Bangladesh J. Fish. Res., 3(2), 1999: 201-208

Development of a new model of feeding strategy analysis of fish incorporating resource availability and use data

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Abstract

A feeding strategy model is proposed using stomach content and resource availability data as a modification to Costello (1990) and Amundsen *et al.* (1996). Incorporation of feeding electivity index (*E*) instead of the prey-specific abundance signifies the importance of resource availability in prey selection as well as the predator`s ability to specialize, generalize or avoid particular prey items at the individual and population level.

Key words : Feeding strategy, Prey importance (electivity), Tilapia

Introduction

Niche breadth in animal are often measured without regard to the relative frequencies of the various resources available to the organisms. Thus these indices lack wide acceptability and objective interpretations, simply because resources thus used by the predators are not simultaneously incorporated in those indices. Feinsinger *et al.* (1981) defined niche width as the degree of similarity between the frequency distribution of resources used by a predator and the frequency distribution of resources available to it. Niche width can appropriately be quantified now with Czekanowski's proportional similarity (PS) index which takes into account the resource available or accessible to the predators and the resource used by the predators as well (Feinsinger *et al.* op. cit.).

Prey abundance and selection are of paramount importance in feeding strategy of any fish. Feeding strategy changes with ontogenetic dietary shifts, variations in morphological adaptations and development of feeding apparatus such as, protrusible jaw mechanisms, pharyngeal teeth's (Wootton 1990), encounter and capture varying with visibility, encounter probability, escape speed, ingestion and retention (Pearre 1986).

In this paper it has been shown that, feeding strategy analysis incorporating Ivlev's (1961) feeding electivity index (*E*) signifies the importance of resource availability in prey selection as well as the predator's ability to specialize, generalize or avoid particular prey item both at individual and population level.

Materials and methods

The data used in this paper was part of a work carried out at the Riverine Station, Chandpur, of the Bangladesh Fisheries Research Institute during 13-15 July'95 in a nursery pond using two size (small and large) categories of *Oreochromis* spp. [*Oreochromis niloticus* (L.) x *O. mossambicus* (Peters) natural hybrid]. The fish and sub-surface plankton were sampled every 3 h from the nursery pond for 48 h to analyze their gut contents, food consumption, feeding electivity and available food.

Pond preparation and fish stocking

The pond was a nursery type, about 1,620 m^2 in size (water area 990 m^2), 1.85 m in maximum depth and was kept weed-free for easy netting. The pond was prepared in June 1995 by completely drying, liming (250.0 kg. ha^{-1}) and manuring once (cow-dung 10.0 t. ha^{-1}, urea 16.0 kg. ha^{-1} and triple super phosphate 32.0 kg. ha^{-1}). Two sizes of *Oreochromis* spp. juveniles, collected from the Riverine Station's other nursery ponds, were stocked at a density of 7.0 juveniles. m^{-2} (3,465 individuals of each size). Before stocking in the pond, fishes were kept in a flow-through system for 48 h to completely empty their gut contents. The small fishes were 4.3-9.3 cm in total length (TL) and 1.6-15.5 g in weight and the large fishes were 9.5-13.5 cm in TL and 14.4-46.4 g in weight. Prior to stocking in the pond the fish had been fed a supplemental feed composed of 40% rice bran, 40% wheat bran and 20% fish meal at 2-5% of body weight (bw), once daily but not during our experiment. Two days after stocking, 10 fishes of each size were sampled every 3 h for 48 h with a cast net (3x6 m, mesh 0.5 cm). In total, 320 fishes (160 of each size) were collected.

Stomach content 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 TL (mm), and weighed ($\pm$ 1 mg) using a Sartorius electronic balance within two weeks after collection and no correction factor for fixation was used. Only 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 as digestion is less advanced in this portion and food items remain mostly identifiable. Tilapias are reported to have a relatively long and coiled intestine up to 14 times the body length (Edwards 1987), and food digestion and assimilation is completed in the first half of the intestine (Bowen 1981). Similar methods have also been adopted by McComish (1967) and Minckley *et al.* (1970) for buffalo fish; Dewan *et al.* (1977, 1985 and 1991) for carps and Dewan and Saha (1979) for tilapia.

