence of competition among species. It is the condition under which data are collected, rather than the method of calculation. Hence, our metrics are virtual niche measurements as we exploited natural conditions as closely as possible in the absence of other competitors. Such clarification between actual and virtual measurements is essential when expressing niche overlap, which by any means is a measure of competition.

In the present study resource availability and use estimated by counting discrete individuals seemed adequate. Discrete counts are more apt to explain the degree of discrimination than are values calculated from energy contents of items (Feinsinger *et al.* 1981, Wallace 1981, Martin 1984). However, these measurements are vulnerable to bias due to patchiness of the plankton and to digestion rates of particular items (Strauss 1979).

As our present study on the two sizes of *B. gonionotus*, two sizes of *Oreochromis* spp. and between *B. gonionotus* and *Oreochromis* spp. were separately done these indices are not directly comparable towards either small sizes of *B. gonionotus* versus small or large sizes of *Oreochromis* spp. or large sizes of *B. gonionotus* versus small or large sizes of *Oreochromis* spp. However, interspecific niche measures estimated with a single median size range of *B. gonionotus* and *Oreochromis* spp., as shown in Table 3, gives an indication of what degree of overlap may be expected.

Significant interspecific dietary overlap of silver barb on tilapia cautions for mixed-species stocking in the same system. It seems that there are less opportunities for habitat segregation between the *B. gonionotus* and *Oreochromis* spp. when stocked together in a rice-fish system. Haroon and Alam (1992) reported poor yield of tilapia with mixed-stock of silver barb and tilapia in concurrent rice-fish culture in Bangladesh. Mixed rearing of barbs and tilapia in the same habitat will likely result in a suppression of the growth of tilapia, due to their high degree of specialization on items with low nutrient value and their dietary overlap with barbs which have a broader niche width.

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