Food and feeding ecology of hilsa (*Tenualosa ilisha*) in Bangladesh's Meghna River basin

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Hilsa shad (*Tenualosa ilisha*) is one of the most important tropical fish of the Indo-Pacific region, especially in Bangladeshi waters. The hilsa fishery has declined significantly since 2002 mainly due to overfishing, habitat destruction and pollution; the Government of Bangladesh and researchers are therefore working to ensure its sustainable management. This study on hilsa food and feeding ecology offers essential information for policymaking and the effective management of the hilsa fishery. to hilsa It is based on a year-long study of hilsa specimens collected from the Meghna River at Chandpur across a range of age groups, from fry to adult. An analysis of the specimens' gut contents, and of the water itself, identified a range of phytoplankton and zooplankton genera; it also established the hilsa's food preferences at various stages in the life cycle using Ivlev's 'electivity index'.

Contents

1 Introduction

The hilsa shad (*Tenualosa ilisha*), popularly known as hilsa, belongs to the sub-family Alosinae of the Clupeidae family. It inhabits freshwater rivers, estuaries and marine environments. The hilsa is a unique commercial fish in the Indo-Pacific region, especially in Bangladesh, India and Myanmar. It is an important migratory species in the Bay of Bengal, Persian Gulf, Red Sea, Arabian Sea, Vietnam Sea and China Sea. Its riverine habitats include the Satil Arab; the Tigris and Euphrates of Iran and Iraq; the Indus of Pakistan; the Irrawaddy of Myanmar; the Ganga, Bhagirathi, Hooghly, Rupnarayan, Brahmaputra, Godavari, Narmada, Tapti and other coastal rivers of India; and the Padma, Jamuna (Brahmaputra), Meghna, Tetulia, Karnafuly Andhermanik, Bashkhali, Baleshor, and other coastal rivers of Bangladesh. The hilsa fishery in Bangladesh is dependent on this single species that contributes up to 99 per cent of the total hilsa catch from the Padma-Brahmaputra and Meghna River basins, coastal zones, and the Bay of Bengal region (Rahman *et al*., 2012).

Hilsa mainly migrate through the largest water body – the Padma-Meghna river system – for breeding and feeding purposes. They spend their different life stages in different habitats, therefore food and feeding strategies may vary in different ecosystems. Food composition and feeding habits vary according to the time of day, season, fish size, ecological factors and food substances present in the water body (Hynes, 1950). A knowledge of the hilsa's food and feeding habits has manifold advantages for the efficient management and exploitation of the fish (Khan and Fatima, 1994). Understanding the relationship between the fish and their favourite food items, seasonal distribution and availability of food items in nature, helps to locate the occurrence, distribution and abundance of fish stock – which will eventually help in the exploitation of these resources. Analysing gut contents and features of the alimentary system provides information on hilsa food and feeding habits, as well as on selective feeding (Kuruppasamy and Menon, 2004). Gut content analysis also helps to understand the tropic dynamic and prey-predator interaction in the ecosystem, which facilitates ecosystem-based fisheries management.

The food and feeding habits of hilsa have been attracting the attention of fisheries biologists and ecologists of the South Asian countries for decades. Many researchers have carried out studies on the food and feeding habits of hilsa shad *T. ilisha* in different water bodies (Pillay and Rao, 1962; Halder, 1968; Ramakrishnaiah, 1972; De and Datta, 1990; De *et al*., 2013; Dutta *et al*., 2013 from India; Rahman *et al*., 1992, from Bangladesh; and Jafri *et al*., 1999, and Narejo *et al*., 2005, from Pakistan). Knowledge of food and feeding habits of the species is still confined to the scientific reports of Hora (1938), Nair (1939), Pillay (1958), Pillay and Rao (1962), Halder (1968), Rahman *et al.* (1992), Jafri *et al.* (1999) and De *et al.* (2013). However, detailed information on *selective* feeding – or food preference and avoidance – in the context of hilsa food and feeding ecology is not yet available for the Padma-Meghna river basins in Bangladesh waters.

The aim of this study was to provide a quantitative and qualitative estimation of the food and feeding habits of *T. ilisha*, with a special emphasis on selective feeding, for the Meghna River system in Bangladesh.

2

Materials and methods

2.1 Collecting fish specimens

Fish specimens of different size groups were collected randomly by fishers in Meghna River at Chandpur, a confluence of two large rivers (the Padma and the Meghna) which goes on to form the widest estuary in the country as it flows into the Bay of Bengal. This area is one of the most important hilsa fish sanctuaries declared by the Government of Bangladesh. Mature hilsa take this route on their freshwater migration to spawn in upstream rivers. The fish were sampled once a month for a year, from January to December 2014. The freshly caught specimens were preserved in ice in an insulated box and brought to the laboratory. The fish were then categorised by size. Each month 25–30 fish, from a total of 318 specimens of hilsa, were selected for gut content analysis. They varied in length from 7 to 48 centimetres and in weight from 40 to 1,309 grams.

