

Diel Feeding Pattern and Ration of Two Sizes of Tilapia, *Oreochromis* spp. in Pond and Paddy Field

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Abstract

The diel feeding pattern, electivity and ration of tilapia, *Oreochromis* spp. (4.3-9.3 and 9.5-13.8 cm total length) were investigated to determine the ontogenetic shifts in diet and the importance of habitat on diet and feeding along with water quality characteristics from a nursery pond and a ricefield in Bangladesh. Feeding activity was continuous with diurnal variation in stomach content and per cent of fish feeding. Small tilapia were more active feeders than large ones. Both sizes exhibited a single feeding peak around afternoon-dusk in the pond but irregular feeding peaks in the ricefield. Stomach content did not differ qualitatively with size, ontogenetic shift in diet apparently was lacking, although resource exploitation was different in the two habitats. Periphytic detrital aggregate was the principal diet in the paddy field while filamentous and colonial algae (*Anabaena* sp. and *Melosira* sp.) occurring as periphytic epipelton were the main food in the pond. Zooplankton was an insignificant dietary component in both habitats. *Oreochromis* spp. was found to be an omnivorous opportunistic-generalistic benthophagic browser or surface grazer. Its detritivory should not be confused with illiophagy. Feeding intensity and food consumption decreased with the increased fish size. Daily rations for small and large fish were estimated at 2.2 and 2.3% of bw in the pond and 0.91 and 0.45% of bw in the paddy field. Stomach content was computed to be completely evacuated in about 9-13 h in the pond and 1-4 h in the paddy field at water temperatures of 29.0-33.3°C. Total plankton density was higher in the pond than in the ricefield. Phytoplankton densities were higher in the pond while zooplankton densities were higher in the ricefield. Water quality properties were well within the acceptable ranges for aquaculture in both habitats. Lack of an ontogenetic dietary shifts suggest that caution should be taken in mixed-size rearing of tilapia.

Introduction

Integrated agriculture-cum-aquaculture in the same land and water resource seems to hold the best promise to augment and resurrect per unit rice and fish yield in developing Asian countries. Resource-poor marginal farmers in Asia, including Bangladesh, are reluctant to choose the high technology systems of the West for obvious reasons and prefer culturing herbivorous, omnivorous, planktivorous and detritivorous fishes in the concurrent rice-fish

systems and seasonal ponds because the stocked fishes utilize both autochthonous and allochthonous food sources.

Food and feeding habits are important biological factors for stocking fish in any type of water body where competition for food and maximum utilization of all available food in the water column is desired. Feeding varies with the time of day as well as season, and is of great theoretical and practical importance to understand the daily meal of fishes. Changes in sunshine photoperiod and physico-chemical condition influence available forage, both qualitatively and quantitatively, and also food ingestion, digestion and gastric evacuation by fish.

The tilapias *Oreochromis mossambicus* [(Peters) and *O. niloticus* (Linnaeus) (Perciformes:Cichlidae)] are exotic fish in Bangladesh and were introduced in 1954 and 1974, respectively, from Thailand (Rahman 1989). They are now widely cultured in ponds, seasonal water bodies and rice paddies. The available reports on the diets of tilapia in ponds in Bangladesh are the works of Doha and Haque (1966), Dewan *et al.* (1977, 1985), Saha and Dewan (1979) and Dewan and Saha (1979).

Studies on the diets of tilapia from various habitats in different countries have indicated that both *O. mossambicus* and *O. niloticus* are omnivorous. However, some controversy remains with regard to feeding habits and resources exploited. In some cases, *O. mossambicus* were found to be detritivorous (Vass and Hofstede 1952; Bowen 1981; Hofer and Newrkla 1983; Otto Infante 1985; Bitterlich 1985) while, in other cases, they were found to prefer phytoplankton and aquatic macrophytes (Doha and Haque 1966; Premjith *et al.* 1987; Dempster *et al.* 1993). Contrarily, *O. niloticus* were reported as phytophagous (Yashouv and Chervinski 1961; Moriarty 1973; Harbott 1982; Getachew 1987; Khallaf and Alne-na-ei 1987), while Saha and Dewan (1979), Dewan and Saha (1979), and Chapman and Fernando (1994) reported *O. niloticus* having preferences for detritus. In both species, food items of animal origin were of less importance in the gut contents.

The present study was undertaken to ascertain the diets, consumption and digestion rate of forage items and daily ration of two sizes of *Oreochromis* spp. (*O. mossambicus* x *O. niloticus* natural hybrid) along with the water chemistry both in the pond and paddy field. A step toward further understanding of the feeding dynamics and the impact of the tilapia can be gained when the daily feeding pattern of various sizes are investigated, and may contribute to an empirical basis for improved fish productivity through better management and stocking practices.

Materials and methods

The present work was carried out at the Riverine Station, Chandpur, of the Fisheries Research Institute of Bangladesh during 13-15 July 1995 in a nursery pond and 19-21 July 1995 in an experimental paddy field using two size (small and large) categories of fish. The fish, sub-surface plankton and water from both the pond and paddy field were sampled every 3 h for 48 h to analyze their gut contents along with the available natural food and physicochemical conditions of the water.

Site preparation and fish stocking

Pond: The pond was a nursery type, about 1,620 m² in size (water area 990 m²), 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 total density of 7.0 juveniles·m² (3465 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 9.5-15.5 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 bw 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.

Paddy field: Paddies (transplant aman: Pajam - a local variety of *Oryza sativa*) were planted in an experimental field of 166 m², having a refuge canal of 1.0 m breadth and 0.5 m depth on one side of the plot, according to farmer's standard practice (Haroon et al. 1989). Once the paddy tillers reached a height of 0.5 m and the field conditions established were as close as possible to those of natural wet-season paddies (water depth of 0.25 m in the paddy field and 0.70 m in the refuge), the two sizes of *Oreochromis* spp. juveniles procured from the Riverine Station's other nursery ponds were stocked at a total density of 7.0 juveniles·m⁻² (581 individuals of each size). Stocked fishes were treated as for the nursery pond, prior to release in the ricefield. The fish had been fed a similar supplemental feed at similar rates prior to the experiment but not during the study. The small fishes were 4.9-8.0 cm in TL and 1.9-8.2 g in weight and the large fishes were 10.3-13.8 cm in TL and 17.7-46.2 g in weight. A similar 48 h sampling regime was followed but using a knotless nylon hapa net (3x2x1.5 m, mesh 0.5 cm) for capture. A total of 320 fishes (160 of each size) were sampled.

Stomach content

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 (± 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 was less advanced in this portion and food items remained 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), Minckley *et al.* (1970) and Dewan *et al.* (1991). 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) and 1.0 (full). The entire gut contents were then carefully transferred to a Petri dish or 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). Gut contents were expressed as $\text{mg} \cdot \text{g}^{-1}$ of bw of the fish (wet weight of both). Food items of animal origin were usually counted under a dissecting stereo microscope, but in the case of tiny items (such as rotifers), three 1-ml subsamples were processed. For counting of items of plant origin, the gut contents were well-mixed, and 1-ml subsamples (three per fish) were examined in a Sedgwick-Rafter cell (1000 mm^3 , $50 \times 20 \times 1 \text{ mm}$) and 100 randomly chosen cells out of 1000 were counted under an inverted microscope. All organisms were identified to the 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).

