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ORIGINAL PAPER

The effects of the flood cycle on the diversity and composition of the phytoplankton community of a seasonally flooded Ramsar wetland in Bangladesh

Sabir B. Muzaffar · Fakhruddin A. Ahmed

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Abstract Freshwater wetlands in Bangladesh are strongly influenced by the monsoons and the annual flood cycle has measurable impacts on the abiotic and biotic components of these ecosystems. The northeastern Haor Basin of Bangladesh is particularly rich in seasonally flooded freshwater wetlands that support a wide diversity of flora and fauna. These wetlands are of great importance to the local economy due to the abundance of rich floodplain fisheries. Little is known about the phytoplankton communities of these wetlands that are known to be linked with zooplankton and fish productivity. We investigated the seasonal variation in the diversity and abundance of phytoplankton assemblages in Tanguar Haor, a Ramsar wetland in northeastern Bangladesh during the period of inundation (June–December). A total of 107 genera of phytoplankton representing five classes were recorded. Blooms of *Microcystis* dominated the phytoplankton community throughout the study period but were particularly acute during the early part of the high water period. Among the Bacillariophyceae, *Melosira* was the most dominant, reaching bloom proportions early in the high water period. Factor analysis of physicochemical variables separated the flood cycle into four distinct periods: early high water, mid high water, late high water and low water periods. Phase of the flood cycle, nutrient availability, the physicochemical variables combined with the dominance of *Microcystis* seemed to be important in controlling the abundance, diversity and dynamics of the phytoplankton genera. The abundance of genera of desmids and some Bacillariophyceae is indicative of the relatively unpolluted conditions of Tanguar Haor.

Keywords Freshwater wetland · Phytoplankton · Haor Basin · Ramsar Site · Tanguar Haor · Bangladesh

Introduction

Wetlands are recognized as ecosystems that harbor high biological diversity, provide sustenance for millions of people and face ongoing threats as

S. B. Muzaffar (✉)
School of Environmental Science and Management, Independent University, Bangladesh (IUB), Baridhara, Dhaka 1207, Bangladesh
e-mail: v35sbm@mun.ca

Present Address:
S. B. Muzaffar
Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

F. A. Ahmed
Department of Botany, Jahangirnagar University, Savar, Dhaka 1342, Bangladesh

result of human activities throughout the world (Gopal and Chauhan 2001). As ecosystems, wetlands are highly volatile being particularly vulnerable to environmental fluctuations. Wetlands of South Asia are strongly influenced by the seasonal monsoons that vary significantly in intensity and duration depending on the regional climatic variation (Gopal and Krishnamurthy 1993; Nishat et al. 1993; Gopal and Chauhan 2001). Although wetland biodiversity constitutes a significant portion of the total biodiversity of the Indian Subcontinent (e.g., 15–20%, Gopal and Krishnamurthy 1993), studies of wetland ecosystems are limited and generally biased towards fisheries (Tsai and Ali 1997; Gopal and Zutshi 1998; Gopal and Chauhan 2001; de Graaf and Marttin 2003). Wetland biodiversity studies in Bangladesh consist primarily of surveys providing taxonomic lists and little or no analyses of ecological relationships (NCSIP-1 2001a, b; de Graaf et al. 2001; Alam et al. 2002, de Graaf and Marttin 2003). A limited number of studies investigate the role of habitat in determining aquatic fish diversity (e.g. EGIS/WARPO 1997) and their management (de Graaf et al. 2001; Thompson et al. 2003). These studies nevertheless illustrate very rich aquatic communities that change in relation to the seasonal flood cycle. The Haor Basin of Bangladesh is a large assemblage of wetlands in the northeastern districts of Sylhet, Sunamganj, Hobiganj and Moulvi bazaar in Sylhet Division and to a certain extent in Netrokona district in Dhaka Division. These wetland complexes remain flooded for a period of about 6–8 months following the monsoons (NERP 1993a) and are very rich in aquatic flora, wildlife and fish (e.g. NCSIP-1 2001a, b).

