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Intraspecific Dietary Breadth, Overlap Indices and Feeding Strategies of *Puntius gonionotus* Bleeker and *Oreochromis* spp. in a shallow pond from Bangladesh

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Abstract

Intraspecific virtual dietary breadth, degree of diet similarity, dietary overlap and feeding strategies of the silver barb *Puntius gonionotus* and the tilapia *Oreochromis* spp. were estimated in a pond from Bangladesh and compared using various niche indices. Appropri-ateness, ease of interpretation and explanation of different indices were evaluated. Dietary breadths were relatively higher in small sizes of *P. gonionotus* than large ones, though neither size class could be considered as a generalist feeder. There was a significant di-etary overlap between large and small barbs. Niche breadths were similar for both sizes of *Oreochromis* spp., a little higher for the small sizes, although as with the barbs, neither size class could be considered as a generalistic feeder. Dietary overlap of large tilapia on small ones was much greater but significant in both ways. Czekanowskis′ Proportional Similarity (PS) index reveals a much broader aspect of the ecological determinants of niche breadth as it incorporates resource availability and resource use and has got the ease of biological interpretation. Similarly, Levins′ dietary overlap indices reveal clearly both the significance, strength and direction of dietary overlap between competitors. According to the PS index, both species are opportunistic feeders, although tilapias are relatively more generalist than the silver barbs. Evidence of significant dietary overlap between the large and small sizes of both species reflects strong competition and indicates caution for mixed-size stocking of tilapia in pond polyculture. Feeding pattern of silver barb reflected a mixed strategy with a combination of both high between- and within-phenotype contributions to the niche width, but with the between-phenotype contribution as the largest. While tila-pias reflected high within-phenotype contributions to the niche width, a generalized feed-ing strategy showed a trend of specialization of a population for periphytic food.

Introduction

The spectrum of prey items consumed by the different life stages of fish species in a particular environment helps to define the ecological niches and interactions with cohabiting species and sizes (Cortes and Gruber 1992; Knight and Ross 1994). Interspecific niche overlap among fishes is usually low (Keast 1978a, 1985; Pen *et al.* 1993) due to differences in foraging habit and the morphology of feeding apparatus, although considerable dietary overlap occurs when a preferred food item is abundant (Keast 1977; Pen *et al.* 1993). Although fish may broaden their dietary breadth when food resources are scarce, it may still remain sufficiently partitioned for competition to be avoided (Keast and Fox 1990). In general, intraspecific niche overlap among different size classes decreases with ontogenetic shift in diets, i.e. differences in habitat utilization by young and adults, and increasing disparity in size (Keast 1977; Pen *et al.* 1993; Esteves and Galetti 1995). Understanding of spatial and temporal variation in the performance of individual fish is essential for studies of habitat profitability for fishes (Easton *et al.* 1996). This also depends on the spatial and temporal heterogeneity of the habitats.

The silver barb or tawes, *Puntius gonionotus* Bleeker (formerly *P. javanicus*) and the tilapias [*Oreochromis mossambicus* (Peters) and *O. niloticus* (Linnaeus)] are exotic to Bangladesh and are very popular because of their rapid growth performance in comparison to the indigenous carps (Rahman 1989). However, under stress of polyculture, these species often do not maintain their usual feeding habits (Sandhu and Toor 1983). Haroon and Pittman (1997, 1998) studied the feeding chronology (pattern), daily ration and gastric evacuation rates of *P. gonionotus* and *Oreochromis* spp. in rice-fish and pond culture. The only available report on the interspecific dietary overlap of Chinese and Indian major carps in pond polyculture from Bangladesh is of Dewan *et al.* (1991).

The present study was undertaken to estimate and compare the intraspecific dietary breadth of two sizes of *P. gonionotus* and *Oreochromis* spp. [*O. mossambicus* x *O. niloticus* natural hybrid] as well as the degree of diet similarity, overlap and feeding strategies in relation to niche width in a shallow, seasonal pond condition. Different niche measures are compared and evaluated for appropriateness, ease of biologically significant interpretation and explanation of different indices.

Materials and methods

The present work was carried out in a nursery pond at the Riverine Station, Chandpur, of the Fisheries Research Institute, Bangladesh, during 8-10 May 1994 using two size categories (around 6 and 12 cm, total length) of *P. gonionotus* and during 13-15 July 1995 with two size categories (same as above) of *Oreochromis* spp. We have chosen these two sizes because fish farmers look first for (the fish) size rather than weight when choosing for culture. The fish and sub-surface plankton were sampled every three hours for a further 48 h to analyze gut contents and available resource states in the plankton, respectively.