Elliott and Persson's (1978) consumption model was used for food consumption estimation:

$$C_t = \frac{(S_t - S_0 e^{-kt})kt}{1 - e^{-kt}}$$

where C_t is food consumption between two sampling times (every 3 h) in $\text{mg} \cdot \text{g}^{-1}$ of bw, S_0 and S_t are the amounts of food present in the gut at the beginning and at the end of a sampling interval of t hours and k is the coefficient of exponential gastric evacuation rate (Elliott 1972).

A 5th order polynomial regression line was fitted to the mean stomach content data to determine the period when fishes were assumed to be evacuating their stomach contents. Habitat and size-wise mean k was calculated with the formula, $k = (1/t) \log_e (S_0 / S_t)$ where S_0 and S_t are the maximum and minimum stomach content values taken from the descending part of the polynomial best fit (Fig. 1) and t is the time interval in h between the maximum and minimum values. Only fishes with food in their stomachs were considered in the calculation of k and daily ration.

The daily ration was calculated by summing the values for C_t and expressed as $\text{g} \cdot \text{kg}^{-1}$ of $\text{bw} \cdot \text{day}^{-1}$ or % of $\text{bw} \cdot \text{day}^{-1}$. This model is most appropriate for species with "fine grained" diet (i.e. large numbers of small particles) such as planktivores, detritivores, herbivores and omnivores (Adams and Breck 1990; Dettmers and Stein 1992) and appears to be most applicable for estimating daily ration of collected fish in the field if: i) feeding is more or less continuous during daylight hours; ii) the amount of food in the stomach at the start and at the end of a sampling interval is not necessarily the same; and iii) the digestion rate is exponential.

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

$$E = r_i - p_i / r_i + p_i$$

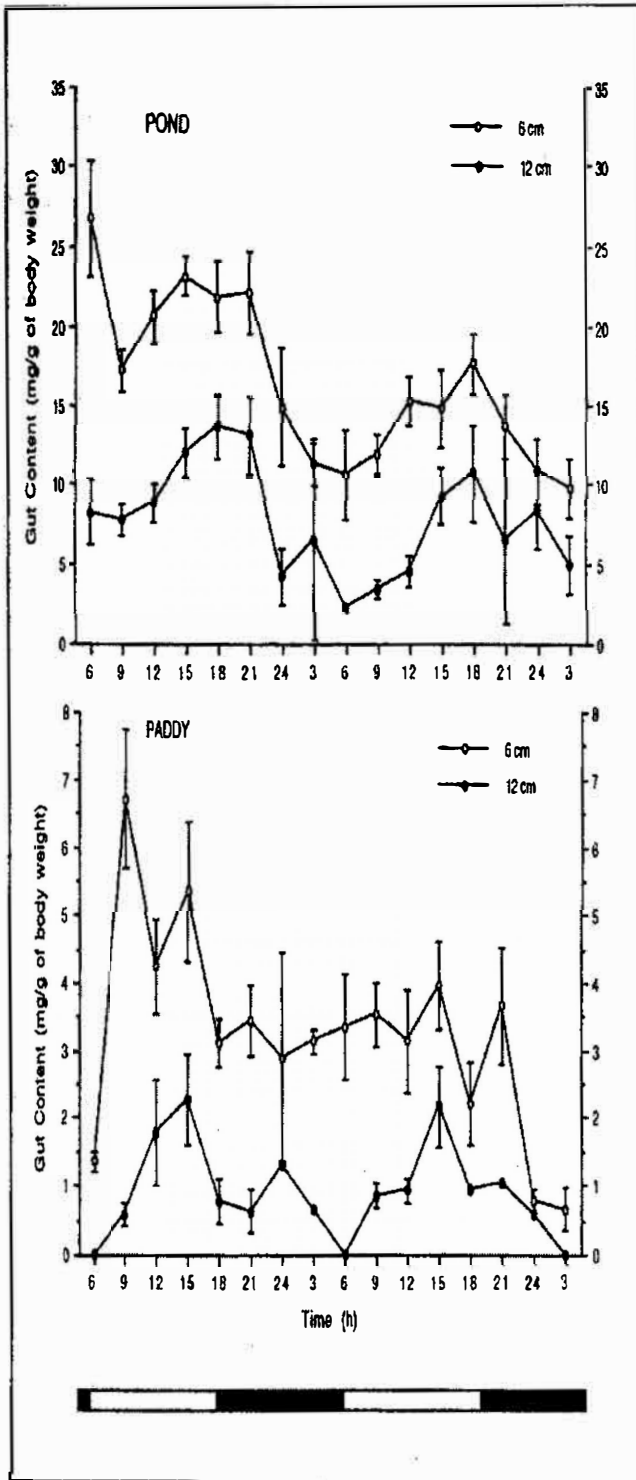


Fig 1. Best fitted 5th order polynomial regression of the mean gut content data of two size classes (6 and 12 cm TL) of tilapia *Oreochromis* spp. in a nursery pond (13-15 July 1995) and a ricefield (19-21 July 1995) in Bangladesh showing the time of the day when fishes were assumed evacuating. The shaded portions of the time bar indicate nighttime.

where r_i and p_i are the relative proportion of the prey category i in the ration and in the environment, respectively. Positive values indicate selection, negative values indicate avoidance and values close to 0 indicate random ingestion.

Plankton

Five 1-l samples of surface to sub-surface water (within 0.02 m depth) were taken from three places of both the pond (near the bank, middle and other side) and the paddy field (refuge canal, middle of the field and other side) every three hours prior to fish sampling, filtered through a 15 mm 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.

Water quality

Air and water temperature, dissolved oxygen, carbon dioxide, pH, total alkalinity, total hardness and ammonia-nitrogen were monitored every three hours prior to fish sampling in both habitats. Surface to sub-surface (0.02 m) water samples from three similar places in each habitat were analyzed each time and the mean calculated. Temperature and pH were measured by a centigrade alcohol thermometer and a portable pH meter (Janeway 3060, U.K.), respectively. Dissolved oxygen, free carbon dioxide, total alkalinity and hardness (as $CaCO_3$) and ammonia-nitrogen were measured by a HACH water kit (FF-2, U.S.A.).

Statistical analyses

Water quality, plankton and gut content data of every sampling interval were averaged according to size class and habitat. Two-way ANOVA were run on gut content values to determine feeding differences between the two size classes in the two habitats. Significant differences found by ANOVA were subjected to Newman-Keuls multiple comparison test. A linear regression was run between the ln-transformed gut content data and fish size to find out the slope of the feeding intensity (food consumption per unit bw).

Results

Water quality

Pond: Air temperature ranged within 26.6-31.7°C and water temperature within 30.0-33.2°C. Water temperature was always higher than the air, a characteristic condition of the rainy season in Bangladesh. Dissolved oxygen content varied between 5.5 and 11.2 $mg \cdot l^{-1}$ with higher values in the prenoon, lower values after dusk and again increasing around midnight. Free carbon dioxide content ranged from 11.5 to 30.6 $mg \cdot l^{-1}$ with higher values in the early morning and lower values during the afternoon-dusk, showing an inverse relationship with dissolved oxygen. Water pH fluctuated within a narrow

range of 8.0-8.5 with higher values in the afternoon hours. Total alkalinity varied between 120.3 and 154.7 $\text{mg}\cdot\text{l}^{-1}$ as CaCO_3 and total hardness between 121.0 and 158.0 $\text{mg}\cdot\text{l}^{-1}$ as CaCO_3 both with higher values during sunset through morning hours and lower values during noon through afternoon. Ammonia-nitrogen ranged within 0.3 to 0.5 $\text{mg}\cdot\text{l}^{-1}$ and could only be traced during sunset through next morning.