2.2 Collecting water samples

To analyse the plankton, water samples were collected from the Meghna River system at a depth of two metres using a flexible plastic tube 2.5 centimetres in diameter. The collected water was passed through a plankton net with a mesh size of 15 micrometres and the concentrated plankton sample was transferred to a plastic bottle and preserved in 10 per cent buffered formalin.

2.3 Analysis of water plankton and gut contents

2.3.1 Food organism analysis in water samples

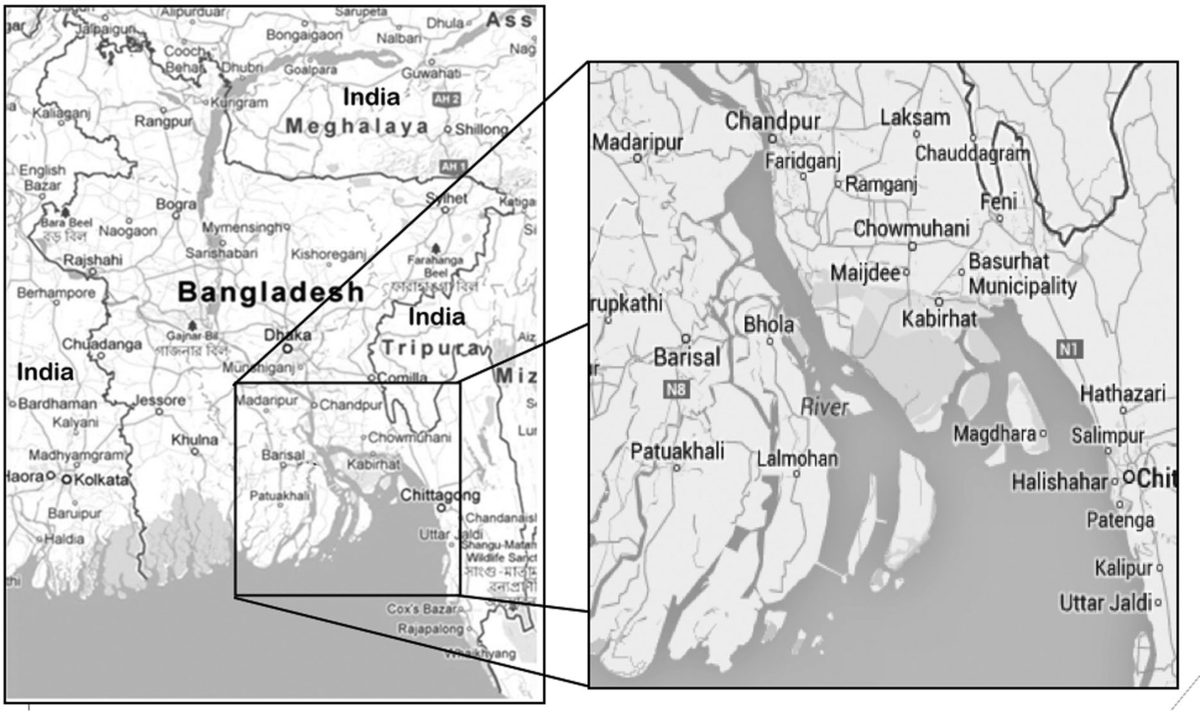
Researchers identified and counted the plankton using the Sedgwick-Rafter counting cell,[1] following the standard methods (APHA, 1992). Plankton were identified up to genus level following the determination keys of Ward and Whipple (1959), Needham and Needham (1962), Prescott (1962) and Bellinger (1992).

2.3.2 Gut content analysis

Researchers dissected the alimentary canals of the preserved fish from the oesophagus to the anus and preserved them in 10 per cent buffered formalin. The gut contents (collected from the pyloric stomach to the gizzard) from each fish were then dissolved in water, and any available food organisms (plankton) examined under an electrical microscope (Olympus BH2) using a Sedgwick-Rafter counting cell for qualitative and quantitative analysis. For the qualitative analysis, researchers matched plankton with the available

[1] Model 550, Fisons

Figure 1. Location of the study: Meghna River, Chanpur District'



photographs and literature. Plankton were identified up to genus level following the determination keys of Ward and Whipple (1959), Needham and Needham (1962), Prescott (1962) and Bellinger (1992). Researchers made a quantitative estimation of the gut contents using the frequency of occurrence method and the numerical method (Hynes, 1950; Pillay, 1952; Dewan and Shaha, 1979; Hyslop, 1980; Dewan *et al.*, 1991; Kariman *et al.*, 2009).

Numerical method

For this method, the number of each food item is expressed as a percentage of the total number of food items found in the stomach (Windell and Bowen, 1978; Costal *et al.*, 1992; Kariman *et al.*, 2009; Hyslop, 1980).