Pond preparation, fish stocking and sampling

1994: The pond was a nursery type about 1620 m^2 in size (water area 980 m^2), 1.85 m in depth, kept weed-free for easy netting. The pond was prepared in March 1994 by completely drying, liming (250.0 $kg \cdot ha^{-1}$) and fertilizing once (cow-dung 10.0 $t \cdot ha^{-1}$, urea 16.0 $kg \cdot ha^{-1}$ and triple super phosphate 32.0

kg•ha^{-1}). Two size categories of *P. gonionotus* juveniles procured from the Riverine Station's hatchery were stocked in the experimental pond at a density of 7.0 juveniles •m^{-2} (3430 numbers of each size). Before stocking in the experimental pond, the fishes were kept in a flow-through system for 48 h with flowing tap water to completely empty their guts. Prior to the experiment, the fish had been fed a supplemental feed composed of rice bran (40%), wheat bran (40%) and fish meal (20%) at 2-5% of body weight (bw)•day^{-1}. Two days after stocking, 10 fishes of each size were sampled every 3 h for a further 48 h with cast net (3x6 m, mesh 0.5 cm). The small fishes were 5.0-6.9 cm in total length (TL) and 2.4-5.6 g in weight and the large fishes were 12.0-13.6 cm in TL and 26.6-40.8 g in weight at stocking. A total of 320 fishes (160 of each size) were sampled.

1995: For experiments with tilapia, the same pond (water area was 990 m^2 this year) was prepared in June 1995 in the same manner as before. Two sizes of *Oreochromis* spp. juveniles collected from the Riverine Station's other ponds were stocked in the experimental pond at a density of 7.0 juveniles•m^{-2} (3465 numbers of each size). Before stocking in the experimental pond, the fish were similarly pre-treated for 48 h to completely empty their stomachs. Prior to stocking in the pond, the fish were fed a similar supplemental feed at the similar rates. Two days after stocking, a similar sampling regime was followed every 3 h for a further 48 h. The small fishes were 4.3-9.3 cm in TL and 1.60-15.46 g in weight and the large fishes were 9.5-13.5 cm in TL and 14.37-46.42 g in weight at stocking. A total of 320 fishes (160 of each size) were collected.

Gut analysis

Fishes were checked immediately after capture for regurgitation (if positive, the fish was replaced), and preserved in 10% buffered formalin until examined. Each fish was measured for TL (mm), and weighed using a Sartorius electronic balance (± 0.001 g) within two weeks after collection and no correction factor for fixation was used.

As *P. 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 as digestion is less advanced in the anterior portion and food items remain mostly identifiable. Silver barbs 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. Tilapia are reported to have a relatively long and coiled intestine up to 14 times their body length (Edwards 1987). Bowen (1981) reported that in *O. mossambicus* food digestion and assimilation is completed in the first half of the intestine. Similar methods have also been adopted by McComish (1967), and Minckley *et al.* (1970) for buffalo fish; Dewan *et al.* (1991) for carps and Dewan and Saha (1979) for tilapia.

Each gut or stomach was blotted uniformly with tissue paper, opened longitudinally and entire gut or stomach contents were then carefully transferred to a petri dish or vial with the standard 10 ml of distilled water. Food items of animal origin were usually counted under a stereo dissecting microscope (Wild Herbrugg), 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^3, 50x20x1 mm) and 100 out of 1000 randomly chosen cells were counted under an inverted microscope (Olympus CK2). Three such sub-samples were enumerated per fish. All organisms were identified to the genus level and percentage composition by number (the percentage of abundance) was used for calculating the proportion of each food item in the gut or stomach (Windell and Bowen 1978; Bowen 1983). Fishes with food in their gut or stomach were only considered for calculation of the proportion of each food item.