Each stomach was blotted uniformly with tissue paper and weighed once along with the gut contents, then opened longitudinally and gut fullness assessed on a visual scale of 0 (empty), 0.25 (1/4th full), 0.5 (1/2 full), 0.75 (3/4th full) and 1.0 (completely full). The entire gut contents were then carefully transferred to a petri dish or a vial with a standard 10 ml of distilled water. Cleared guts were weighed again to calculate the weight of the gut contents (Dettmers and Stein 1992). Stomach contents were expressed as mg. g^{-1} of bw of the fish (wet weight of both). Larger food items of animal origin were usually counted under a dissecting stereo microscope (Wild Herbrugg), but in the case of tiny items (such items of plant origin, rotifers) the gut contents were well mixed, and 1 ml was sub-sampled by a digital Finn pipette to a Sedgwick-Rafter counting cell (1,000 mm^3, 50x20x1 mm) and 100 randomly chosen grids out of 1,000 were examined and counted under an inverted microscope (Olympus CK2). Three such sub-samples were enumerated per fish. All organisms were identified to genus level (Prescott 1962; Ward and Whipple 1978) and the percentage of each category determined. Percentage composition by number (the percentage abundance) was used for calculating the relative abundance (%) of food item in the stomach (Windell and Bowen 1978, Bowen 1983).

Selection of available plankton by fish was calculated using Ivlev's (1961) electivity index (E).

$$E = St_i - P_i / St_i + P_i$$

where St_i and P_i are the relative proportion of the prey category i in the fish gut (ration) and in the environment, respectively. The resultant index reflects random ingestion (around 0), weak to strong selection (up to +1.0) and weak to strong avoidance (down to -1.0) of a particular food item.

Plankton

Five one litre samples of surface to sub-surface water (within 0.02 m depth) were taken from three places of the pond (near the bank, middle and other side) every three hours prior to fish sampling, filtered through a 15 µm 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 such 1 ml sub-samples were taken from each plankton sample and the mean numbers. l^{-1}, relative abundance (%) and identification of each food item were done in the same way as for stomach content.

Costello (1990) and Amundsen et al. (1996) approach

Costello's method incorporates frequency of occurrence (FO) of a given prey type (expressed as a frequency of the total number of stomachs in which prey are present) in the x-axis and percentage abundance of a given prey type (defined as the percentage of total stomach contents in volume, weight or numbers in all predators comprised by that given prey) ingested by fish in the y-axis (Fig. 1a). In the Costello plot, generalized feeding strategy (a high within-phenotype contribution to the niche width) is indicated by data points distributed along the entire x-axis, rather than just to the lower right quadrant. In practice, specialized feeding strategy (a high between-phenotype contributions to the niche width) will rarely be determined, as the data points of prey abundance and FO rarely fall into the upper left quadrant (Amundsen *et al.* 1996).

An amendment to the Costello (1990) method was developed by Amundsen *et al.* (1996) by only substituting prey-specific abundance (defined as the percentage in volume, weight or number a given prey taxon comprises out of all prey items in only those predators in which that given prey occurred) for percentage abundance on the y-axis (Fig. 1b) and keeping the FO in the x-axis as such.

In Costello (1990) and Amundsen *et al.* (1996) methods nothing is told about the affect of resources available, accessible or selectivity to a fish's feeding strategy. Presumably it should be considered as, equal availability and electivity of all resources. In nature and field level studies, this assumption is unwarranted and thus describes inappropriately the feeding strategy in respect to both components of the total niche width.

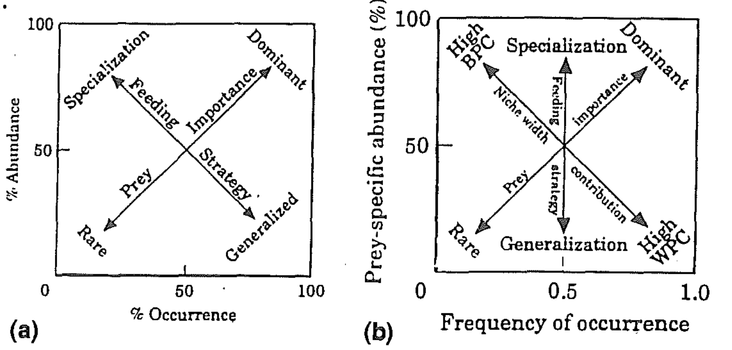

Fig. 1. Explanatory diagram for the (a) Costello (1990) and (b) Amundsen *et al.* (1996) methods (BPC= between-phenotype component, WPC= within-phenotype component).