Frequency of occurrence

This is the number of stomachs in which a given category of food items is present, expressed as a percentage of the total number of non-empty stomachs examined (Hynes, 1950; Hyslop, 1980; Windell and Bowen, 1978; Bowen, 1983).

Frequency of occurrence: $Qi = 100*(Ji*P^{\wedge}-1)$

Where:

Qi = frequency of occurrence (per cent) of the i food item in the sample
Ji = number of stomachs in which the i item is found
P = total number of stomachs with food in the sample.

2.3.3 Electivity index

The recorded food organisms were compared with the food organisms collected from the natural environment. Food preferences were analysed for each stage of growth as well as at each site using Ivlev's food preference index, known as the 'electivity index' (E) (Ivlev, 1961).

The E value is determined using the following equation:

$$E = \frac{Pg - Pw}{Pg + Pw}$$

Where:

Pg = percentage of a particular food organism in the gut
Pw = percentage of a particular food organism in the water
E values vary between −1 to +1. Positive values indicate selection for a certain food item while negative values indicate avoidance.

3

Results

3.1 Plankton compositions in the gut analysis

Researchers recorded 56 genera of phytoplankton in the analysis of hilsa guts, including Bacillariophyceae (or diatoms; 18 genera), Chlorophyceae (or green algae; 24 genera), Cyanophyceae (9 genera), Euglenophyceae (2 genera), Xanthophyceae (2 genera) and Dinophyceae (1 genus). There were 17 genera of zooplankton, including Rotifera (7 genera), Cladocera (5 genera), Copepoda (4 genera) and Protozoan (1 genus) (Table 1). Chlorophyceae therefore occurred most frequently among the various groups of phytoplankton, whereas Rotifera was the most numerous group for zooplankton. The combined analysis of hilsa gut contents revealed that hilsa mainly feed on phytoplankton (98.08 per cent) with a small quantity of zooplankton (1.92 per cent) (Table 3). Chlorophyceae was the most common (58.04 per cent) among the phytoplankton, followed by Bacillariophyceae (38.57 per cent), Cyanophyceae (1.24 per cent), Euglenophyceae (0.1 per cent), Xanthophyceae (0.03 per cent) and Dinophyceae (0.1 per cent). Among the zooplankton Cladocera (0.77 per cent) dominated in the gut contents, followed by Rotifera (0.56 per cent), Copepoda (0.52 per cent) and Protozoa (0.06 per cent) (Table 3).

3.2 Food and feeding habits of hilsa at different sizes

The numerical study of hilsa gut contents for different size groups revealed that Bacillariophyceae (diatoms), Chlorophyceae (green algae) and crustaceans (Copepoda and Cladocera) formed the major constituents of their food (see Table 2). It was observed that considerable amounts of Chlorophyceae (53.67 per cent), Bacillariophyceae (42.44 per cent), Cyanophyceae (0.5 per cent), Copepoda (1.75 per cent), Cladocera (0.9 per cent), Rotifera (0.7 per cent) and Protozoa (0.05 per cent) were found in the gut contents of juvenile hilsa (jatka) below 10 centimetres in size, whereas for hilsa measuring 11–20cm, food consisted of Chlorophyceae (57.23 per cent), Bacillariophyceae (39.17 per cent), Cyanophyceae (0.99 per cent), Euglenophyceae (0.05 per cent), Xanthophyceae (0.04 per cent), Copepoda (1.04 per cent), Cladocera (0.85 per cent), Rotifera (0.59 per cent) and Protozoa (0.02 per cent). Jatka in the 21–30 centimetre group contained Chlorophyceae (58.34 per cent), Bacillariophyceae (37.65 per cent), Cyanophyceae (1.66 per cent), Euglenophyceae (0.06 per cent), Cladocera (0.89 per cent), Rotifera (0.87 per cent), Copepoda (0.44 per cent) and Protozoa (0.04 per cent). Adult hilsa of 31–40 centimetres fed on Chlorophyceae

Table 1. Plankton genera observed in the hilsa gut analysis

PLANKTON GROUP	GENUS
Phytoplankton	
Bacillariophyceae	*Amphora, Asterionella, Bacillaria, Coscinodiscus, Cyclotella, Diatoma, Fragillaria, Gomphonema, Gyrosigma, Melosira, Navicula, Nitzschia, Pleorosigma, Rhizosolenia, Surirella, Synedra, Tabellaria, Triceratium*
Chlorophyceae	*Actinastrus, Ankistrodesmus Botryococcus, Chlorella, Closterium, Coelastrum, Micractinium, Microspora, Muogeotia, Oedogonium, Oocystis, Palmella, Pediastrum, Pleorococcus, Scenedesmus, Selenestrum, Spirogyra, Staurastrum, Stichococcus, Tetraedron, Ulothrix, Uroglena, Volvox, Zygnema*
Cyanophyceae	*Anabaena, Aphanizomenon, Aphanocapsa, Chroococcus, Gomphosphaeria, Merismopedium, Microcystis, Oscillatoria, Spirulina*
Euglenophyceae	*Euglena, Phacus*
Xanthophyceae	*Botrydium, Tribonema*
Dinophyceae	*Ceratium*
Zooplankton	
Copepoda	*Cyclops, Diaptomus, Laptodora, Naupleus*
Cladocera	*Bosmina, Diaphanosoma, Daphnia, Moina, Sida*
Rotifera	*Asplanchna, Brachionus, Filinia, Hexarthra, Keratilla, Poliarthra, Trichocerca*
Protozoa	*Difflugia, Favella*