Phytoplankton are integral components of freshwater wetlands, which significantly contribute towards succession and dynamics of zooplankton and fish (Payne 1997). Community structure, dominance and seasonality of phytoplankton in tropical wetlands are highly variable and are functions of nutrient status, water level, morphometry of the underlying substrate and other regional factors (Gopal and Zutshi 1998; Zohary et al. 1998; Agostinho et al. 2001). The stage of flooding is an important determinant of phytoplankton communities in South American (Neiff 2001; Carvalho et al. 2003; Zalocar de Domitrovic 2003) and South Asian floodplains (Paul and Mazid 1997; Gopal and Zutshi 1998). The floodplain water cycle associated with wetlands in Bangladesh has been divided into four phases (I–IV) in a given year (Paul and Mazid 1997). Phase I, occurring between January and March, represents a latent period, when water levels are very low, with locally drying water bodies. Phase II spans from April to June, when many water bodies are completely dry. The latter part of phase II through phase IV represents the high water period, corresponding with the on-set of the monsoons (July–September). Phase III represents the peak growth period for phytoplankton and floating vegetation, followed by the recession of water levels, characterized by a decline in phytoplankton densities (Phase IV, October–December). Very little is known on how phytoplankton communities in wetlands of Bangladesh change in relation to the various phases of the flood cycle. Periods of high water, in general, tend to mobilize nutrients that enhance growth of phytoplankton (Zohary et al. 1998). Most wetlands in Bangladesh have high levels of eutrophication due to leaching chemical fertilizers used extensively in agricultural lands (Gain 2002). Many of the existing wetlands in the northeastern Haor Basin are surrounded by village communities that participate in seasonal agriculture with the use of chemical fertilizers (Gain 2002) making them eutrophic (Islam 1991). Gaining a baseline understanding of how phytoplankton and other aquatic communities change in relation to flooding therefore poses a challenge since nutrient levels of the aquatic habitat are unnaturally enhanced. Fortunately, one wetland complex, Tanguar Haor (one of two Ramsar sites in Bangladesh), located at the very north of the Haor Basin is almost unaffected by fertilizer input since its location at the foothills of the Meghalaya makes large-scale seasonal agriculture unsuitable (Geisen et al. 2000; NCSIP-1 2001a, b).

In this study, we investigated the variation of phytoplankton communities in relation to the high water period of the flood cycle in Tanguar Haor. We hypothesized that massive growth of phytoplankton occurred during the high water period, when the hydrological conditions support a high diversity and abundance of phytoplankton. Changes in the flood cycle would also be reflected in the phytoplankton community and the physicochemical variables of the water during the high water period.

Study area

The northeastern Haor basin of Bangladesh contains the floodplains of Meghna tributaries and is characterized by numerous, shallow water bodies known locally as *beels* (Rashid 1977; NERP 1993a; NERP b; Geisen et al. 2000). During the dry season (from mid October to March), these beels are part of a distinct depression, collectively referred to as a *haor*. With the advent of the monsoons (generally late May–mid-October), the beels coalesce forming expansive water bodies, sometimes resulting in the merger of one or more haors. These wetlands vary in size from as little as a few hectares to many thousands of hectares, interconnected with one another by shallow canals or rivers.

Tanguar Haor is located near the foothills of the Meghalaya at the northern reaches of the Haor basin (NERP 1993a; Geisen et al. 2000, Fig. 1). With a total area of 9,527 hectares it is among the least disturbed of water bodies in the area. Most of Tanguar Haor falls within the district of Sunamganj within the Sylhet Division, with a small portion on the southwest occurring within the district of Netrokona in Dhaka Division (NCSIP-1 2001b). The monthly temperature in Tanguar Haor ranges from as low as 8.5°C in the winter to as high as 32°C in the summer. Humidity ranges from 64% in the dry season to higher than 83% throughout the wet season. Rainfall in this area is perhaps the most intense phenomenon influencing all aspects of the ecosystem and its inhabitants. With an average annual rainfall of over 500 cm (NCSIP-1 2001a), the bulk of the rain occurs from June through August. Figure 2 illustrates the monthly rainfall of the greater Sylhet Division for the year 2002. Tanguar Haor receives backwater from the Bauli, Patnai and Jadukata river systems during these wettest of months. Extensive stands of open water and emergent marsh vegetation occur in this wetland with *Hydrilla veriticilla* as the dominant species, with varying amounts of *Trapa*, *Nymphoides*, *Potamogeton* and other aquatic genera