Paddy field: Air temperature ranged from 25.3 to 30.8°C and water temperature from 29.0 to 33.3°C. Here also, the water temperature was always higher than the air temperature. Dissolved oxygen content varied between 2.56 and 6.4 $\text{mg}\cdot\text{l}^{-1}$, having higher values around afternoon-dusk, lower values between sunset and predawn, and higher values again after dawn. Free carbon dioxide content ranged from 16.6 to 31.7 $\text{mg}\cdot\text{l}^{-1}$ with an inverse relationship to oxygen levels. pH also fluctuated within a narrow range of 7.0-7.5, with lower values during morning. Total alkalinity varied between 72.0 and 87.0 $\text{mg}\cdot\text{l}^{-1}$ as CaCO_3 , with lower values once after sunset and again during early noon. Hardness varied from 71.0 to 91.0 $\text{mg}\cdot\text{l}^{-1}$ as CaCO_3 with higher values once in the morning and again after sunset and lower values once in the noon and again in midnight. Ammonia-nitrogen varied between 0.3 and 0.4 $\text{mg}\cdot\text{l}^{-1}$ with no obvious fluctuation.

Feeding activity

In both habitats, feeding activity continued throughout the day and night with most fishes feeding during sunlit hours and with reduced feeding activity during night hours. The mean index of gut fullness and gut content were generally higher for the small than for the large and higher in the pond than in the paddy field.

In the pond, both sizes were found to feed round the clock. Most fish fed from dawn to dusk while fewer fed during dusk to next sunrise. Mean index of stomach fullness ranged between 0.3 and 0.9 for the small fish with higher values during sunrise through sunset and lower values during dusk through next dawn (Table 1). Mean stomach content of the small fish varied between 9.8 and 26.7 $\text{mg}\cdot\text{g}^{-1}$ of bw with higher values during daylight hours showing a trend of gradual increasing feeding activity after sunrise (except at 0900 h of the first day of the sampling) giving a dome-shaped single feeding peak slightly skewed towards the dusk (Fig. 2). Mean index of stomach fullness for large fish ranged from 0.01 to 0.97 with higher values during sunrise through sunset and lower values from dusk to dawn (Table 1). Mean stomach content of the large fish ranged from 2.3 to 13.7 $\text{mg}\cdot\text{g}^{-1}$ of bw with lower values during dusk to dawn and having a clearly skewed, single feeding peak around sunset (Fig. 2).

In the paddy field, most fish were feeding similarly from dawn to dusk and fewer during dusk to dawn (Table 2). Small fish were again found to feed round the clock while large fish did not feed around sunrise (Fig. 2). Mean index of stomach fullness of the small fish ranged between 0.01 and 0.7, with higher values during morning through afternoon and minimum values during 2400-0600 h (Table 2). Mean stomach content of

Table 1. Diel variation in feeding of *Oreochromis* spp. in the pond during 48 h. Data are mean \pm 95% confidence limits. Ct is the rate of food consumption per interval, using only those fish feeding, and longer interval times for periods of 0 gut fullness. Gut = anterior portion of the digestive tract lying between esophagus and first major bend of small intestine, just after the stomach.

Date & Hour	6 \pm 1cm					12 \pm 1cm				
	Fish size(cm)	Fish wt.(g)	% Fish Feeding	Index of gut fullness	Ct(mg/gbw/interval)	Fish size(cm)	Fish wt.(g)	% Fish Feeding	Index of gut fullness	Ct(mg/gbw/interval)
13.7.95										
06:00	5.99 \pm 0.35	4.73 \pm 1.06	100.0	0.89 \pm 0.15		12.12 \pm 0.29	33.35 \pm 2.90	100.0	0.74 \pm 0.22	2.13
09:00	5.98 \pm 0.68	4.73 \pm 1.51	100.0	0.90 \pm 0.10		11.64 \pm 0.51	29.46 \pm 3.82	100.0	0.97 \pm 0.04	3.75
12:00	6.69 \pm 0.63	6.07 \pm 1.49	100.0	0.80 \pm 0.17	7.3	11.56 \pm 0.55	28.46 \pm 3.49	100.0	0.88 \pm 0.14	6.49
15:00	6.73 \pm 0.55	6.30 \pm 1.08	100.0	0.91 \pm 0.10	7.15	11.40 \pm 0.63	28.77 \pm 4.33	100.0	0.92 \pm 0.14	5.73
18:00	7.19 \pm 0.64	6.36 \pm 2.11	100.0	0.81 \pm 0.14	3.41	11.42 \pm 0.84	28.54 \pm 5.37	100.0	0.86 \pm 0.12	3.70
21:00	6.89 \pm 0.49	5.70 \pm 1.23	100.0	0.74 \pm 0.20	4.88	12.02 \pm 0.63	31.34 \pm 5.27	60.0	0.53 \pm 0.29	
24:00	6.58 \pm 0.45	4.96 \pm 1.13	80.0	0.37 \pm 0.20	1.09	11.58 \pm 0.78	28.74 \pm 5.72	40.0	0.12 \pm 0.12	
14.7.95										
03:00	7.09 \pm 0.51	6.32 \pm 1.51	80.0	0.45 \pm 0.17		10.96 \pm 0.61	23.61 \pm 3.98	20.0	0.09 \pm 0.15	3.96
06:00	6.57 \pm 0.43	4.71 \pm 1.08	70.0	0.33 \pm 0.15	1.57	11.64 \pm 0.47	25.45 \pm 3.53	10.0	0.01 \pm 0.02	
09:00	6.11 \pm 0.43	4.24 \pm 1.14	100.0	0.57 \pm 0.08	3.62	10.96 \pm 0.71	24.05 \pm 4.27	90.0	0.33 \pm 0.12	2.03
12:00	6.63 \pm 0.39	6.23 \pm 1.37	100.0	0.78 \pm 0.14	6.34	12.44 \pm 0.69	33.28 \pm 5.37	100.0	0.58 \pm 0.22	2.42
15:00	7.21 \pm 0.41	6.17 \pm 1.10	100.0	0.77 \pm 0.14	2.63	11.69 \pm 0.59	26.08 \pm 4.49	70.0	0.38 \pm 0.20	6.94
18:00	6.64 \pm 0.47	4.90 \pm 1.00	100.0	0.78 \pm 0.14	6.29	11.89 \pm 0.57	28.51 \pm 5.21	90.0	0.57 \pm 0.23	4.65
21:00	7.63 \pm 0.74	8.04 \pm 2.53	80.0	0.73 \pm 0.25		12.09 \pm 0.78	31.11 \pm 5.19	20.0	0.11 \pm 0.20	
24:00	7.44 \pm 0.45	7.07 \pm 1.43	90.0	0.61 \pm 0.20		11.68 \pm 0.69	28.05 \pm 4.47	70.0	0.44 \pm 0.23	4.31
15.7.95										
03:00	7.42 \pm 0.47	6.88 \pm 1.35	90.0	0.66 \pm 0.21	1.05	11.60 \pm 0.69	27.95 \pm 3.86	20.0	0.18 \pm 0.23	

Table 2. Diel variation in feeding of *Oreochromis* spp. in the paddy during 48 h. Data are mean \pm 95% confidence limits. Ct is the rate of food consumption per interval, using only those fish feeding, and longer interval times for periods of 0 gut fullness. Gut = anterior portion of the digestive tract lying between esophagus and first major bend of small intestine, just after the stomach.