Plankton

Five 1-l samples of surface to sub-surface water (0.02 m) were taken from three areas of the pond (near the bank, middle and other side of the pond), every three hours prior to fish sampling, filtered through a 15 m mesh plankton net, carefully 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 enumerated from each plankton sample and the mean numbers $\cdot l^{-1}$ determined. Identification and calculation of the proportion (relative abundance) 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 indices, B and B_n (Hurlbert 1978; Keast 1978b; Easton *et al.* 1996).

$$B_x = 1/\Sigma\,(p_{xi}^{\,2}) \tag{1a}$$

$$B_y = 1/\Sigma\,(p_{yi}^{\,2}) \tag{1b}$$

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

$$B_{nx} = 1/[R\Sigma\, p_{xi}^{\,2}] \tag{2a}$$

$$B_{ny} = 1/[R\Sigma\, p_{yi}^{\,2}] \tag{2b}$$

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

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

$$PS_x = 1\text{-}0.5\ \Sigma\ |p_{xi} - q_i| \qquad (3a)$$

$$PS_y = 1\text{-}0.5\ \Sigma\ |p_{yi} - q_i| \qquad (3b)$$

where p_{xi} and $p_{yi,}$ respectively, are the proportion of resource items in category i out of all items used by the x or y, and q_i is the proportion of i items in the resource base available to the population. Values for *PS* range 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 α_{xy}, α_{yx} (after Keast 1978b; Wallace 1981) and Schoener's α (Schoener 1970; Colwell and Futuyma 1971; Hurlbert 1978; Wallace 1981). These are as follows:

The Levin's overlap indices are represented by α_{xy} (overlap of x on y) and α_{yx} (overlap of y on x).

$$\alpha_{xy} = \Sigma(p_{xi} . p_{yi}) / \Sigma\ p_{yi}^2 \qquad (4a)$$

$$\alpha_{yx} = \Sigma(p_{xi} . p_{yi}) / \Sigma\ p_{xi}^2 \qquad (4b)$$

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

Schoener's overlap (1970) index is denoted by α.

$$\alpha = 1\text{-}0.5\ (\Sigma\ |p_{xi} - p_{yi}|) \qquad (5)$$

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

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 (Colwell and Futuyma 1971). These are the conditions under which data are collected, rather than the method of calculation. Hence, we refer to the indices used in this study as 'virtual niche' measurements as we exploited the natural condition as close as possible and 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.

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 regarding values for dietary overlap indices above the arbitrary level of 0.60 as representing a biologically significant overlap.

Feeding strategy

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

$$F_i = (N_i / N) \text{ and} \qquad (6)$$

$$\%P_i = (\Sigma S_i / \Sigma S_{ti}) \times 100 \qquad (7)$$

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) and S_{ti} is the total stomach content in only those predators with prey type i in their stomach. Unidentifiable digested food were excluded from the analysis.

Results

Niche measures

P. gonionotus: Both sizes consumed quite large amounts of macrophytes (0.351 in small vs. 0.513 in large; fraction of total items used). There were distinct differences in feeding on zooplankton by the two sizes. Small fish ate *Brachionus* and *Monostyla* of the rotifers, *Cyclops*, *Moina*, *Diaptomus* and some crustacean nauplii whereas large fish avoided rotifers and crustacean nauplii. Large fish did consume *Cyclops* (0.26), *Moina*, and *Diaptomus* and only the large sizes consumed *Cypris* (ostracod). Insects were a larger component of the diet for small fish (0.10) compared to the larger fish. Both sizes avoided most of the phytoplankton, except *Microcystis* (blue-green algae) which was consumed in much greater proportions by the small fish (0.33) than by the large fish. Silt and sand was a larger proportion of the gut content of larger fish (Table 1).

Dietary breadth (both B and B_n) values were higher in small sizes than in the large representatives. Czekanowski's PS index also reflected that small fishes are apt to use a broader range of the available resources (though not by comparison with the proportion of resource abundance). On the other hand, large fish discriminated against several food categories but chose ostracods, thus making use of a relatively narrower niche than the small size class (Table 2). Numerically small fish have about 4 times greater PS value or 1.3

Table 1. Resource category availability and use by two sizes of *Puntius gonionotus* during 8-10 May 1994 and two sizes of *Oreochromis* spp. during 13-15 July 1995, from a nursery pond in Bangladesh. (Unid.= unidentified, rem.= remains; empty guts or stomachs were not included in calculation).