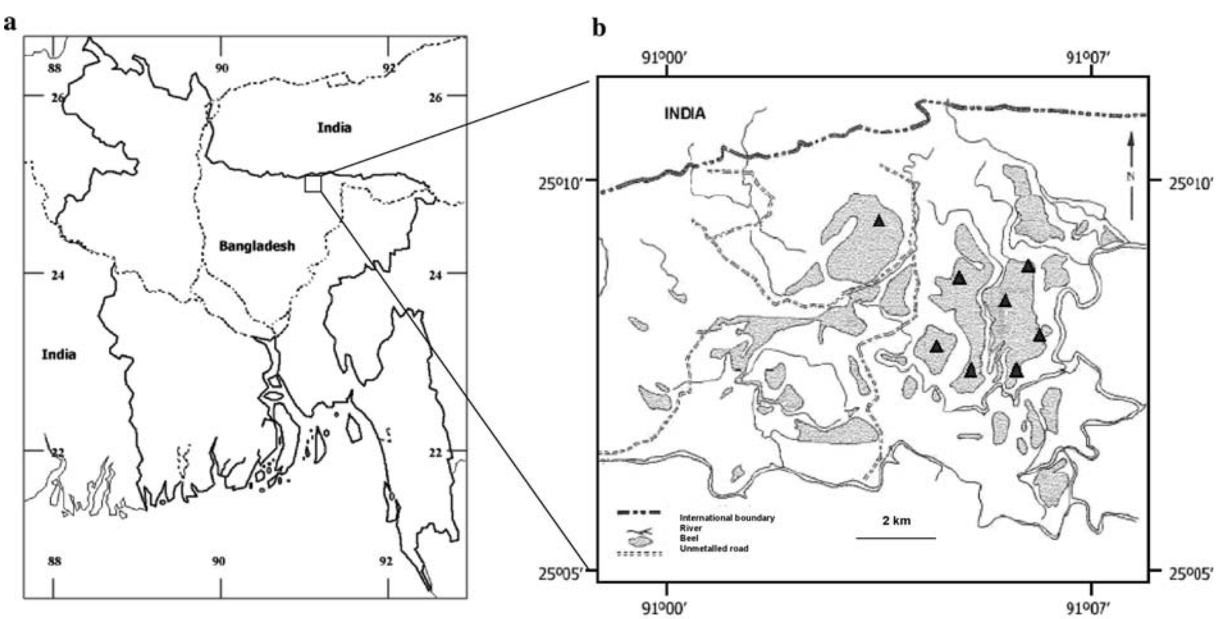

Fig. 1 Tanguar Haor in winter, showing the water bodies (beels) that join up during the monsoons to form a large water body (haor). The triangles represent the sampling sites

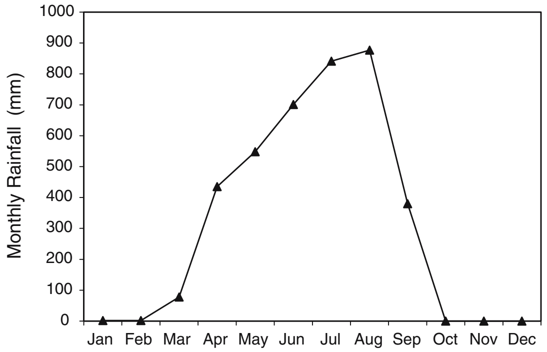

Fig. 2 Monthly rainfall (mm) in the greater Sylhet Division in 2002 (Bangladesh Meteorological Office)

(NCSIP-1 2001a). The emergent vegetation is dominated by *Persicaria* spp., whereas the most abundant natural reed vegetation consists of *Phragmites karka*, with a wide diversity of other reeds occurring in scattered aggregations. The receding floodwaters reveals more than 40 beels of varying sizes within the Tanguar Haor complex and the high vegetation and fish diversity attracts large concentrations of wintering waterbirds such as ducks, geese, shorebirds, herons and egrets (Khan 1997; NCSIP-1 2001b). Some beels within this complex may become completely dry, exposing areas of dried *Hydrilla* and other aquatic vegetation that is particularly attractive to shorebirds feeding on benthic and littoral invertebrates. Villages surrounding Tanguar Haor and villagers often harvest exposed snails as fodder for domestic ducks (Geisen et al. 2000). Additionally, dried areas within the haor are also used for selective small-scale agriculture, while cattle and ducks are allowed to graze and feed freely in areas unsuitable for agriculture.

Methods and materials

Eight sites within Tanguar Haor complex were chosen randomly for phytoplankton sampling at bi-monthly intervals from June to December, 2002. Surface water was collected using a 1.5 l plastic container and then sieved through a 20 μm plankton-net. Thirty such sub-samples were collected with a total of 45 l of water being sieved in each sample. The samples were labeled and preserved in Lugol's Iodine and 4% Formaldehyde and kept in the dark.

At each sampling site, the following variables relating to water quality were also measured: pH, Dissolved Oxygen, Alkalinity, Nitrite, Ammonia, Hardness, Carbon Dioxide and Chloride following APHA (1992) guidelines. Titrimetric methods using Hach's water quality testing kit (Model FF-1A, Hach USA) were used to determine these variables. Additionally, the temperature and Sechhi depth was measured to assess water clarity. Depth is highly variable within the Tanguar Haor complex (ranging from 5 to 10 m during the high water period) and we estimated the depth for one of the eight sites to allow interpretation of the data with respect to the changing water level. Additionally, we provide the mean monthly rainfall data for the greater Sylhet Division (of which Tanguar Haor is part, Fig. 2) as a reference for variation in rainfall patterns (water level in relation to observed changes in the various physicochemical variables measured. A total of 66 samples were analyzed for phytoplankton and individuals were identified to the generic level using the following references: Needham and Needham (1962), Prescott (1964), Khondokar (1997). All genera were enumerated using a Sedgwick-rafter cell counter and the numbers were then converted to densities (cells/filaments/colony forming units l^{-1}) for statistical analyses.

Quantification and statistical analyses

All data on physicochemical variables (except pH) were standardized (by subtracting the mean and dividing by the standard deviation) allowing better visualization of patterns in subsequent analyses (McGarigal et al. 2000). Factor analysis was used to assess the variation in different physicochemical variables with respect to time. In this technique the different variables are effectively combined to produce a smaller number of composite variates called 'factors'. When plotted against one another, these factors help reduce 'noise' in the data. Usually, the first 2–3 factors account for most of the variability of the data. Variables are first plotted as a loading plot, whereby each variable is plotted as a single point arising from the center and represents the degree to which it is correlated with either factor. This gives an idea of how strongly each variable contributes towards each factor. Subsequently, a scatter plot of the factors shows whether there are differences between measurements taken at different times. If there are differences in the variables, then the scatter plot of the factors are expected to show clustering during these different time periods, whereas similarities will reveal overlaps. Physicochemical variables measured during the four sampling periods would therefore be expected to cluster separately in each period, if there were major differences in these periods. For an in-depth treatment of Factor analysis, see McGarigal et al. (2000). The generic richness and relative abundance of each major taxonomic group, density (number of individuals or colony forming units per milliliter) were calculated. Genera that constituted more that 5% of the total abundance of all genera (except *Microcystis* and *Mellosira*) during any of the sampling periods were selected to examine patterns of variation in phytoplankton across these periods. All differences in the means of different taxa were compared across the four sampling periods using one way analysis of variance (ANOVA) (Sokal and Rolph 1981).