Date & Hour	6 \pm 1cm					12 \pm 1cm				
	Fish size (cm)	Fish wt. (g)	% Fish feeding	Index of gut fullness	Ct(mg/gbw/interval)	Fish size (cm)	Fish wt. (g)	% Fish feeding	Index of gut fullness	Ct(mg/gbw/interval)
19.7.95										
06:00	6.86 \pm 0.39	4.89 \pm 0.62	30.0	0.01 \pm 0.01	6.47	11.92 \pm 0.45	26.27 \pm 3.17	0	0	0
09:00	6.94 \pm 0.24	5.24 \pm 0.78	90.0	0.67 \pm 0.24		12.49 \pm 0.43	30.10 \pm 4.43	50.0	0.09 \pm 0.08	0.71
12:00	6.98 \pm 0.48	5.21 \pm 0.88	90.0	0.59 \pm 0.19	2.39	12.34 \pm 0.43	29.76 \pm 3.09	30.0	0.09 \pm 0.12	1.74
15:00	7.20 \pm 0.26	5.74 \pm 0.72	90.0	0.56 \pm 0.21		12.46 \pm 0.57	30.09 \pm 4.17	50.0	0.20 \pm 0.14	1.34
18:00	6.95 \pm 0.64	5.38 \pm 1.08	80.0	0.51 \pm 0.23		12.02 \pm 0.76	28.08 \pm 4.98q	30.0	0.05 \pm 0.05	0.14
21:00	6.84 \pm 0.35	5.21 \pm 0.78	50.0	0.37 \pm 0.28	1.20	12.61 \pm 0.45	32.14 \pm 2.88	30.0	0.05 \pm 0.05	0.14
24:00	7.29 \pm 0.29	5.85 \pm 0.68	30.0	0.10 \pm 0.17	0.31	12.24 \pm 0.43	29.47 \pm 3.62	10.0	0.02 \pm 0.04	1.09
20.7.95										
03:00	6.70 \pm 0.34	4.62 \pm 0.57	20.0	0.18 \pm 0.23	1.04	11.26 \pm 0.74	23.05 \pm 4.29	10.0	0.01 \pm 0.02	
06:00	7.23 \pm 0.24	5.37 \pm 0.40	50.0	0.30 \pm 0.26	1.08	11.98 \pm 0.55	30.23 \pm 5.04	0	0	
09:00	6.99 \pm 0.24	5.19 \pm 0.58	90.0	0.49 \pm 0.20	1.11	11.20 \pm 0.74	25.96 \pm 3.21	40.0	0.02 \pm 0.05	1.04
12:00	6.89 \pm 0.24	5.06 \pm 0.53	100.0	0.52 \pm 0.16	0.50	12.00 \pm 0.61	29.38 \pm 3.96	70.0	0.14 \pm 0.07	0.45
15:00	6.13 \pm 0.49	3.68 \pm 0.88	80.0	0.43 \pm 0.19	1.78	12.27 \pm 0.59	30.37 \pm 4.72	40.0	0.15 \pm 0.15	1.91
18:00	6.23 \pm 0.40	4.54 \pm 0.77	40.0	0.07 \pm 0.07		11.49 \pm 0.86	23.89 \pm 4.62	10.0	0.01 \pm 0.02	
21:00	6.44 \pm 0.54	4.92 \pm 0.92	20.0	0.09 \pm 0.12	2.25	11.77 \pm 0.41	25.29 \pm 3.02	10.0	0.02 \pm 0.04	0.51
24:00	6.78 \pm 0.47	4.81 \pm 0.92	20.0	0.01 \pm 0.01		12.19 \pm 0.61	27.45 \pm 4.53	10.0	0.01 \pm 0.02	
21.7.95										
03:00	6.70 \pm 0.42	4.58 \pm 0.82	20.0	0.01 \pm 0.01	0.06	11.68 \pm 0.53	23.96 \pm 4.25	0	0	

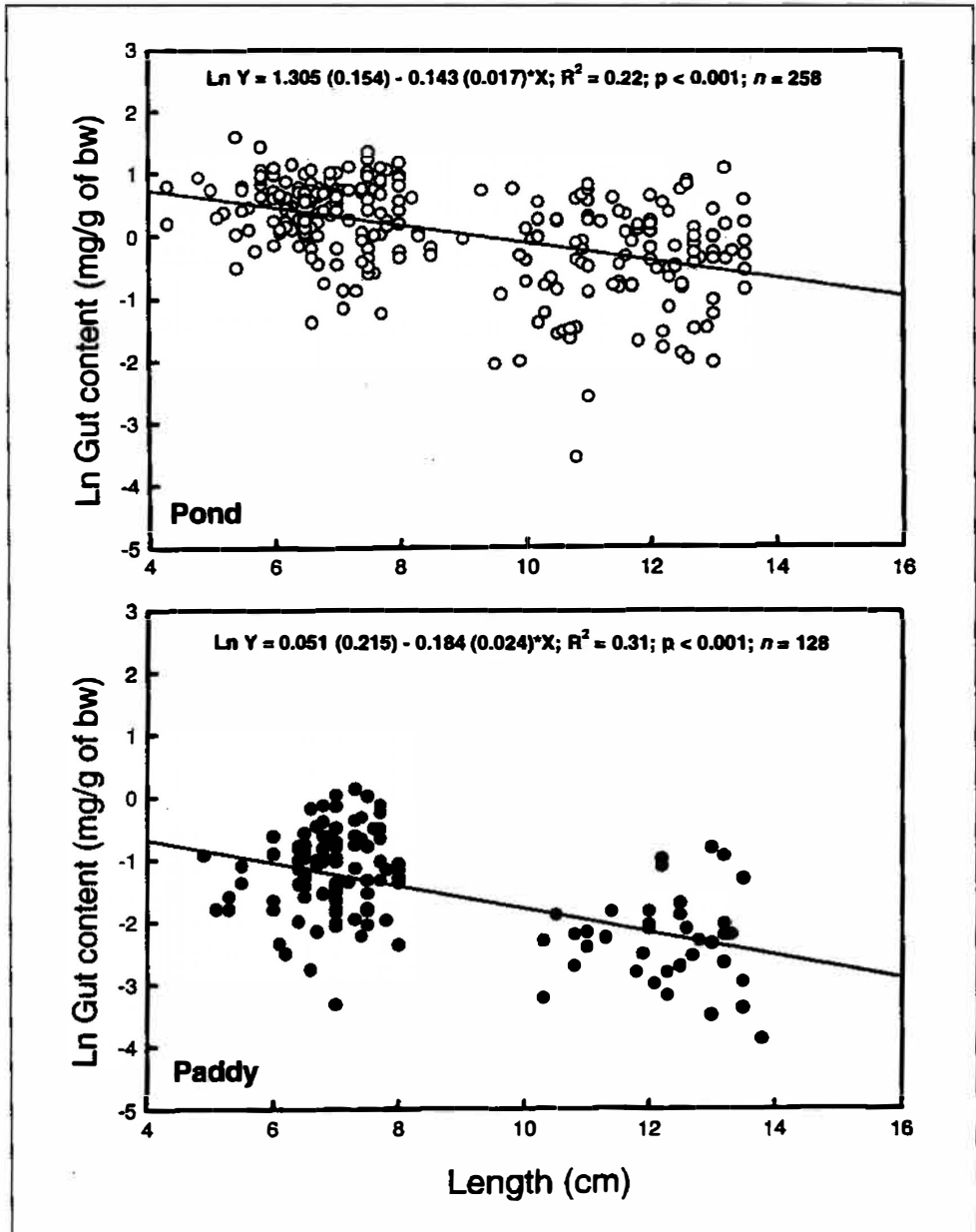


Fig. 2. Diel pattern of stomach content (mean \pm SEM) of two sizes of *Oreochromis* spp. in the pond (13-15 July 1995) and paddy field (19-21 July 1995) in Bangladesh. The shaded portions of the time bar indicate nighttime. Note the differences in the scales of the Y-axes in the two figures.

this size varied from 1.0 to 6.6 mg·g⁻¹ of bw, with lower values during midnight through next sunrise, showing three possible feeding peaks, at 0900 h, 1500 h and 2100 h (Fig. 2). Mean index of stomach fullness for large fish ranged from 0.01 to 0.2, peaking around 15.00 h and declining sharply after that. Stomachs were empty prior to sunrise (Table 2). Mean stomach content of this size varied between 0.5 and 2.4 mg·g⁻¹ of bw, with one feeding peak at 1500 h and possibly another around midnight (Fig. 2).