(58.67 per cent), Bacillariophyceae (38.44 per cent), Cyanophyceae (1.20 per cent), Euglenophyceae (0.11 per cent), Xanthophyceae (0.05 per cent), Dinophyceae (0.01 per cent), Cladocera (0.7 per cent), Rotifera (0.46 per cent), Copepoda (0.31 per cent) and Protozoa (0.05 per cent). The large hilsa group of 41–50 centimetres contained Chlorophyceae (57.71 per cent), Bacillariophyceae (38.15 per cent), Cyanophyceae (1.17 per cent), Euglenophyceae (0.18 per cent), Xanthophyceae (0.02 per cent), Cladocera (0.91 per cent), Rotifera (0.89 per cent) Copepoda (0.82 per cent) and Protozoa (0.19 per cent).

The gut contents analysis using the frequency of occurrence method (also in Table 2) shows that the percentage of feeding individuals was found to be higher among the young or fry-sized hilsa (less than 10 centimetres long). The highest occurrence (100 per cent) of Bacillariophyceae and Chlorophyceae were found in this group, followed by Copepoda (85.71 per cent), Cladocera (85.71 per cent), Rotifera (71.43 per cent), Cyanophyceae (57.14 per cent) and Protozoa (14.19 per cent). In the 11–20 centimetre group, Bacilariophyceae had the highest occurrence (91.84 per cent), followed by Chlorophyceae (89.8 per cent), Cyanophyceae (71.43 per cent), Copepoda (51.02 per cent), Rotifera (51.02 per cent), Cladocera (48.98 per cent), with the lowest occurrence by Protozoa (6.12 per cent), Euglenophyceae (2.04 per cent) and Xanthophyceae (2.04 per cent) groups. In the guts of fish between 21 and 30 centimetres long, Chlorophyceae constituted the major food item (97.92 per cent) followed by Bacillariophyceae (86.46 per cent), Cyanophyceae (69.79 per cent), Copepoda (36.46 per cent), Cladocera (37.50 per cent), Rotifera (47.92 per cent) and Protozoa (6.25 per cent). Bacillariophyceae was found to have the highest (92.41 per cent) occurrence as a food item for fish between 31 and 40 centimetres, followed by Chlorophyceae (87.34 per cent), Cyanophyceae (68.35 per cent), Cladocera (39.24 per cent), Copepoda (35.44 per cent), Rotifera (30.38 per cent) and Protozoa (7.59 per cent). In the guts of fish longer than 41 centimetres there were occurrences of Bacillariophyceae (96.43 per cent), Chlorophyceae (89.29 per cent), Cyanophyceae (78.57 per cent), Copepoda (35.71 per cent) and

Table 2. Plankton composition found in hilsa at different sizes

	HILSA SIZE GROUPS (BY TOTAL LENGTH)									
	BELOW 10cm		11–20cm		21–30cm		31–40cm		41–50cm	
Food items	% No.	% O	% No.	% O²	% No.	% O	% No.	% O	% No.	% O
Phytoplankton	**96.61**	**100**	**97.48**	**100**	**97.75**	**97.92**	**98.48**	**100**	**97.23**	**100**
Bacillariophyceae	42.44	100	39.17	91.84	37.65	86.46	38.44	92.41	38.15	96.43
Chlorophyceae	53.67	100	57.23	89.8	58.34	97.92	58.67	87.34	57.71	89.29
Cyanophyceae	0.50	57.14	0.99	71.43	1.66	69.79	1.20	68.35	1.17	78.57
Euglenophyceae	0	0	0.05	2.04	0.06	4.17	0.11	11.39	0.18	10.71
Xanthophyceae	0	0	0.04	2.04	0.01	1.04	0.05	2.53	0.02	3.57
Dinophyceae	0	0	0	0	0.03	1.04	0.01	1.27	0	0
Zooplankton	**3.39**	**100**	**2.52**	**67.35**	**2.25**	**65.63**	**1.52**	**55.7**	**2.77**	**42.86**
Copepoda	1.75	85.71	1.06	51.02	0.44	36.46	0.31	35.44	0.81	35.71
Cladocera	0.90	85.71	0.85	48.98	0.89	37.50	0.70	39.24	0.90	25
Rotifera	0.70	71.43	0.59	51.02	0.87	47.92	0.46	30.38	0.87	25
Protozoan	0.05	14.29	0.02	6.12	0.04	6.25	0.05	7.59	0.19	14.29

Notes: No. – number of individual plankton or food items in the guts; O – occurrence of individual items in the guts

Cladocera (25 per cent). Rotifera (25 per cent) and Protozoa (14.29 per cent) were also observed. The percentage of occurrence method also indicated that at the early stages, feeding intensity was highest for Bacillaripophyceae and Chorophyceae among phytoplankton, and for Copepoda and Cladocera in the zooplankton group.