Results

Physicochemical variables

The changes in the different physicochemical variables are shown in Fig. 3. Values for pH remained close to neutral from June to October, 2002 but increased sharply to about 9.0 in December. Alkalinity and total hardness showed a gradual decline across the 4 months, whereas other variables showed variation without any general trend. Factor analysis showed that the first two factors accounted for 66.2% of the variance, suggesting that the first two factors were sufficient to account for the differences observed in physicochemical variables (McGarigal et al. 2002). Ammonia-N, pH, D.O. and Chloride correlated negatively and temperature correlated positively with the Factor 1 (Fig. 4). Hardness correlated positively with Factor 2. Plotting the principal component scores for Factors 1 and 2 showed that scores for December clustered separately from the rest of the three sampling periods (Fig. 5) (corresponding to high water levels). Additionally, June clustered separately from August to October within the high water period.

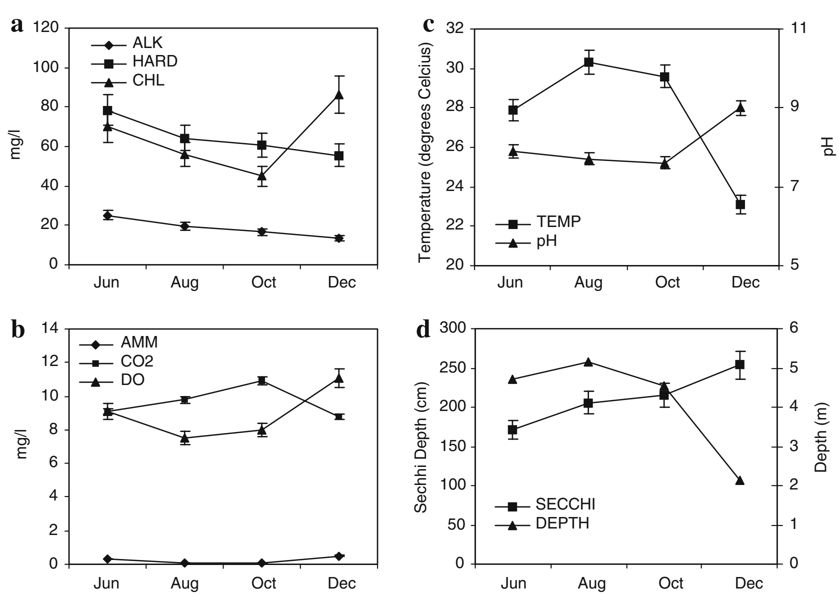

Fig. 3 Comparison of the physicochemical variables of water in Tanguar Haor. (**a**) ALK, Alkalinity; HARD, hardness; CHL, Chloride measured (mg/l); (**b**) AMM, Ammonium nitrogen; CO_2, carbon dioxide; DO, dissolved oxygen measured in (mg/l); (**c**) TEMP, temperature (°C) and pH; and (**d**) Sechhi Depth (cm) and approximate water depth (m). All variables were measured in each of the eight sites. The depth of water was estimated in one of the eight sites (see text for details)

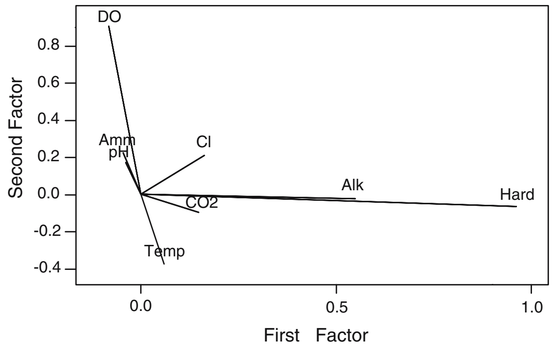

Fig. 4 Loading plot of the different physicochemical variables in relation to the first two factors. Dissolved Oxygen was strongly related to the Factor 2 while Alkalinity and Hardness were strongly related to Factor 1. Temperature was weakly negatively related to Factor 2. All other variables had weak relationships with either factors. (DO = Dissolved Oxygen; Amm = Ammonium Nitrogen; Cl = Chloride; CO_2 = Carbon dioxide; Temp = Temperature; Alk = Alkalinity; Hard = Total hardness; see text for explanations)