Resource category	Fraction available	*Puntius gonionotus* Fraction used by		Fraction available	*Oreochromis* spp. Fraction used by	
		small[1]	large[2]		small[3]	large[4]
Green algae						
Ankistrodesmus				0.069	0.0367	0.0261
Closterium					0.0006	0.0001
Cosmarium						0.0006
Dictyosphaerium					0.0058	
Pediastrum	0.0072			0.0671	0.079	0.0774
Scenedesmus	0.0155			0.0702	0.0147	0.0155
Selenestrum				0.0003		
Sphaerocystis	0.0026					
Spirogyra				0.0005		
Blue-green algae						
Anabaena	0.434			0.0661	0.5123	0.4511
Coelosphaerium	0.001					
Gloeocapsa	0.002					
Merismopedia				0.1441	0.0255	0.0016
Microcystis	0.4497	0.331	0.0815			
Oscillatoria	0.018					0.0001
Spirulina	0.0026					
Diatoms						
Asterionella					0.0021	
Melosira				0.5542	0.2842	0.3989
Euglenoid						
Euglena	0.0001				0.0025	0.0001
Phacus				0.0002	0.0008	0.0033
Unid. macrophytes	0.351	0.5134			0.0009	
Rhizopods						
Diffulgia					0.012	
Rotifera						
Brachionus	0.0274	0.081		0.0113	0.0088	0.0109
Filinia	0.0275			0.0003	0.0038	0.0024
Keratella	0.001			0.0043	0.0093	0.0088
Monostyla		0.0008				
Polyarthra				0.0011	0.0002	0.0001
Trichocerca				0.0004	0.0003	
Crustacea						
Cyclops	0.0026	0.0631	0.264	0.0023	0.0001	0.0001
Diaptomus	0.0032	0.0026	0.01			
Diphanosoma				0.0006		
Moina	0.0024	0.015	0.014			0.0001
Unid. nauplii	0.0038	0.0003		0.0083	0.0012	0.0019
Unid. Mysis larvae						
Ostracods						
Cypris			0.0012			
Unid. insect rem.		0.10	0.0217			
Silt and sand		0.056	0.0971			
Total	1.0	1.0	1.0	1.0	1.0	1.0

[1] n= 126, [2] n= 54, [3] n= 149 and [4] n= 109 fishes with food in the stomach.

Table 2. Intraspecific virtual dietary breadth and overlap indices* of two size categories of *Puntius gonionotus* (8-10 May, 1994) and *Oreochromis spp.* (13-15 July, 1995) in a shallow nursery pond from Bangladesh. (x= small, y= large; B_x and B_y= Levin's dietary breadths of x and y ; B_{nx} and B_{ny} = Levin's dietary breadths of x and y ; PS_x and PS_y= Czekanowski's Proportional Similarity of x and y, respectively; α_{xy} = Levin's dietary overlap of x on y, α_{yx}= Levin's dietary overlap of y on x and α= Schoener's dietary overlap index. For definition of various indices, see text.

Niche indices	Czekanowski's		Levin's				Schoener's		
Fish species	PS_x	PS_y	B_x	B_y	B_{nx}	B_{ny}	α_{xy}	α_{yx}	α
Puntius gonionotus	0.37	0.09	3.85	2.86	0.17	0.12	0.66*	0.89*	0.59
Oreochromis spp.	0.52	0.59	2.86	2.69	0.11	0.10	0.95*	1.01	0.86*

*diet overlap values >0.60 are considered to be biologically significant.

times greater B or B_n value than the large fish (Table 2). B, B_n and PS indices all reflect that both sizes of *P. gonionotus* are emphasizing some particular resource items, though small ones have a relatively greater capability to exploit resources. They are not generalistic feeders in that they do not utilize all resource states without preferences.

Overall dietary overlap of large fishes on the small ones (α_{yx}=0.89) were much greater than the reverse (α_{xy}=0.66), but were biologically significant in each case. Schoener's α index (0.59) also reflected this trend of biologically significant intraspecific overlap (Table 2).

Oreochromis spp.: Numerically, about half of the diet of both sizes of *Oreochromis spp.* consisted of *Anabaena* (blue-green algae) with lesser amounts of *Melosira* (diatom). *Microcystis* (blue-green algae) was avoideded though they were quite abundant, as was filamentous green algae. Some of the planktonic forms of green and blue-green algae were consumed by both sizes, of which *Pediastrum* and *Ankistrodesmus* (green algae) were consumed in relatively greater amounts than other plankton. Of the euglenoids, *Phacus* was consumed in greater amounts by the large fish than the small fish while *Euglena* was preferred more by the small than the large fishes. Macrophytes were incidentally consumed by large fishes only. Both sizes ate small amounts of rotifers and crustacean nauplii rather than adult crustacean. Both sizes avoided *Cypris* (ostracod), aquatic insects and silt and sand during feeding (Table 1).