Results and discussion

New approach

We suggest the use of electivity index, *E* (Ivlev 1961) on the *y*-axis, and maintaining the FO on the *x*-axis (Fig. 2) of the Amundsen *et al.* (1996) plot. We have followed a similar principle (as indicative of biologically significant dietary overlap, coined by Zaret and Rand (1971) in considering the electivity index beyond the arbitrary level of +0.4 and -0.4, respectively representing a biologically significant selection and avoidance, and between -0.4 and +0.4 as generalization. The FO of a particular prey item in the fish's stomach will direct the trends of either individual (low FO) or population (high FO) strategies.

This approach has been applied to the resultant Ivlev's electivity index derived from feeding data (Tables 1 and 2) of two sizes of tilapia, *Oreochromis* spp. and plankton availability data from a nursery pond (Haroon and Pittman 1998). The graphical feeding strategy thus obtained with this new model are shown in Figures 3a and 3b.

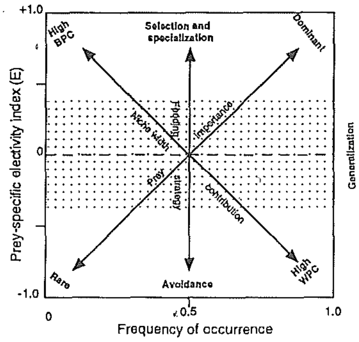

Fig. 2. Explanatory diagram of feeding strategy, niche width contribution and prey electivity for the proposed new method.

Table 1. Diel mean plankton composition (P_i%), stomach composition (St_i%) and resultant electivity indices (E) of two sizes (6 and 12 cm) of *Oreochromis* spp. from a nursery pond (13-15 July 1995), Bangladesh

Species	Pond					
	6 cm			12 cm		
	Pi%	Sti%	E	Pi%	Sti%	E
Chlorophyceae						
Ankistrodesmus	6.90	3.67	-0.31	6.90	2.58	-0.46
Scenedesmus	7.02	1.47	-0.65	7.02	1.53	-0.64
Dictyosphaerium	0.0	0.58	+1.0			
Selenestrum	0.0	0.03	+1.0			
Pediastrum	6.71	7.88	+0.08	6.71	7.64	+0.06
Pleurotaenium						
Closterium	0.0	0.06	+1.0	0.0	0.006	+1.0
Spirogyra	0.05	0.0	-1.0	0.05	0.0	-1.0
Cosmarium				0.0	0.06	+1.0
Cyanophyceae						
Merismopedia	14.41	2.55	-0.70	14.41	0.16	-0.98
Anabaena	6.61	51.23	+0.74	6.61	44.54	+0.74
Oscillatoria				0.0	0.006	+1.0
Bacillariophyceae						
Melosira	55.42	28.42	-0.32	55.42	39.40	-0.17
Asterionella	0.0	0.21	+1.0			
Euglenoid						
Euglenophyceae						
Euglena	0.0	0.25	+1.0	0.0	0.008	+1.0
Phacus	0.02	0.08	+0.60	0.02	0.33	+0.88
Total Phytoplankton	97.14	96.43	-0.003	97.14	96.26	-0.004
Unidentified macrophyt remain				0.0	0.09	+1.0
Rhizopoda						
Diffulgia	0.0	1.20	+1.0			
Rotifera						
Polyarthra	0.11	0.02	-0.69	0.11	0.004	-0.93
Brachionus	1.13	0.88	-0.12	1.13	1.08	-0.02
Keratella	0.43	0.93	+0.37	0.43	0.87	+0.34
Filinia	0.03	0.38	+0.85	0.03	0.24	+0.78
Trichocerca	0.04	0.03	-0.14	0.04	0.0	-1.0
Crustacea						
Moina				0.0	0.01	+1.0
Diaptomus	0.06	0.0	-1.0	0.06	0.0	-1.0
Cyclops	0.23	0.01	-0.92	0.23	0.006	-0.95
Unidentified nauplii	0.83	0.12	-0.75	0.83	0.19	-0.63
Total Zooplankton	2.86	3.57	+0.11	2.86	2.40	-0.09
Digested food					1.25	