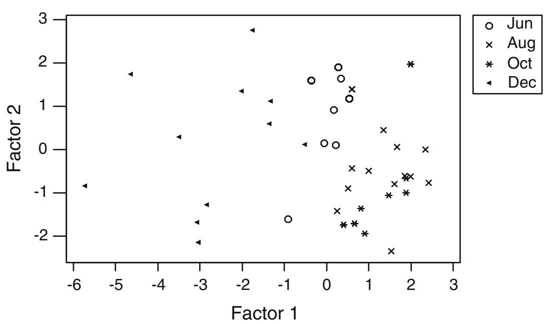

Fig. 5 Variation in the net physicochemical variables over the over the four sampling periods. June (open circle) and December (triangle) cluster separately from August (cross) and October (asterisk)

Generic richness

A total of 107 genera of phytoplankton were recorded, with the largest number of genera being recorded in June (74 genera) (Table 1). The mean richness of genera differed significantly between the four periods studied (Df = 3, $F = 8.70$, $P < 0.001$, Fig. 6) with the greatest mean richness being recorded in June followed by a sharp decline in August. Among the major taxa, all (except the Bacillariophyceae) underwent significant changes in their richness of genera (Fig. 6, One way ANOVA $P \ll 0.01$ in all cases).

Table 1 Phytoplankton genera recorded from Tanguar Haor between June and December 2002

	June	August	October	December
Chlorophyceae				
Radiofilum	*			
Eudorina	*	*	*	
Gonium	*	*		
Pandorina	*	*		
Pleodorina	*	*	*	
Platydorina		*	*	
Volvox	*		*	*
Pyrobotrys		*		
Sphaerocystis	*	*	*	*
Gloeocystis	*			
Palmodictyon	*	*	*	*
Nannochloris	*			
Ulothrix	*			*
Chlorococcum	*		*	
Mycanthococcus		*		
Golenkinia	*	*	*	*
Dictyosphaerium	*	*	*	*
Characium	*			
Pediastrum	*	*	*	*
Euastropsis	*			
Ankistrodesmus	*		*	
Cerasterias		*		
Glaucocystis		*		
Kirchneriella	*	*		*
Pachycladon	*	*		
Selenestrum	*	*	*	*
Trochiscia		*		
Westella	*			
Coelastrum		*	*	
Crucigenia	*	*		
Scenedesmus	*	*	*	
Mougeotia	*	*		*
Eremosphera	*	*	*	
Spirogyra	*			*
Gonatozygon	*			
Closterium	*			
Pleurotaenium	*			*
Cosmarium	*	*	*	*
Sirocladium				*
Micrasterias	*			
Staurastrum	*	*	*	*
Xanthidium	*	*	*	
Arthrodesmus	*	*	*	
Spondylosium	*			
Desmidium	*	*	*	
Hyalotheca	*			
Sphaerosozma			*	*
Euglenoidea				
Trachelomonas		*		
Pyrobotrys		*		
Xanthophyceae				
Botryococcus	*	*	*	
Chrysophyceae				
Synura	*			
Uroglenopsis	*			

Table 1 continued

	June	August	October	December
Dinobryon	*	*	*	*
Gloeobotrys			*	
Phaeosphaera	*			*
Bacillariophyceae				
Melosira	*	*	*	*
Coscinodiscus	*	*		*
Biddulphia	*			
Fragilaria	*		*	*
Synedra	*	*		*
Navicula	*	*	*	*
Pinnularia			*	
Nitzschia	*	*	*	*
Amphora		*	*	*
Cymbella			*	*
Suriella				*
Dinophyceae				
Ganyaulux	*	*		*
Ceratium	*	*	*	*
Peridinium	*	*		
Glenodinium	*	*	*	*
Attheya	*			
Cyanophyceae				
Chrooccus	*	*	*	*
Gloeocapsa	*	*	*	*
Synechocystis	*			
Aphanocapsa	*	*	*	*
Synechococcus				*
Microcystis	*	*	*	*
Merismopedia			*	
Eucapsis	*			
Dactylococcopsis	*			
Coelosphaerium	*	*	*	*
Spirulina	*	*		
Oscillatoria	*	*		*
Borzia	*	*		*
Lyngbia	*		*	
Schizothrix				*
Trichodesmium	*			
Anabaena	*	*	*	*
Nostoc	*			*
Anabaenopsis			*	
Nodularia	*			*
Tolypothrix	*			
Rivularia	*			*
Gloeotrichia	*			*
Total genera	72	51	42	44

The Chlorophyceae, Cyanophyceae, Dinophyceae and Chrysophyceae all showed sharp significant declines in their richness of genera between June and August (One way ANOVAs, $P \ll 0.02$ in all cases). The Chlorophyceae was the richest from June to October (compared to all other major groups). The generic richness of the Bacillariophyceae were similar throughout the study period with a slight increase between October and December (One way ANOVA, $P>0.05$). The Cyanophyceae rose significantly between October and December ($\mathrm{Df} = 1$, $F = 16.41$, $P = 0.001$). The Chrysophyceae were low in generic richness throughout the duration of the study, with an overall declining trend from June to December. The richness of genera was also very low in the Dinophyceae.