Niche breadth, both B and B_n values, were almost similar (a little higher for the small) for both sizes (Table 2). PS indices yielded a similar trend in dietary breadth but indicated that large fish used more of the resource items than the small fish. Both Levin's and Czekanowski's indices reveal this trend of dependency on some selective resource items (higher specialization of both sizes for *Anabaena* and *Melosira*), discriminating against others of the resource spectrum. The principal interpretation here seems to be that, like *P. gonionotus*, both sizes of *Oreochromis* spp. have specialized feeding preferences. Dietary breadths of *Oreochromis* spp. may be relatively broader than the dietary breadth of *P. gonionotus*, although these comparisons are not valid since data were not taken from a single system at the same time (Table 2).

Dietary overlap indices α_{xy} and α_{yx} revealed that both sizes of *Oreochromis spp.* had biologically significant overlaps. The overlap strength of the large size on the small (α_{yx}) was about 1.06 times greater than the reverse (α_{xy}). Schoener's a index was 0.86, indicating biologically significant intraspecific dietary overlap between the sizes. Feeding competition between the sizes for the same resource item (e.g. *Anabaena* and *Melosira*, primarily occurring as periphytic epipelon, but later as plankton) seemed to significantly affect the selection of the resource. The dietary overlap of large size on the small depends mainly on the consumption of *Anabaena* and *Melosira*.

Feeding strategy

P. gonionotus: Feeding strategy of both sizes of *P. gonionotus* indicates specialization of individual fish on food items of high specific abundance and low occurrence (Figs. 1a and 1b). Here, most of the prey dots are on the left half of the graph with at least two dots on the upper left side, for aquatic macrophytes and *Brachionus* (rotifer) in case of small sizes, and for detritus, silt and sand in case of large sizes. Nonetheless, some important prey points are located below the diagonal from lower left to upper right.

Oreochromis spp.: Both small and large tilapia showed a generalistic feeding strategy (Figs. 1c and 1d). Here, food items with low to moderate specific abundance and frequency of occurrence have been consumed occasionally by most individuals (most dots on the lower part and right hand side of the graph). However, there seems to be an indication of population specialization for *Anabaena* (blue-green algae) and *Melosira* (diatom) [Fig. 1].

Discussion

The small sizes of both species were more active feeders, capable of using more of the resource categories and having broader niches than the larger fish. This reflects large sizes′ specialization on certain items with increasing size and competitive ability. Tilapias′ present feeding preferences were similar to the previous reports (Dewan and Saha 1979). Due to lack of any previous work, silver barbs′ feeding preferences could not be checked out. Colwell and Futuyma (1971) stated that minimum niche breadth refers to maximum specialization. Broader dietary breadth was recorded for smaller sizes of *Galaxis occidentalis*, *Bostockia porosa*, *Edelia vittata*, *Gambusia holbrooki*, and *Perca fluviatilis* than the larger sizes from an Australian river (Pen *et al.* 1993). Our results disagree with the observations of Esteves and Galetti (1995) that small fish would be forced to specialize on certain food items to assure their survival although the time factor involved may have affected habitat utilization. Nonetheless, our result indicate that the large sizes were already narrowing their prey selectivity, while the small ones were consuming a broader range of items. It must be noted that the present study is based on data of 48 h periods. As seasonality in food habits occur in fish (De Silva *et al.* 1980), results of the present study are valid only for the sampling period.