3.3 Electivity index of food preference

The electivity index was used to determine hilsa food preferences. The overall electivity index results showed that hilsa preferred phytoplankton over zooplankton, and among the phytoplankton, Bacillariophyceae or diatoms (+0.06) and Chlorophyceae or green algae (+0.04) were preferred. The rest of the food groups showed negative values (Table 3). This indicates that Bacillariophyceae is the hilsa's most preferred food item in general. Breaking down the data by hilsa size and life stages gives a more detailed picture (Table 4). In the early stages of the hilsa life cycle, the highest electivity index (+0.18) was found among the zooplankton in the form of Copepoda. Among the phytoplankton, a high electivity index (+0.11) was found for Bacillariophyceae; as the hilsa grew, the electivity index for this item decreased. In the early stages of the hilsa life cycle there was neutral selection for Chlorophyceae (Table 4), but this became positive during the adult stages. The fish responded positively to Bacillariophyceae and Chlorophyceae, but negatively to Cyanophyceae, Euglenophyceae and other groups. Among zooplankton, Copepoda and Cladocera were positively selected as food preferences at the early stages (below 10 centimetres in length). In other size groups (11–50 cm long), Copepoda was found frequently in hilsa guts, although the electivity index suggested a negative selection. Of the individual species of planktoner, hilsa showed positive selection for *Amphora*, *Coscinodisscus, Cyclotella, Melosira, Nitzchia* and *Tabellaria* in the Bacillariophyceae group, *Microspora, Tetraedron* and *Ulothrix* among the Chlorophyceae, and *Bosmina* from the Cladocera; with a negative or neutral selection for the rest of the other types of plankton (see Table 1).

Table 3. Ivlev's electivity index values showing hilsa food preferences for different plankton groups

GROUPS	PLANKTON IN GUT		PLANKTON IN WATER		ELECTIVITY INDEX (E)
	No. (per gut)	(% in gut)	No. (per litre)	(% in water)	
Phytoplankton	10,15,972	98.08	34,795	94.05	0.02
Bacillariophyceae	3,99,505	38.57	12,534	33.88	**0.06**
Chlorophyceae	6,01,171	58.04	20,019	54.11	**0.04**
Cyanophyceae	12,847	1.24	1964	5.31	−0.62
Euglenophyceae	1,081	0.10	83	0.22	−0.36
Xanthophyceae	360	0.03	62	0.17	−0.66
Dinophyceae	1009	0.10	134	0.36	−0.58
Zooplankton	19,873	1.92	2,201	5.95	−0.51
Copepoda	5,389	0.52	448	1.21	−0.40
Cladocera	8,006	0.77	322	0.87	−0.06
Rotifera	5,805	0.56	1,260	3.40	−0.72
Protozoan	672	0.06	163	0.44	−0.75