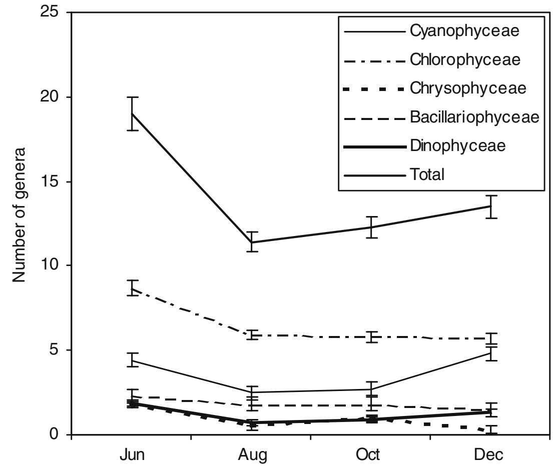

Fig. 6 Variation in the richness of genera of major phytoplankton taxa. (error bars represent standard errors of the mean)

Abundance

The Cyanophyceae showed the highest abundance throughout the study period, with densities reaching as high as 8.8×10^6 cells l^{-1} in June, with a gradual decline occurring throughout the period to levels of 2.7×10^6 cells l^{-1} in December (Fig. 7). The Cyanophyceae also represented the most dominant group, with more than 97% of all taxa being represented in all periods of the study. The bulk of the Cyanophyceae consisted of the genus *Microcystis* with particularly high densities occurring in June and August, followed by gradual declines by December (Table 2). Other genera such as *Chroococcus*, *Gloeocapsa*, *Aphanocapsa*, *Lyngbia*, *Coelosphaerium* and *Anabaena* were also abundant but showed a range of trends (Table 2). *Lyngbia*, declined to very low densities by December, although *Anabaena*, *Coelosphaerium* and *Aphanocapsa* increased significantly,

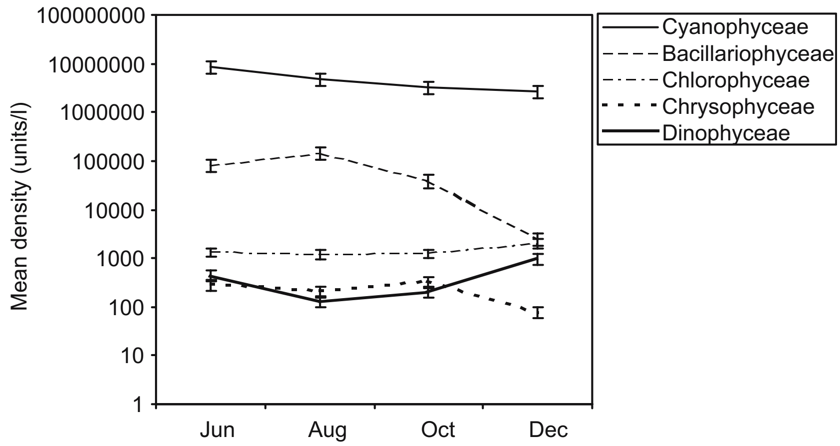

Fig. 7 Changes in the mean densities (number of cells/filaments/colony-forming units l^{-1} of water sampled) of the five major taxa of phytoplankton and the total number of individuals in all taxa in relation to time. (error bars represent standard errors of the mean)

causing the overall abundance of the Cyanophyceae to be high in December.

The Bacillariophyceae showed the highest mean densities in June and August, with the peak occurring in August (Fig. 7). In October, the densities of Bacillariophyceae declined and was not significantly different from the Chlorophyceae or Cyanophyceae. The Bacillariophyceae was dominated by the genus *Melosira* between June and October, with two major blooms in June and August (Table 2). The drastic reduction of *Melosira* by December corresponded with a rise in other genera such as *Nitzschia*, *Fragilaria* and *Coscinodiscus*. Even then the overall density of *Melosira* was still higher than all other genera combined.

The Chlorophyceae, in contrast, reached a peak in their densities in December, although their densities in the preceding months were also very high (Fig. 7). Among the Chlorophyceae, *Pediastrum* and desmid genera such as *Closterium*, *Cosmarium*, *Staurastrum*, *Xanthidium*, *Arthrodesmus* and *Desmidium* were very abundant (Table 2). *Cosmarium* and *Staurastrum* both declined between June and October, but increased again to very high densities by December. The rest of the genera gradually declined and were either reduced to low densities or were absent in December. Genera such as *Volvox*, *Eudorina*, *Palmodictyon*, *Chlorococcum* were all present in relatively lower densities in June and August, but declined by December.

The Chrysophyceae were lower in densities compared to most other taxa, although in August and October, their densities were similar to the Dinophyceae (Fig. 7 and Table 2). Chrysophyceae that were dominant in June included *Synura* and *Dinobryon*. *Synura*, however became scarce after August whereas *Dinobryon* continued to be relatively more abundant, although the overall declining trend was evident with the approach of December.

The Dinophyceae occurred in low densities, with highest densities occurring in June and a major increasing occurring in December (Fig. 7). The dominant genus was *Ceratium*, and changes in its density were reflected in the overall densities of the Dinophyceae (Table 2).