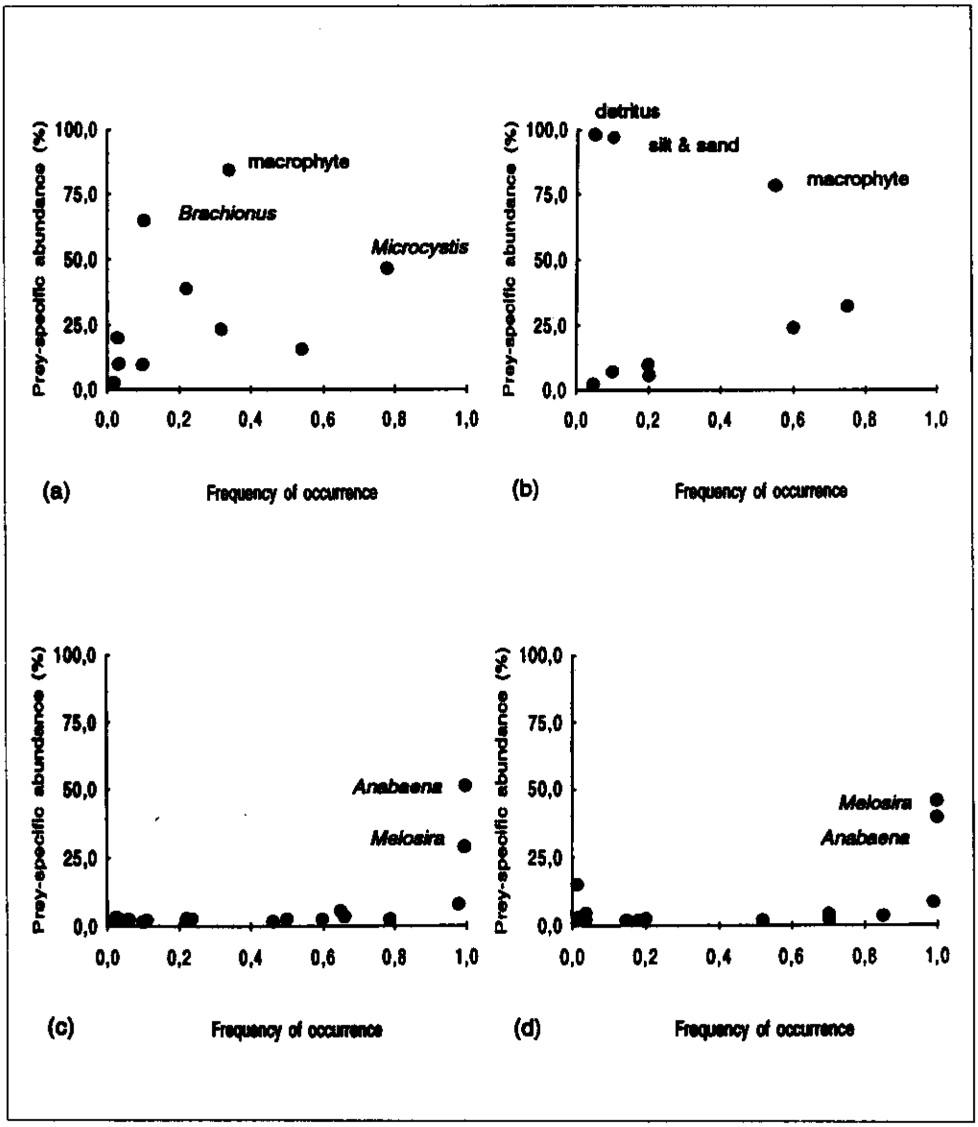

Fig. 1. The feeding strategy diagram: prey-specific abundance plotted against frequency of occurrence of different food items in the diet of two sizes of *Puntius gonionotus* (8-10 May 1994) and two sizes of *Oreochromis* spp. (13-15 Jul 1995) from a nursery pond in Bangladesh. (a) *P. gonionotus*, 5.0-6.9 cm (n=118); (b) *P. gonionotus*, 12.0-13.6 cm (n=40); (c) *Oreochromis* spp., 4.3-9.3 cm (n=149) and (d) *Oreochromis* spp., 9.5-13.5 cm (n=106). The points represent different food items (only the important items are labeled on the graph).

The high degree of intraspecific dietary overlap between small and large sizes of *P. gonionotus* and *Oreochromis* spp. may reflect concentration and competition for the same food. Similar intraspecific dietary overlaps were reported for *Astyanax bimaculatus, Moenkhausia intermedia* and *Cheirodon stenodon* in Brazilian rivers (Esteves and Galetti 1995). Groups of individuals from one or many species, when having 80% similarity in selection of food items, are clustered into an ontogenetic trophic unit and various sizes of one species may also occupy several trophic units depending on its ontogenetic progression in diet (Eggold and Motta 1992).

Use of B_n is more useful than B as the former incorporates the number of resource categories available while the latter does not. The use of Czekanowski's PS index reveals more about the ecological determinants of niche breadth as it simultaneously incorporates the availability and use of the particular resource category. For example, values of B and B_n for both sizes of *P. gonionotus* and *Oreochromis* spp. are not clearly interpretable in biological terms. The values of 0.37 and 0.09, respectively, for PS indices of small and large sizes of silver barbs, and 0.52 and 0.59, respectively, for PS indices of small and large sizes of tilpias are easily interpretable: of all the resource categories available, 1/2.7 (0.37) and 1/11 (0.09) were obtained by the small and large silver barbs, while 1/2 (0.52) and 1/1.7 (0.59) part of resources were obtained by the small and large tilapias. Hence, large tilapias have the broadest niche followed by small tilapias and small and large silver barbs.