Table 4. Ivlev's electivity index of hilsa food preferences at different sizes

	BELOW 10 CM SIZE GROUPS				11–20 CM SIZE GROUPS				21–30 CM SIZE GROUPS				31–40 CM SIZE GROUPS				ABOVE 40 SIZE GROUPS			
	Mean plankton	% in gut	%P in water	E	Mean plankton	% in gut	% in water	E	Mean plankton	% in gut	% in water	E	Mean plankton	% in gut	% in water	E	Mean plankton	% in gut	% in water	E
Phytoplankton	**552857**	**96.61**	**94.05**	**0.01**	**602122**	**97.50**	**94.05**	**0.02**	**568063**	**97.75**	**94.05**	**0.02**	**1945506**	**98.48**	**94.05**	**0.02**	**1809857**	**97.23**	**94.05**	**0.02**
Bacillariophyceae	242857	42.44	33.88	0.11	241918	39.17	33.88	0.07	218667	37.65	33.88	0.05	759333	38.44	33.88	0.06	710071	38.15	33.88	0.06
Chlorophyceae	307143	53.67	54.11	0.00	353510	57.23	54.11	0.03	339479	58.34	54.11	0.04	1159358	58.67	54.11	0.04	1074286	57.71	54.11	0.03
Cyanophyceae	2857	0.50	5.31	−0.83	6122	0.99	5.31	−0.69	9375	1.66	5.31	−0.56	23481	1.20	5.31	−0.64	21786	1.17	5.31	−0.64
Euglenophyceae	0	0.00	0.22	−1.00	327	0.05	0.22	−0.62	333	0.06	0.22	−0.59	2198	0.11	0.22	−0.33	3286	0.18	0.22	−0.12
Xanthophyceae	0	0.00	0.17	−1.00	245	0.04	0.17	−0.62	21	0.01	0.17	−0.96	988	0.05	0.17	−0.54	429	0.02	0.17	−0.76
Dinophyceae	0	0.00	0.36	−1.00	0	0.00	0.36	−1.00	188	0.03	0.36	−0.98	148	0.01	0.36	−0.96	0	0.00	0.36	−1.00
Zooplankton	**19429**	**3.39**	**5.95**	**−0.27**	**15469**	**2.50**	**5.95**	**−0.41**	**13063**	**2.25**	**5.95**	**−0.45**	**29975**	**1.52**	**5.95**	**−0.59**	**51571**	**2.77**	**5.95**	**−0.36**
Copepoda	10000	1.75	1.21	0.18	6449	1.04	1.21	−0.07	2583	0.44	1.21	−0.46	6222	0.32	1.21	−0.59	15000	0.81	1.21	−0.20
Cladocera	5143	0.90	0.87	0.02	5265	0.85	0.87	−0.01	5188	0.89	0.87	0.01	13802	0.70	0.87	−0.11	16857	0.91	0.87	0.02
Rotifera	4000	0.70	3.40	−0.66	3633	0.59	3.40	−0.71	5063	0.87	3.40	−0.59	9062	0.46	3.40	−0.76	16214	0.87	3.40	−0.59
Protozoan	286	0.05	0.44	−0.80	122	0.02	0.44	−0.91	229	0.04	0.44	−0.84	889	0.05	0.44	−0.81	3500	0.19	0.44	−0.40

Notes: %Pg – Percentage of a particular food organism in the gut; %Pw – percentage of a particular food organism in the water; E – electivity index value

4

Comparing findings across hilsa feeding studies

4.1 Plankton compositions as food items in the gut

The gut content analysis of hilsa from the early stages (fry and juvenile) to adult revealed 51 genera of phytoplankton: Bacillariophyceae (18 genera), Chlorophyceae (20 genera), Cyanophyceae (9 genera), Euglenophyceae (2 genera), Xanthophyceae (1 genus) and Dinophyceae (1 genus). It also found 17 genera of zooplankton: Copepoda (4 genera), Rotifera (7 genera), Cladocera (5 genera) and Protozoan (1 genus). This study observed a greater generic abundance of plankton, both phytoplankton and zooplankton, in the hilsa gut than the Rahman *et al.* (1992) study, which identified only 39 genera; 27 phytoplankton and 12 zooplankton.

The organisms found in hilsa guts, constituting their main identifiable food items, were Bacillriophyceae (*Amphora, Cosciondisscus, Cyclotella, Diatoma, Navicula, Nitzchia, Rhizosolenia, Surirella, Fragillaria, Tabellaria, Melosira*), Chlorophyceae (*Tetraedron, Stichococcus, Microspora, Padiastrum, Chlorella, Ulothrix*), Cyanophyceae (*Aphanizomenon, Mycrocystis, Gomphosphaeria, Osillatoria*), Copepoda (*Cyclops, Diaptomus, Naupleus*) Cladocera (*Bosmina, Daphnia, Diaphanosoma, Moina*), Rotifera (*Keratilla, Brachionus, Polyarthra, Trichocerca*). But Pillay and Rao (1962) observed different groups of phytoplankton such as *Spirogyra, Oscillatoria, Microcystis* and *Merismopedia* in the gut contents of *H. ilisha.* Halder (1968) identified the food items as *Cyclotella, Melosira, Gyrosigma, Microcystis, Aphanocapsa, Oscillatoria* and *Spirogyra* in *T. ilisha* stomachs in the 120 to 160 millimetre and 180 to 200mm size ranges in the Hooghly estuarine system. On the other hand, Narejo *et al.* (2005) reported that hilsa selected some genera of phytoplankton such as Bacillariophyta *(Cyclotella, Cymbella, Gyrosigma, Melosira* and *Navicula* species), Cyanophyta *(Aphanocapsa, Chroococus, Lyngbya, Merismopedia, Microcystis,* and *Oscillatoria)* and Chlorophyta *(Odogonium, Rhizoclonium* and *Scendesmus)*. They also mentioned that *Tenualosa ilisha* avoided zooplankton; whereas present findings reveal that hilsa prefer zooplankton in the early stages, and their choice diverts towards phytoplankton as they mature.