Discussion

Very few studies document the composition and diversity of phytoplankton taxa in relation to physicochemical characters of freshwater wetlands in Bangladesh (Islam 1991). The changes in phytoplankton assemblages in Tanguar Haor observed in this study were related to the flood cycle and its associated nutrient status. Rainfall in Tanguar Haor usually increases in early June, with the arrival of the monsoons (NERP 1993a, b). The Surma-Bauai, Patnai and Jadukata river systems all provide backwaters into Tanguar Haor. The flow rate is low with a small sediment load, making the waters of Tanguar Haor relatively clear that was clearly evident in our measures of water clarity (Mean Sechhi depths of about 171 cm in June and 254 cm in December,

Table 2 Variation in the densities (cells/filaments/colony-forming units l^{-1}) of selected phytoplankton genera with respect to time

Class	Genus	Jun	August	October	December
Cyanophyceae	*Chroococcus*	33.5 ± 19.7	105.8 ± 34.3	32.9 ± 19.5	123.4 ± 106.8
	Gloeocapsa	35.3 ± 15.0	7.1 ± 7.1	32.9 ± 18.6	78.2 ± 30.1
	Aphanocapsa	89.9 ± 21.6	60.0 ± 27.0	45.3 ± 23.9	90.5 ± 27.7
	Microcystis	8.2×10^6 ± 1.1×10^6	5.0×10^6 ± 1.0×10^6	3.3×10^6 ± 5.5×10^5	2.8×10^6 ± 5.4×10^5
	Coelosphaerium	60.0 ± 17.1	63.5 ± 29.0	20.6 ± 14.2	41.2 ± 22.6
	Oscillatoria	14.1 ± 6.1	3.5 ± 3.5		119.3 ± 52.4
	Borzia	60.0 ± 34.3	3.5 ± 3.5		24.7 ± 16.6
	Lyngbia	149.9 ± 26.9		24.7 ± 24.7	
	Anabaena	17.6 ± 14.2	38.8 ± 22.1	164.6 ± 55.8	444.4 ± 90.6
Chlorophyceae	*Eudorina*	30.0 ± 9.3	24.7 ± 15.3	24.7 ± 16.6	
	Volvox	75.8 ± 16.7		86.4 ± 46.3	20.6 ± 20.6
	Sphaerocystis	8.8 ± 6.2	42.3 ± 23.1	8.2 ± 8.2	4.1 ± 4.1
	Palmodictyon	22.9 ± 9.7	7.1 ± 7.1	69.9 ± 25.4	20.6 ± 14.2
	Ulothrix	3.5 ± 3.5			115.2 ± 35.6
	Chlorococcum	65.3 ± 26.2		12.3 ± 12.3	
	Golenkinia	19.4 ± 6.9	151.7 ± 34.1	65.8 ± 30.0	8.2 ± 8.2
	Dictyosphaerium	14.1 ± 7.1	105.8 ± 31.4	115.2 ± 28.1	164.6 ± 28.1
	Pediastrum	266.3 ± 21.9	317.4 ± 41.0	255.1 ± 33.2	164.6 ± 30.0
	Coelastrum		35.3±24.0	24.7±17.7	
	Mougeotia	7.1 ± 4.9	3.5 ± 3.5		152.2 ± 37.7
	Eremosphera	37.0 ± 14.7	31.7 ± 21.7	28.8 ± 28.8	
	Cosmarium	84.7 ± 18.3	21.2 ± 17.7	107.0 ± 50.4	847.7 ± 334.8
	Staurastrum	269.8 ± 29.8	225.7 ± 29.2	292.2 ± 58.1	300.4 ± 77.5
	Xanthidium	67.0 ± 15.7	3.5 ± 3.5	28.8 ± 15.4	
	Arthrodesmus	42.3 ± 16.8	7.1 ± 7.1	12.3 ± 12.3	
	Desmidium	58.2 ± 14.4	17.6 ± 12.3	82.3 ± 26.7	
Chrysophyceae	*Dinobryon*	185.2 ± 27.1	194.0 ± 82.6	304.5 ± 66.8	70.0 ±4 1.4
Bacillariophyceae	*Melosira*	8.2×10^4 ± 1.1×10^4	1.5×10^5 ± 5.0×10^4	4.0×10^4 ± 7.8×10^3	2.3×10^3 ± 1.9×10^3
	Coscinodiscus	33.5 ± 11.4	60.0 ± 23.3		28.8 ± 21.5
	Fragilaria	31.7 ± 9.6		28.8 ± 19.7	28.8 ± 15.4
	Synedra	15.9 ± 6.3	7.1 ± 7.1		24.7 ± 24.7
	Navicula	12.3 ± 7.9	21.2 ± 21.2	32.9 ± 23.0	8.2 ± 8.2
	Nitzschia	30.0 ± 19.7	10.6 ± 7.6	32.9 ± 23.0	86.4 ± 38.0
	Amphora		3.5 ± 3.5	8.2 ± 8.2	61.7 ± 42.6
Dinophyceae	*Ganyaulux*	10.6 ± 4.7	21.2 ± 15.3		20.6 ± 20.6
	Ceratium	134.0 ± 22.0	52.9 ± 23.4	131.7 ± 33.5	930.0 ± 214.9
	Peridinium	14.1 ± 6.1	3.5 ± 3.5		
	Glenodinium	283.9 ± 77.6	52.9 ± 28.6	70.0 ± 39.6	37.0 ± 25.2