However, we sampled only plankton, which contained mostly minute forms. Had we taken benthos and macrovegetation into the entire resource availability account, the dietary breadth indices with PS would have been different due to changes in the proportion of resource categories. However, because of the use of absolute differences between resource use and availability in Eqns. 3a and 3b, there will be a corresponding PS value for a certain resource item even though that particular food item was not ingested by the species or sizes concerned.

Until now, the principal means of comparing fishs′ diet with resource availability has been Ivlev's (1961) electivity index, which considers only one resource state at a time. It is reported to be significantly biased when the sizes of the prey samples from the fish gut or stomach and the habitat are unequal (Strauss 1979). PS measures most accurately the actual area of intersection between two frequency distributions and is therefore more robust than Levin's B, B_n and Ivlev's electivity indices. It is 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 and 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 species or size concerned shows the same selectivity over time regardless of changes in resource states (Hurlbert 1978; Petraitis 1979; Feinsinger *et al.* 1981). The constraint is that niche breadth is measured by looking into the variability in resource use while the conceptual basis for variation in niche breadth is resource selectivity by the individuals (Petraitis 1979).

For future work on niche measures, the appropriate index would thus seem to be Czekanowski's PS (Eq. 3a and 3b) for the niche breadth and Levin's α_{xy} (Eq. 4a) and α_{yx} (Eq. 4b) for the niche overlaps which define these metrics in the context of resource availability and use, and the overlap of resource utilization curve between the competitors, respectively. Although Schoener's index is widely used, we also agree with Wallace (1981) and Martin (1984) that it is the least controversial of the indices only when resource availability data are not present. Niche breadth and overlap in resource utilization is a relative measure, hence they depend on specific resource availability and how accurately an organism's power of discrimination is gauged (Petraitis 1979).

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).

As our present study on the two sizes of *P. gonionotus* and two sizes of *Oreochromis* spp. were separately done in two phases during different months in 1994 and 1995, respectively, we acknowledge these indices are not directly comparable towards either small sizes of *P. gonionotus* versus small or large sizes of *Oreochromis* spp. or large sizes of *P. gonionotus* versus small or large sizes of *Oreochromis* spp. We feel it necessary to study in the future the actual dietary breadth and overlap of these two exotic species from a single system under polyculture conditions for ascertaining their intra- and interspecific competition.

Feeding pattern of silver barb is indicative of a mixed strategy with a combination of both between- and within-phenotype contributions to the niche width, but with the between-phenotype contribution as the largest. This shows their individual specialization, not for the population, for certain food types. The feeding strategy of tilapia is indicative of high within-phenotype contributions to the niche width. In other words, most of the individuals have utilized many food types simultaneously, a generalized feeding strategy of the population. Yet, the tilapia population seem to have a trend of specialization for periphytic foods.

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References

Amundsen, P. -A., H. -M. Gabler and F. J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data - modification of the Costello (1990) method. Journal of Fish Biology 48:607-614.

Bowen, S. H. 1981. Digestion and assimilation of periphytic detrital aggregate by *Tilapia mossambica*. Transactions of the American Fisheries Society 110(2):239-245.

Bowen, S. H. 1983. Quantitative description of the diet. In: Fisheries techniques (eds. L. A. Nielsen and D. L. Johnson), pp. 325-336. American Fisheries Society, Bethesda.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Costello, M.J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. Journal of Fish Biology 36:261-263.

Cortes, E. and H. Gruber. 1992. Gastric evacuation in the young lemon shark, *Negaprion brevirostris*, under field conditions. Environmental Biology of Fishes 35:205-212.

De Silva, S.S. P.R.T Cumaranatunga and C.D. De Silva. 1980. Food, feeding ecology and morphological features associated with feeding of four co-occurring cyprinids (Pisces:Cyprinidae). Netherlands Journal of Zoology 30:54-73.

Dewan, S. and S. N. Saha. 1979. Food and feeding habits of *Tilapia nilotica* (L.) (Perciformes: Cichlidae). II. Diel and seasonal patterns of feeding. Bangladesh Journal of Zoology 7:75-80.

Dewan, S., M. A. Wahab, M. C. M. Beveridge, M. H. Rahman and B. K. Sarkar. 1991. Food selection, electivity and dietary overlap among planktivorous Chinese and Indian major carp fry and fingerlings grown in extensively managed rain-fed ponds in Bangladesh. Aquaculture and Fisheries Management 22:277-294.