Table 2. Frequency of occurrence (Freq. Occurr.) and prey-specific Ivlev's (1961) electivity indices data of two sizes (4.3-9.3 cm TL and 9.5-13.5 cm TL) of tilapia, *Oreochromis* spp. from a nursery pond (13-15 July 1995), Bangladesh

Food items	Small size*		Large size*	
	Freq. Occurr.	Electivity	Freq. Occurr.	Electivity
Chlorophyceae				
Ankistrodesmus	0.15	-0.31	0.85	-0.46

Scenedesmus	0.79	-0.65	0.70	-0.64
Dictyosphaerium	0.22	+1.0		
Selenestrum	0.02	+1.0		
Pediastrum	0.98	+0.08	0.99	+0.06
Closterium	0.06	+1.0	0.01	+1.0
Cosmarium			0.03	+1.0
Spirogyra	0	-1.0	0	-1.0
Cyanophyceae				
Merismopedia	0.66	-0.70	0.04	-0.98
Anabaena	1.0	+0.74	1.0	+0.74
Oscillatoria			0.01	+1.0
Euglenophyceae				
Euglena	0.11	+1.0	0.01	+1.0
Phacus	0.09	+0.60	0.20	+0.88
Unidentified macrophytes			0.01	+1.0
Rhizopoda				
Diffulgia	0.60	+1.0		
Rotifera				
Polyarthra	0.01	-0.69	0.03	-0.93
Brachionus	0.46	-0.12	0.70	-0.02
Keratella	0.50	+0.37	0.52	+0.34
Filinia	0.23	+0.85	0.15	+0.78
Trichocerca	0.03	-0.14	0	-1.0
Crustacea				
Moina			0.01	+1.0
Diaptomus	0	-1.0	0	-1.0
Cyclops	0.006	-0.92	0.01	-0.95
Crustaceans nauplii	0.10	-0.75	0.18	-0.63