Table 3. Diel mean plankton composition (PI%), stomach composition (St%) and resultant electivity indices (E) of two sizes (6 and 12 cm) of *Oreochromis* spp. from both pond and paddy field.

Habitat Species	POND					PADDY				
	6 cm			12 cm		6 cm			12 cm	
	PI%	St%	E	St%	E	PI%	St%	E	St%	E
Green										
Chlorophyceae										
<i>Ankistrodesmus</i>	6.90	3.67	-0.31	2.58	-0.46	4.87	0.0	-1.00	0.0	-1.0
<i>Scenedesmus</i>	7.02	1.47	-0.65	1.53	-0.64	3.74	0.007	-0.99	0.0	-1.0
<i>Dictyosphaerium</i>	0.0	0.58	+1.0							
<i>Selenestrum</i>	0.0	0.03	+1.0							
<i>Pediastrum</i>	6.71	7.88	+0.08	7.64	+0.06	0.84	0.0	-1.0	0.02	-0.95
<i>Pleurotaenium</i>									0.02	+1.0
<i>Closterium</i>	0.0	0.06	+1.0	0.006	+1.0	0.0	0.12	+1.0		
<i>Spirogyra</i>	0.05	0.0	-1.0	0.0	-1.0	0.0	0.14	+1.0		
<i>Rhizoclonium</i>						0.0	7.21	+1.0	0.03	+1.0
<i>Pithophora</i>						0.0	3.45	+1.0		
<i>Cosmarium</i>	0.0			0.06	+1.0					
Blue-green										
Cyanophyceae										
<i>Merismopedia</i>	14.41	2.55	-0.70	0.16	-0.98	14.64	0.0	-1.0	0.0	-1.0
<i>Anabaena</i>	6.61	51.23	+0.74	44.54	+0.74	0.26	0.0	-1.0	0.05	-0.68
<i>Oscillatoria</i>	0.0			0.006	+1.0					
Diatom										
Bacillariophyceae										
<i>Melosira</i>	55.42	28.42	-0.32	39.40	-0.17	1.85	0.19	-0.81	0.12	-0.88
<i>Asterionella</i>	0.0	0.21	+1.0							
Euglenoid										
Euglenophyceae										
<i>Euglena</i>	0.0	0.25	+1.0	0.008	+1.0					
<i>Phacus</i>	0.02	0.08	+0.60	0.33	+0.88	0.37	0.0	-1.0	0.0	-1.0
Phytoplankt. Tot.	97.14	96.43	-0.003	96.24	-0.004	26.57	11.12	-0.41	0.24	-0.98
Unid. macroph. rem.	0.0			0.09	+1.0					
Rhizopoda										
<i>Diffulgia</i>	0.0	1.20	+1.0							
Rotifera										
<i>Polyarthra</i>	0.11	0.02	-0.69	0.004	-0.93	1.56	0.0	-1.0	0.0	-1.0
<i>Brachionus</i>	1.13	0.88	-0.12	1.08	-0.02					
<i>Keratella</i>	0.43	0.93	+0.37	0.87	+0.34	0.37	0.0	-1.0	0.0	-1.0
<i>Filinia</i>	0.03	0.38	+0.85	0.24	+0.78					
<i>Trichocerca</i>	0.04	0.03	-0.14	0.0	-1.0					
Crustacea										
<i>Moina</i>	0.0			0.01	+1.0	0.52	0.07	-0.76	0.0	-1.0
<i>Bosmina</i>						0.31	0.33	+0.03	0.0	-1.0
<i>Alona</i>						0.89	0.0	-1.0	0.0	-1.0
<i>Daphnia</i>						0.78	0.02	-0.95	0.0	-1.0
<i>Diphanosoma</i>						0.57	0.0	-1.0	0.0	-1.0
<i>Diaptomus</i>	0.06	0.0	-1.0	0.0	-1.0	42.92	0.0	-1.0	0.0	-1.0
<i>Cyclops</i>	0.23	0.01	-0.92	0.006	-0.95	3.44	0.05	-0.97	0.0	-1.0
Unid. eggs						0.0	0.69	+1.0		
Unid. nauplii	0.83	0.12	-0.75	0.19	-0.63	20.50	0.82	-0.92	0.47	-0.96
Ostracoda										
<i>Cypris</i>						1.57	0.14	-0.84	0.12	-0.86
Zooplankton Tot.	2.86	3.57	+0.11	2.40	-0.09	73.43	2.12	-0.94	0.59	-0.98
Unid. insect rem						0.0	3.39	+1.0		
Digested food				1.25						
Detrital aggreg.						0.0	83.37	+1.0	99.17	+1.0

Phytoplankt. = Phytoplankton, Tot. = Total, Unid. = Unidentified, macroph. = aquatic macrophytes, rem. = remains and aggreg. = aggregate.

Food consumed per unit body weight of both sizes were significantly higher in the pond than in the paddy field and small fish fed significantly more than the large ones in either habitat (two-way Anova followed by Newman-Keuls test, $p < 0.001$). Linear regression of \ln transformed gut content data revealed significant decreases ($p < 0.0001$) in feeding with the increase in fish size in both habitats (Fig. 3).

Stomach content and electivity

In the pond, both sizes consumed relatively large amounts (>95% of gut content) of algal matter (Table 3). There was an overall random selection of algae (-0.003 for the small and -0.004 for the large fishes), although *Anabaena* sp. and *Melosira* sp., both occurring as periphytic epipelon, and *Pediastrum* sp. occurring as plankton, were most frequently found in the stomachs. Filamentous green algae (*Spirogyra*, *Rhizoclonium* and *Pithophora*) were totally avoided while some of the planktonic forms of the green, blue-green and diatom were often positively and often negatively (though weak) selected by both sizes. *Euglena* sp. and *Phacus* sp. of the Euglenoids were selected by both sizes and aquatic macrophytes were incidentally consumed only by the large fish. Small and large fish showed overall random selection (+0.11 and -0.09, respectively) for zooplankton, although *Brachionus*, *Keratella* and *Filinia* (Rotifers) were found in the stomachs of both sizes. Crustaceans were generally avoided by both sizes, and crustaceans nauplii were strongly avoided (-0.75 in small and -0.63 in large) while crustacean eggs, and insects were never consumed by the either size (Table 3).