The present study found that hilsa feed mainly on phytoplankton (98.08 per cent) with a small quantity of zooplankton (1.92 per cent). Diatoms, algae and crustaceans formed the major constituents of food in the guts of hilsa of all size groups; small amounts of sand particles and debris were also observed in the gut, but were not taken into consideration. Chlorophyceae appeared with the highest percentage (58.04 per cent) among phytoplankton, followed by Bacillariophyceae (38.57 per cent), Cyanophyceae (1.24 per cent), Euglenophyceae (0.1 per cent), Xanthophyceae (0.03 per cent) and Dinophyceae (0.1 per cent). Among zooplankton, Cladocera (0.77 per cent) dominated in the gut contents, followed by Rotifera (0.56 per cent), Copepoda (0.52 per cent) and Protozoa (0.06 per cent).

Similar results were observed by Rahman *et al.* (1992), who stated that hilsa were predominantly a planktonic filter feeder, although sand and debris were also seen in their guts. A few studies on the food and feeding habits of hilsa indicate that hilsa shad is a filter feeder and feeds on plankton (Hora, 1938; Jones and Sujansingani, 1951). The feeding adaptation of *T. ilisha* and the structure of its digestive tract also suggest the planktivorous feeding habit of palla (Jafri, 1987; Halder, 1968; Bapat and Bal, 1958). Some genera of phytoplankton, such as green algae, diatoms, blue-green algae and zooplankton (mainly copepods) were observed in the guts of *T. ilisha* from different water bodies (Jafri *et al.*, 1999; Qureshi, 1968), which were more or less similar to the present findings. But the present results do not match the findings of Ramakrishnaiah (1972), who described the food and feeding habits of *H. ilisha* as consisting of organic detritus (48.56 per cent), copepods (25.82 per cent), algae (10.32 per cent), molluscan larvae (7.85 per cent), mysids (5.34 per cent) and diatoms (2.10 per cent) in the 50–150 mm size range in Chilka Lake. Rahman *et.al* (1992) mentioned the food composition as 42 per cent algae, 36 per cent debris with sand, 15 per cent diatoms, 3 per cent rotifers, 2 per cent crustaceans, 1 per cent protozoan and 1 per cent miscellaneous. A more recent document has shown hilsa guts containing 41–65 per cent algae, 36.28 per cent sand particles, 15.36 per cent diatoms, 1.89 per cent crustaceans, 1.22 per cent protozoa and 0.41 per cent miscellaneous items (BFRI, 2011). In terms of food items, the present findings are more or less similar to the above, although the quantity differs.

4.2 Food and feeding habits of hilsa in different size groups

The gut contents of hilsa in different size groups revealed that Bacillariophyceae (diatoms), Chlorophyceae (green algae) and crustaceans (Copepoda and Cladocera) formed the major constituents of food. Phytoplankton was higher both in number and in occurrence in most of the stomachs across all size groups, but in the case of zooplankton, a higher frequency of occurrences was observed at the early stages of life. The year-long study indicated that both Chlorophyceae and Bacillariophyceae dominated in all the size groups; however zooplankton – mainly crustacean – dominated in the early age group. A small portion of silt and debris of negligible amounts was also observed in the gut contents.

The juvenile hilsa (up to 10 centimetres long) are mostly confined to rivers and the upper reaches of the estuary. In this study, it was observed that hilsa fry and juveniles mainly feed on green algae, diatoms from among the phytoplankton and crustaceans from among the zooplankton, and the frequency of individual food items occurring was much higher than in adults. Similar findings were observed by Hora (1938), who reported that the young hilsa (between 2 and 4 centimetres in length) mostly feed on diatoms and sparingly on crustacean, while the slightly larger specimens (up to 10cm) were found to feed on smaller crustaceans and also on insects and polyzoa. De *et al.* (2013) stated that diatoms were also found as a major food item of *Tenualosa ilisha* from marine, brackish as well as freshwater habitats of India. Shafi *et al.* (1977) reported that the juveniles were voracious eaters and bottom feeders, and their food and feeding habits changed with their increase in size and with changes in the season. Present findings differ from those of Ramakrishnaiah (1972), who said that juveniles (5–15 centimetres) subsisted mainly on organic detritus, and the adults on zooplankton.

The present study found that in **jatka and pre-adult stages** (11–30 centimetres long), hilsa mainly feed on phytoplankton (97.48 per cent, 97.75 per cent) with a small proportion of zooplankton (2.52 per cent, 2.25 per cent). Similar findings were reported by Mazid and Islam (1991) who noted that the relatively large but immature hilsa preferred phytoplankton to zooplankton, and that jatka were voracious feeders. Rahman *et al.* (1992) have also suggested that the diet of the jatka stages of hilsa includes both phytoplankton and zooplankton; the diet of post-jatka hilsa includes mostly phytoplankton. These findings are more or less similar to the present findings. However, the present findings differ from the outcomes of De and Datta (1990), who reported that Copepoda was the most important food item consumed by fry, juvenile and adult hilsa; whereas Narejo *et al.* (2005) found that the adult hilsa (13.8–32.8 centimetres long) feed exclusively on phytoplankton, Bacillariophyceae dominating the diet with a 70 per cent occurrence. But in the present study, Chlorophyceae appeared as the highest percent composition in the guts of all size groups.