* *Smalls n = 149, *Larges n = 106*

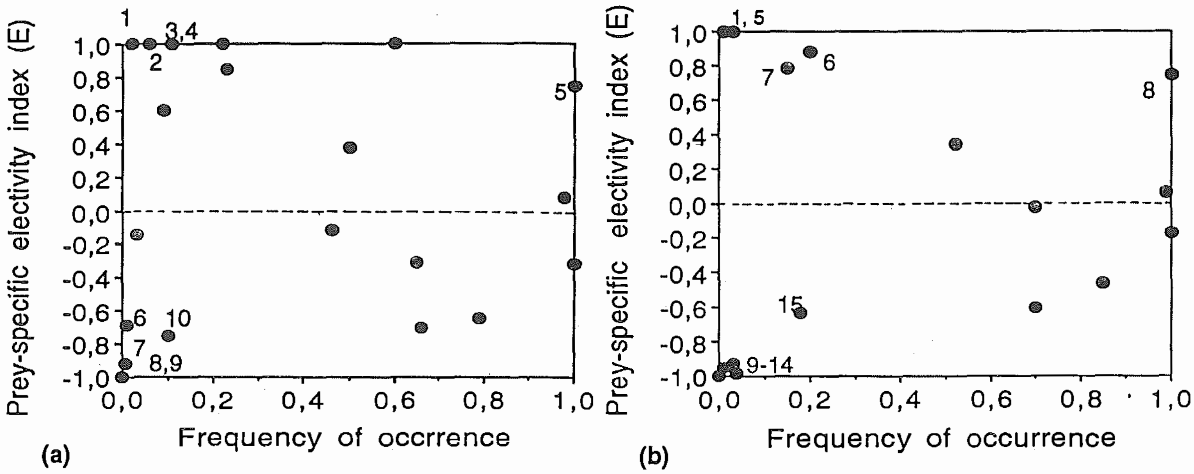

Fig. 3. Application of new feeding strategy analysis method to stomach content data of *Oreochromis* spp. [*O. mossambicus* (Peters) x *O. niloticus* (Linnaeus) natural hybrid] and resource data from a shallow nursery pond (13-15 July 1995), Bangladesh (refer to Tables I and II). The black dots represent different food items (only the important ones are labeled). **(a)** 4.3-9.3 cm TL, *n*= 149 (1= *Selenestrum* sp., 2= *Closterium* sp., 3= *Euglena* sp., 4= *Asterionella* sp., 5= *Anabaena* sp., 6= *Polyarthra* sp., 7= Crustaceans egg, 8= *Diaptomus* sp., 9= *Spirogyra* sp., 10= Crustaceans nauplii); **(b)** 9.5-13.5 cm TL, *n*= 106 (1= Aquatic macrophytes, 2= *Closterium* sp., 3= *Euglena* sp., 4= *Cosmarium* sp., 5= *Moina* sp., 6= *Phacus* sp., 7= *Filinia* sp., 8= *Anabaena* sp., 9= *Trichocera* sp., 10= *Spirogyra* sp., 11= *Diaptomus* sp., 12= Crustaceans egg, 13= *Polyarthra* sp., 14= *Merismopedia* sp., 15= Crustaceans nauplii).

Interpretations

The fish show selection of prey items when the data points are located on the upper part of the plot (+0.4 to +1.0). Data points positioned in the lower part (-0.4 to -1.0) represent food items that are avoided and food items that have been eaten inadvertently or randomly (between the ranges of +0.4 and -0.4) are positioned in the mid part of the plot. Data points located in the upper left quadrant indicate selection and specialization of prey at individual level (though of low occurrence in the gut but those prey have been strongly preferred by few fish), indicating a high between-phenotype component. Data points generally a single point or a few, in the upper right quadrant represent prey selection and specialization by the fish population (high occurrence of the prey in the gut and that food item has been strongly selected), also indicating a high between-phenotype component. Data points in the mid part of the plot (between +0.4 and -0.4) indicate a generalized feeding strategy, similar to Amundsen *et al.* (1996) within-phenotype component.

Data points in the lower left quadrant indicate avoidance of that food type at the population level. An electivity index of -1.0 for any food item would mean that this particular food item was available in the environment (plankton in this experiment) but never in the fish's ration, and thus the frequency of occurrence of that food item is 0. This applies to all the items found in the environment but avoided by the fish population, and correctly leads to a clustering of data points on the lower left corner. Data points closer to the lower right corner would indicate that most fishes are ingesting that food item but in much lower proportions (indicating avoidance) than found in the environment.

Similarly, there will be an electivity index value of +1.0, indicating strong selection for certain prey items, when they are absent in the resource availability spectrum (plankton in this experiment) sometimes because of their rare occurrence and at other times due to biased sampling and enumeration procedure, but present in the fish's gut. Because, there is no single unbiased sampling procedure for quantifying entire resource spectrum (plankton, benthos, detritus, aquatic vegetation, etc.) available or accessible to fish.

Conclusions

Feeding strategy analysis by Amundsen *et al.* (1996) method seems inappropriate because resource availability data are not taken into account, rather considered as irrelevant. The present proposed method would facilitate understanding of the feeding strategies and total niche width components of predators with reference to the resource availability in the environment. Moreover, information about selection and the predator's ability or limitation to specialize, generalize or avoid prey items both at the individual and population level can be obtained and interpreted objectively. This method seemed to meet the necessity of both resource use and selectivity, concurrently. If the problem inherent to sampling procedure and quantification of entire resources available/accessible to the predators could be overcome in future, the feeding strategy analysis with the proposed method would be more robust and accurate than as reported here. It may be opined that Amundsen *et al.* (1996) method can only be used when resource availability data are lacking.

Since niche width can be described in relation to resource availability and use concurrently (Feinsinger *et al.* 1981), why not feeding strategy analysis using resource use and availability data be in accordance with the theoretical concept of total niche width as coined by Hurlbert (1978) and Petraitis (1979).

Acknowledgments

We thank Dr. Geir Blom, Department of Fisheries and Marine Biology, University of Bergen, Norway for critically reviewing the manuscript. The authors also thank the anonymous reviewer for reviewing the final version of this paper.

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(Manuscript received 27 July 1998)