In the paddy field, both sizes fed mainly on the detrital aggregates (83.4% in small and 99.2% in large fish), and had overall strong negative selection for zooplankton (-0.94 in small and -0.98 in large). Phytoplankton was negatively selected by both sizes (small fish -0.41, large fish -0.98). Both sizes avoided *Melosira* sp. of the diatoms, *Merismopedia* sp., *Anabaena* sp. of the blue-greens and *Phacus* sp. of the Euglenoids. Small fish showed positive selection for *Rhizoclonium*, *Pithophora*, *Closterium* and *Spirogyra* of the green algae while large fish chose small amounts of *Rhizoclonium* of filamentous and *Pleurotaenium* of planktonic green algae. Macrophytes were not consumed by the either size in the paddy field. Of the zooplankton, small fish often randomly consumed *Bosmina* but selected crustaceans eggs. Large fish avoided all crustaceans and eggs. Unidentified crustaceans nauplii were avoided by both sizes. Rotifers were avoided by both sizes and insects were consumed (3.4%) by the small fish only (Table 3). There was no evidence of tilapia nibbling on the rice plant or fronds.

Rate of gastric evacuation

In the pond, k values varied up to 0.1 (mean 0.07). h^{-1} for small fish and up to 0.16 (mean 0.10). h^{-1} for large fish (Fig. 1). Both sizes had maximum evacuation after sunset. In the paddy field, k values ranged up to 0.12 (mean 0.09) $\cdot h^{-1}$ for small fish and up to 0.20 (mean 0.14) $\cdot h^{-1}$ for the large (Fig. 1). The small fish showed three possible evacuation peaks daily; at noon, at

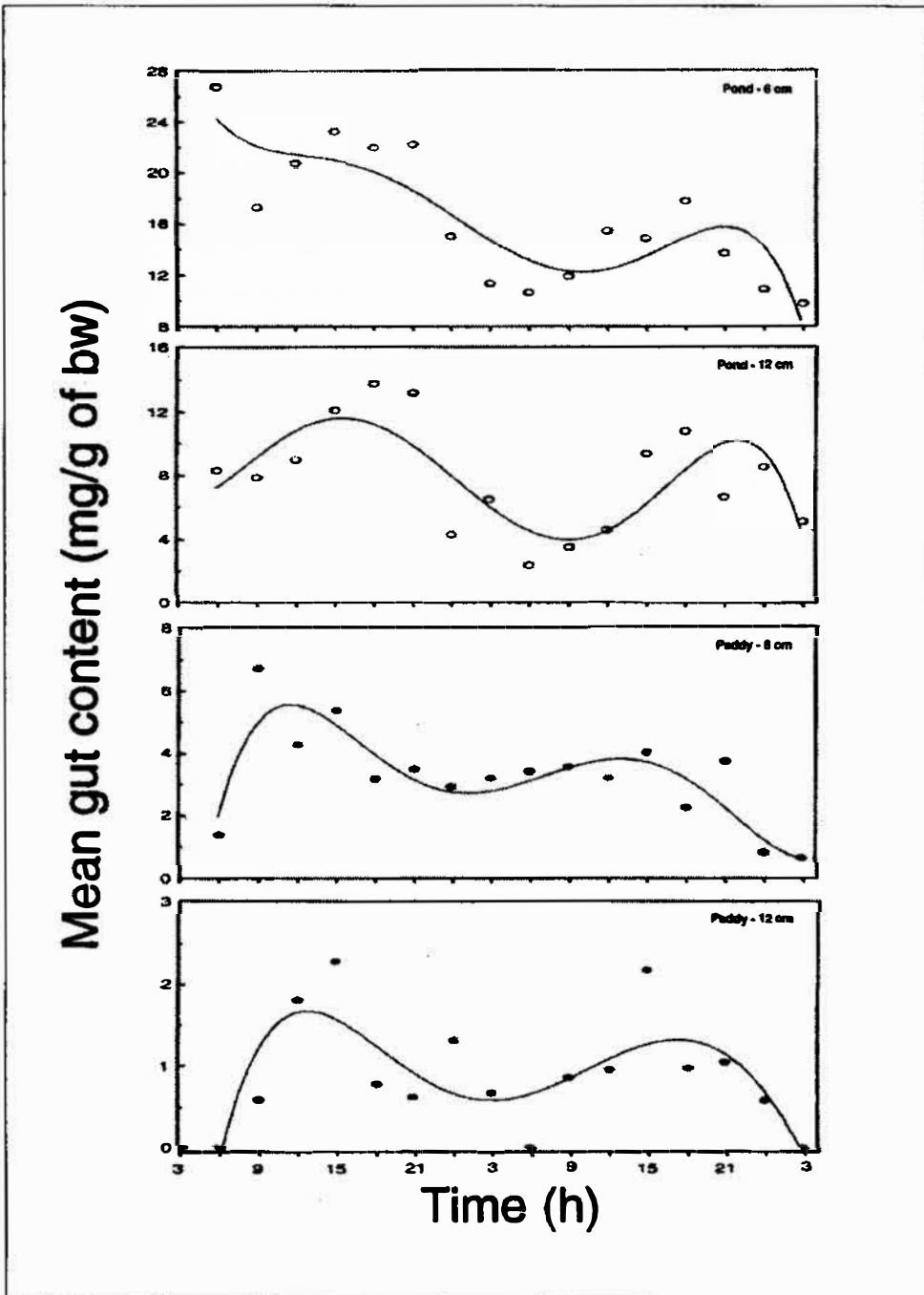


Fig 3. Linear regression of ln transformed gut content data versus size of *Oreochromis* spp. in the pond (13-15 July 1995) and paddy field (19-21 July 1995) in Bangladesh.

sunset, and midnight-early morning (Fig. 2). The large fish showed a single evacuation peak at sunset, and almost no evacuation in the predawn hours (Fig. 2). Stomach contents were estimated to be completely evacuated in about 9-13 h in the pond and in about 1-4 h in the paddy field at water temperatures of 29.0-33.3°C.

Food consumption and daily ration

C_t values for small fish ranged from 1.05 to 7.3 $\text{mg} \cdot \text{g}^{-1}$ of bw. 3 h^{-1} (mean 4.1) and for large fish ranged from 2.0 to 6.9 $\text{mg} \cdot \text{g}^{-1}$ of bw. 3 h^{-1} (mean 4.2) in the pond (Table 1). In the ricefield, C_t values for small fish ranged from 0.06 to 6.5 $\text{mg} \cdot \text{g}^{-1}$ of bw. 3 h^{-1} (mean 1.7) and for large fish between 0.14 and 1.9 (mean 1.0) $\text{mg} \cdot \text{g}^{-1}$ of bw. 3 h^{-1} (Table 2).

Both sizes fed better in the pond than in the paddy field. In the pond, the daily ration of small fish was calculated to be 2.2% of bw, which was about the same as the daily ration of large fish, 2.3% of bw. In the paddy field, the daily ration of small fish was calculated to be 0.9% of bw, which was twice that of the daily ration of the large fishes, 0.45% of bw.