In the present study, the gut contents of **adult fish** (above 30 centimetres long) mostly comprised of phytoplankton (98.48 per cent, 97.23 per cent) with a small proportion of zooplankton (1.52 per cent, 2.77 per cent). Raja (1985) reviewed the food and feeding habits of hilsa, drawing together the findings of a large number of researchers from the late 1930s to the late 1970s (Hora, 1938; Hora and Nair, 1940; Chacko and Ganapati, 1949; Pillay and Rao, 1962; Halder, 1968, 1970; Quereshi, 1968; Shafi *et al.*, 1977). According to them, the dominant food items for hilsa were crustaceans (in particular copepods), diatoms, green and blue green algae, organic detritus, mud and sand. They further mentioned that hilsa gradually adapted to a diet of mainly phytoplankton when they matured. In a more recent review paper, Rahman (2006) stated that hilsa is a predominantly planktonic filter feeder, which is similar to the present findings. The present research revealed that Chlorophyceae and Bacillariophyceae from among the phytoplankton dominated in all the age groups, and among the zooplankton crustacean (Copepoda and Cledocera) mainly dominated in the yearly age group, although Copepoda and Cladocera frequently occurred in adult hilsa guts. De and Datta (1990) studied the hilsa's alimentary tract and described their feeding adaptation attributes as follows: no teeth in the mouth, filter mechanisms in the form of fine gill rakers, a pharyngeal pouch, a modified stomach as a gizzard and a moderately long intestine. All these features indicated that hilsa possess a strainer type of feeding mode adapted to the planktivorous feeding habits of these species.

4.3 Electivity index of food preference

The present study's electivity index showed that hilsa preferred phytoplankton over zooplankton. Among phytoplankton, Bacillariophyceae (diatoms) were the most preferred hilsa food organisms, especially in the early stages of the life cycle. Hilsa showed a neutral preference for Chlorophyceae in the early life stages, but moving towards it in the adult stages. The fish responded positively to Bacillariophyceae and Chlorophyceae, but negatively to Cyanophyceae, Euglenophyceae and other groups. Hilsa showed positive selections for Copepoda and Cladocera in zooplankton groups in the early stages (at less than 10 centimetres long), but a negative selection when sized from 11 to 50cm, although Copepoda and Cladocera were found frequently in the guts. Alhough there was no available review on the electivity index of hilsa food preferences, Jones and Sujansingani (1951) stated that hilsa was essentially a plankton feeder and did not exhibit any selection in feeding. But Narejo *et al.* (2005) reported that hilsa avoided zooplankton and showed a strong preference for some genera of phytoplankton, such as Bacillariophyta, Chlorophyta and Cyanophyta.

5

Summary and conclusion

The study has provided an in-depth understanding of the food and feeding biology of hilsa at different age groups, with insights into selective feeding on different plankton using the electivity index. The year-long study indicated that Bacillariophyceae (diatoms), Chlorophyceae (green algae) and crustaceans (Copepoda and Cladocera) formed the major food constituents in the guts of hilsa in all size groups, with a small amount of silt, debris and unknown particles in negligible quantities. It also indicated that both Chlorophyceae and Bacillariophyceae dominated in general; however, zooplankton (mainly crustacean) dominated in the early age groups. Bacillariophyceae (diatoms) from among the phytoplankton was the most preferred hilsa food group, especially at the early stages of its life cycle, and their neutral response to Chlorophyceae changed to positive when they reached maturity. The hilsa's preferred food items in the form of phytoplankton and zooplankton were available in the environments of the hilsa fishery areas, especially in the sanctuary areas, throughout the year. It was also observed that natural food availability was greatest from January to April, coinciding with higher numbers of hilsa juveniles at those times. Therefore, the government should focus on protecting and conserving juvenile hilsa (jatka) as well as adult hilsa in these areas. These detailed research findings on the food and feeding ecology of hilsa *Tenualosa ilisha* in the Meghna river basin in Bangladesh are essential for the effective management of the hilsa fishery, as well as for domestication and culture to conserve and rehabilitate this declining fishery.

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Hilsa shad (*Tenualosa ilisha*) is one of the most important tropical fish of the Indo-Pacific region, especially in Bangladeshi waters. The hilsa fishery has declined significantly since 2002 mainly due to overfishing, habitat destruction and pollution; the Government of Bangladesh and researchers are therefore working to ensure its sustainable management. This study on hilsa food and feeding ecology offers essential information for policymaking and the effective management of the hilsa fishery. to hilsa It is based on a year-long study of hilsa specimens collected from the Meghna River at Chandpur across a range of age groups, from fry to adult. An analysis of the specimens' gut contents, and of the water itself, identified a range of phytoplankton and zooplankton genera; it also established the hilsa's food preferences at various stages in the life cycle using Ivlev's 'electivity index'.

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