Easton, R. S., D. J. Orth and J. R. Voshell Jr. 1996. Spatial and annual variation in the diets of juvenile smallmouth bass, *Micropterus dolomieu*. Environmental Biology of Fishes 46:383-392.

Edwards, P. 1987. Use of terrestrial vegetation and aquatic macrophytes in aquaculture. ICLARM Conference Proceedings 14. International Center for Living Aquatic Resources Management, Manila.

Eggold, B. T. and P. J. Motta. 1992. Ontogenetic dietary shifts and morphological correlates in striped mullet *Mugil cephalus*. Environmental Biology of Fishes 34: 139-158.

Esteves, K. E. and P. M. Galetti Jr. 1995. Food partitioning among some characids of a small Brazilian floodplain lake from the Parana river basin. Environmental Biology of Fishes 42:375-389.

Feinsinger, P., E. E. Spears and R. W. Poole. 1981. A simple measure of niche breadth. Ecology 62: 27-32.

Haroon, A. K. Y. and K. A. Pittman. 1997. Diel feeding pattern and ration of two sizes of silver barb, *Puntius gonionotus* Bleeker, in the nursery pond and paddy field. Aquaculture Research (accepted, January 1997).

Haroon, A. K. Y. and K. A. Pittman. 1998. Diel feeding pattern and ration of two sizes of tilapia, *Oreochromis* spp. in pond and paddy field. Asian Fisheries Science 10:281-301.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Ivlev, I. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA, 302 pp. (Transl. from Russian by D. Scott).

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environmental Biology of Fishes 2:53-70.

Keast, A. 1978a. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. nvironmental Biology of Fishes 3:7-31.

Keast, A. 1978b. Feeding interrelations between age-groups of pumpkinseed (*Lepomis gibbosus*) and comparisons with bluegill (*L. macrochirus*). Journal of the Fisheries Research Board of Canada 35:12-27.

Keast, A. 1985. Development of dietary specializations in a summer community of juvenile fishes. Environmental Biology of Fishes 13:211-224.

Keast, A. and M. G. Fox. 1990. Fish community structure, spatial distribution and feeding ecology in a beaver pond. Environmental Biology of Fishes 27:201-214.

Knight, J. G. and S. T. Ross. 1994. Feeding habits of the Bayou darter. Transactions of the American Fisheries Society 123:794-802.

Martin, F. D. 1984. Diet of four sympatric species of *Etheostoma* (Pisces:Percidae) from southern Indiana: interspecific and intraspecific multiple comparisons. Environmental Biology of Fishes 11:113-120.

McKomish, T. S. 1967. Food habits of big mouth buffalofish in Lewis and Clark lake and Missouri river. Transactions of the American Fisheries Society 96:70-74.

Minckley, W. L., J. E. Johnson, J. N. Rinne and S. E. Willoughby. 1970. foods of buffalofishes, Genus *Ictiobus*, in central Arizona reservoirs. Transactions of the American Fisheries Society 99:333-342.

Pen, L. J., I. C. Potter and M. C. Calver. 1993. Comparisons of the food niches of three native and two introduced fish species in an Australian river. Environmental Biology of Fishes 36:167-182.

Petraitis, P. S. 1979. Likelihood measures of niche breadth and overlap. Ecology 60:703-710.

Rahman, A. K. A. 1989. Freshwater fishes of Bangladesh. Zoological Society of Bangladesh. C/O. Department of Zoology, University of Dhaka, Bangladesh, 365 pp.

Sandhu, J. S. and H. S. Toor. 1983. Preliminary studies on dietary overlap of fishes in a polyculture. Indian Journal of Ecology 12(2):322-326.

Sattar, M. A. 1987. Paragrass as feed for the herbivorous carp *Puntius gonionotus*. M. Sc. Thesis No. AE 37-38. Asian Institute of Technology, Bangkok, Thailand, 87 pp.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.

Strauss, R. E. 1979. Reliability estimates for Ivlevs' electivity index, the forage ratio and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

Wallace Jr., R. K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110: 72-76.

Windell, J. T. and S. H. Bowen. 1978. Methods for study of fish diets based on analysis of stomach contents. In: Methods for the assessment of fish production in freshwaters (ed. T. Bagenal), pp 219-226. Blackwell Scientific Publications, Oxford, England.

Zaret, T. M. and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

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