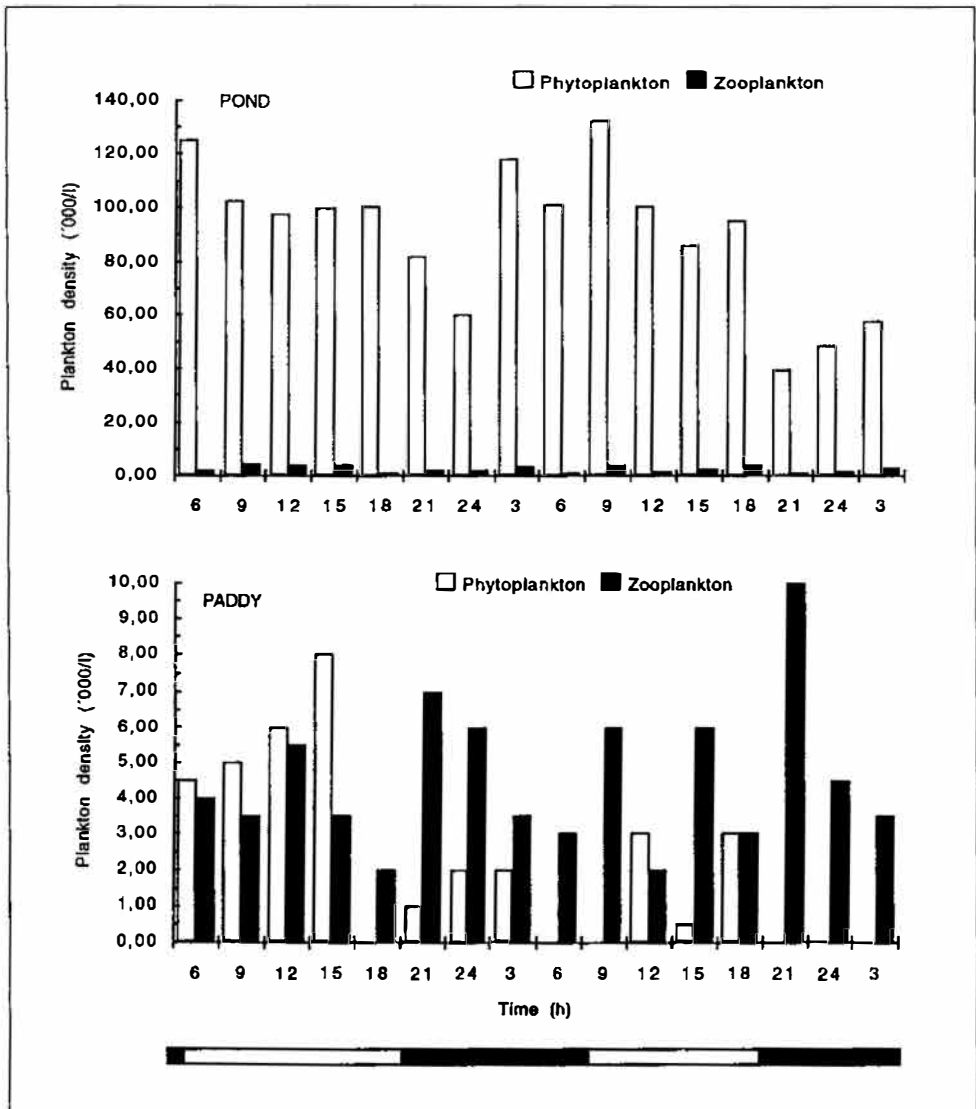


Figure 4. Diel pattern in plankton density in the pond (13-15 July 1995) and paddy field (19-21 July 1995) in Bangladesh. The shaded portions of the time bar indicate nighttime. Note the differences in the scale of the Y-axes in the two figures.

Plankton

Phytoplankton densities were higher in the pond than in the paddy field while zooplankton densities were higher in the paddy field (Fig. 4). Total plankton density was higher in the pond, ranging between $40.5 \times 10^3 \text{ l}^{-1}$ and $136.5 \times 10^3 \text{ l}^{-1}$, of which zooplankton densities were between $1.0 \times 10^3 \text{ l}^{-1}$ and $4.5 \times 10^3 \text{ l}^{-1}$.

In the pond, phytoplankton comprised 97.14% of total plankton numbers with some diel fluctuation (Fig. 4). A total of eight genera of phytoplankton belonging to the Chlorophyceae (4), Cyanophyceae (2), Bacillariophyceae (1) and Euglenophyceae (1) and seven genera of zooplankton belonging to the Rotifera (5) and Crustacea (2) were found in the pond (Table 3). In the paddy field, total plankton densities ranged between $2.0 \times 10^3 \text{ l}^{-1}$ and $11.5 \times 10^3 \text{ l}^{-1}$ of which zooplankton densities were between $2.0 \times 10^3 \text{ l}^{-1}$ and $10.0 \times 10^3 \text{ l}^{-1}$. Zooplankton comprised 73.4% of the total plankton in the paddy field, although phytoplankton were numerically dominant between 06.00-15.00 h of the first day and at 12.00 h of the second day. In the paddy field, zooplankton were most abundant after sunset, peaking around 21.00 h (Fig. 4). A total of seven genera of phytoplankton, comprising Chlorophyceae (3), Cyanophyceae (2), Bacillariophyceae (1) and Euglenophyceae (1), and 10 genera of zooplankton belonging to Rotifera (2), Crustacea (7) and Ostracoda (1) were recorded in the paddy field (Table 3).

Among the Chlorophyceae, *Dictyosphaerium* and *Selenestrum* were present only in the pond while *Pleurotaenium*, *Rhizoclonium* and *Pithophora* were found only in the paddy field. The rest of Chlorophyceae were common to both habitats. Of the Cyanophyceae, *Merismopedia* was abundant in both habitats while *Anabaena* was common in the pond but rare in the ricefield. Of the Bacillariophyceae, *Melosira* was the most dominant plankton in the pond, although it was rare in the paddy field. Among the Euglenophyceae, *Phacus* was found in both habitats (Table 3).

Of the Rotifera, *Brachionus*, *Filinia* and *Trichocerca* genera were recorded only from the pond while *Polyarthra* and *Keratella* were present in both habitats. Among the Crustacea, *Diaptomus* was common in the paddy field and rare in the pond and *Cyclops* was recorded in both habitats. *Moina*, *Bosmina*, *Alona*, *Daphnia* and *Diphanosoma* were recorded only in the paddy field. *Cypris* of the Ostracoda were recorded only from the ricefield. Unidentifiable crustacean nauplii were the second dominant zooplankton in the paddy field but were also found in the pond (Table 3).

Discussion

Physico-chemical and biological properties of water of both habitats were within the acceptable ranges for aquaculture (Hajek and Boyd 1994). Water temperature, dissolved oxygen and carbon dioxide content, and pH ranges as recorded in this study were similar to the characteristics of water from deepwater rice-fish farming in West Bengal, India (Mukhopadhyay *et al.* 1992). The general pattern of higher values of total hardness than alkalinity suggests the dominance of non-carbonate hardness (Boyd 1990). In both habitats, the

concentration of ammonia-nitrogen was about equal to the ranges usually found in fertilized fish ponds (Ali 1992) and was well below the level which might cause toxic effects (Hasan and Macintosh 1986; Boyd 1990).

Feeding activity was continuous in *Oreochromis* spp., with diurnal variation in stomach content and per cent of fish feeding. Small tilapia were more active feeders than large ones. Tilapia are frequent feeders (unlike salmonids and catfish which can consume a big meal every 8-12 h) and because they have small, rudimentary, thin-walled acidic stomachs that benefit from several feedings per day (Lobel 1981; Lovell 1995).

The relative clear pattern of feeding activity in the pond was absent in the ricefield, reflecting greater reliance on periphytic detritus in the paddy field and periphytic epipelon in the pond. Resources exploited by the *Oreochromis* spp. were different in the two habitats. In the ricefield, periphytic detrital aggregate was the principal dietary component of both sizes while, in the pond, algal matter, usually periphytic epipelon such as *Anabaena* sp., was the main food item. Similarly blue tilapia (*O. aureus*) juveniles were reported to graze on *Anabaena* sp. (McDonald 1987). In the paddy field, the diet was supplemented by small amounts of filamentous green algae, unidentified crustacean eggs and nauplii and *Cypris* sp. of the Ostracod. The small contribution from zooplankton reflects the tilapias opportunistic feeding behavior and illustrates a phenomenon found in other fishes, e.g. Hawaiian goby, *Sicyopterus stimpsoni* (Kido 1996). This indicates the benthic feeding habit, as browser or surface grazer, and the importance of periphyton (epipelon) as their food. This sort of feeding habit was also reported earlier for *O. niloticus* (Chapman and Fernando 1994) from Thailand.

Feeding electivity of these size ranges indicated that *Oreochromis* spp. have apparently no ontogenetic shifts in diet in the present study and are reliant on the same food resources in either habitat, with competition or dietary overlap between the small and large size. While other workers (Northcott and Beveridge 1988; Tudorancea *et al.* 1988; Yowell and Vinyard 1993) have found ontogenic dietary shifts in tilapias studying in different habitats and working with wider size groups. *O. niloticus* do undergo a dietary shift at 3-6 cm (Northcott and Beveridge 1988; Tudorancea *et al.* 1988). It could be concluded that *Oreochromis* spp. is an omnivorous opportunistic - generalistic feeder, benthophytophagous in the pond but detritivorous in the paddy field. This detritivorous feeding habit should not be confused as iliophagy - the habit of eating mud which contains organic detritus and associated organisms. Closer examination showed no silt, mud or associated organisms. In this study, *Oreochromis* spp. showed the characteristic feeding selectivity of both *O. mossambicus* and *O. niloticus* by feeding on the algae and detritus depending on their availability, as reported by Vass and Hofstede (1952), Bowen (1981), Otto Infante (1985), Bitterlich (1985) for *O. mossambicus* and by Dewan and Saha (1979) and Saha and Dewan (1979), Harbott (1982) for *O. niloticus*. However, Bishai (1975) from Sudan, Spataru (1978) from Israel, Premjith *et al.* (1987) from India and Ufodike and Wada (1991) from Nigeria reported *O. niloticus* as mainly zooplanktivorous at 2-24 cm sizes. Nonetheless, *O. aureus* was reported as predominantly phytoplanktophagous in Nicaragua (Porrás and

Noguera-Canales 1989) and Cuba (Martinez and Quinones 1988; Polastre-Melgar 1989) while zooplanktivorous from Mexico (Salvadores and Guzman 1983). Dewan and Saha (1979) reported that *O. niloticus* preferred to feed on blue-green and green algae in winter, diatoms in early summer and debris in summer. Generally, the composition of any fish's stomach content varies throughout the year and each important food item tends to have a maximum importance at ascertain season (Hynes 1950).

Based on the regression analyses carried out on the stomach contents we conclude that small fish were more active feeders than large fish and specific feeding (food consumption) decreased with increasing fish size. This contradicts the previous hypothesis of Dewan and Saha (1979) and Saha and Dewan (1979) that specific feeding rate increases with the increase in size. A similar phenomenon of decrease in feeding with respect to fish size was reported for *O. aureus* from Mexico (Salvadores and Guzman 1983), carnivorous grouper, *Epinephelus guttatus* (Pauly 1986) and many other fishes.

Our results are in agreement with the hypothesis that detritivorous species feed continuously, as compensation for the low nutritional value of these resources (Fugi *et al.* 1996). Daily feeding rhythms are reported not to be uniform for many benthivorous species (Fugi *et al.* 1996). In this study, in the paddy field, tilapia was found to feed directly on detrital aggregate. Lobel (1981) reported that *Oreochromis* sp. minimize ingesting sand while browsing on detritus and periphyton. The filter feeding mechanism of *O. niloticus* may be a relatively unimportant method of ingesting food (Dempster *et al.* 1993).

In this study, stomach fullness indices were not always in synchrony with the values of mean stomach content ($\text{mg} \cdot \text{g}^{-1} \text{bw}$). This may be because lighter food items like phytoplankton, zooplankton and pieces of macrophytes need to be ingested in large quantities to affect the index of stomach fullness. We conclude that stomach fullness, particularly visual, is not as appropriate for expressing intensity of feeding activity as stomach content.

Our observations on complete evacuation, 9-13 h in the pond and 1-4 h in the paddy field, support the work of Hofer and Newrkla (1983). They reported that small *O. mossambicus* feeding on detritus and littoral fauna had a mean gut passage time of 1.7 h at water temperatures of 27-28°C and 1.3 h at water temperatures of 32-33°C. Bowen (1981) reported that in *O. mossambicus* periphytic detrital aggregate passes unaltered through the buccal cavity to the stomach and intestinal digestion and assimilation of most organic matter is completed in the first half of the intestine.

In the pond, both sizes fed at common levels, 2.2% of $\text{bw} \cdot \text{day}^{-1}$ for the small fish and 2.3% of $\text{bw} \cdot \text{day}^{-1}$ for the large. This is comparable to feeding rates of 3-5% of $\text{bw} \cdot \text{day}^{-1}$ in *Oreochromis* spp. found by Sastradiwirja (1990).

The consumption model used in this study (Elliott and Persson 1978) is widely accepted and adequate to estimate the daily ration of fish that feed throughout the day on a wide range of prey types (benthivorous and planktivorous fish) and exhibit occasional feeding peaks (Boisclair and Marchand 1993; Andrade *et al.* 1996). Jobling (1981, 1986) and Persson (1986) pointed out the advantages of using exponential models and opined that most

gastric evacuation and daily ration estimation can satisfactorily be described by the exponential model. However, optimal growth rates of stocked fish can only be obtained by consumption of optimal daily rations by the fish, which were not met under our experimental conditions. Since the composition (%) of the diet is based on the discrete number of food items in each category rather than the weight of each item, it is not possible to calculate the amount of protein or energy consumed in the two habitats.

Conclusion

The result of the present study confirm the previous finding of detritivory and omnivory in *Oreochromis* spp. in Bangladesh but contradicts the hypothesis of increasing feeding intensity with increasing fish size. There is apparently no ontogenetic shift in their diet due to less narrow gap in size ranges. Hence, caution should be taken in mixed-size rearing of tilapia. In this pond and paddy condition, Bangladesh *Oreochromis* spp. is a browser or surface grazer and the periphytic epipelon and detrital aggregate are important food resources. The study reveals that the best time for field sampling of tilapia to determine their exploitation of available resources would be around 1500-1800 h in the pond and at 1500 h in the paddy field, which is the period of greatest feeding activity and highest stomach content. However, feeding activity in such shallow paddy environments may be disrupted by external influences such as traffic and lighting and, as such, test samples should be collected. The present study also suggests that a suitable stocking procedure in a paddy field would be to use the smaller size of tilapia when the diet may contain small but important amounts of micro- and filamentous algae and zooplankton, allow the detritus to accumulate as periphyton and let the growing fish feed increasingly on the detritus. In a pond, tilapia are strongly phytoplanktivorous and would compete with other planktivorous popular carp (both endemic and exotic) species if stocked. Further detailed studies are required to evaluate the empirical rate of gastric evacuation, diet overlap with other carps, seasonal feeding pattern and nutritional values of ingested food items.

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