Fig. 3d). As the water level gradually rises through June–August and then starts to decline in September, changes occur in the physicochemical variables that may not be evident unless they are combined in a factor analysis. Hardness, a measure of Calcium and Magnesium carbonates present in natural waters, showed a gradual decline across the period of sampling. Alkalinity, a measure of carbonate ions in the natural waters, showed an even more gradual decline across the four sampling periods and did not seem to be an important driving variable. Temperature and D.O. showed more variable patterns across the sampling periods (Fig. 3). Factor analysis revealed that the combination of physicochemical variables in June and December were different from August to October (Fig. 5). The differences in these combined effects of the physicochemical variables was likely driven by D.O., hardness, alkalinity and temperature, all of which contributed strongly towards either factor 1 or 2 (Fig. 4). Clearly, patterns not evident in individual variables were evident when they were combined into factors and could be related to the individual

sampling periods. High nutrient levels early during the monsoons presumably separated June from the rest of the months. Even though nutrient input is clearly related to physicochemical variables (Payne 1997; Neiff 2001; Gopal and Chauhan 2001), we did not measure nutrients per se and can therefore not be certain about which nutrients were responsible for driving the changes in the physicochemical variables. December clustered separately since conditions were far different during this low water period particularly with respect to water clarity, pH, D.O. and Chloride levels (Figs. 3 and 5). The overall differences in physicochemical variables were reflected in the phytoplankton relative abundance and generic richness, with higher values for total phytoplankton (as well as selected taxa) being recorded during the high water period between June and August. With the progressing season, the nutrients likely became depleted causing the significant reductions in the phytoplankton richness and abundance as the water levels started to subside in September.

Enhanced nutrient levels are characteristic of floodplain habitats, as changes in water level followed by an expansion of the water sheet causes a direct release of nutrients accumulated in the terrestrial zone over the dry period (Payne 1997; Neiff 2001; Gopal and Chauhan 2001; Carvalho et al. 2003; Zalocar de Domitrovic 2003). In South American wetlands, the flood pulse characterizes distinct low water (limnophase) and high water (potamophase) periods (Neiff 2001; Carvalho et al. 2003; Zalocar de Domitrovic 2003). The water level, coupled with the increased nutrients drive an explosive growth of phytoplankton (Neiff 2001) although the dilution effect of the water may cause an initial decline in the microbiota (Zalocar de Domitrovic 2003). In South Asian wetlands, the monsoons are less predictable since the timing of arrival, duration and intensity of the monsoons and the associated flooding patterns vary from year to year (Gopal and Chauhan 2001; Dudgeon 2001). The changes in the phytoplankton observed in Tanguar Haor reflected a situation similar to the South American floodplain wetlands, with the high and low water periods supporting characteristic phytoplankton assemblages as a result of the distinct nature of the physicochemical variables (Zalocar de Domitrovic 2003). The flood cycle classification of Paul and Mazid (1997) matched particularly well with our data. The latter part of phase II (June) and phase III represents the peak high water period (July–September), showed high diversity of phytoplantkton as well as blooms of two genera. The receding waters corresponded with declines in total phytoplankton abundance, as predicted by phase IV characteristics (Paul and Mazid 1997). Water bodies in the Indian subcontinent are known to sometimes go through one or more peaks in the phytoplankton densities (Zafar 1986; Gopal and Zutshi 1998). We observed high densities of phytoplankton in June, which continued to decline gradually through to December.

Our study showed a dominance of Cyanophyceae throughout the study period, but particularly in the high water period. Subsequently, as the water levels started to subside, the Cyanophyceae declined, although levels were still high in December. The generally high diversity and dominance of the Cyanophyceae in freshwater ecosystems in Bangladesh has been recorded by others (Islam 1973; Islam and Begum 1981; Aziz and Tanbir 1999). Bacillariophyceae were extremely high in abundance during the high water period but declined dramatically with the progress of the season (Fig. 7). The high densities of Bacillariophyceae indicated relatively unpolluted conditions (Islam 1969; Islam 1991; Gopal and Zutshi 1998), supporting the idea that Tanguar Haor is less polluted with fertilizers (Geisen et al. 2000), a common cause of hyper-eutrophication in most wetlands in the country (Islam 1991).

Low total Nitrogen to total Phosphorus ratios (TN:TP) are regarded as a cause of cyanobacterial blooms, particularly of the genus *Microcystis* (Shapiro 1972; Smith 1983), although it has been argued that nutrient uptake by Cyanophyceae during blooms may cause the observed low TN:TP ratios (Xie et al. 2003). We did not measure total Nitrogen or total Phosphorus in this study, but the values of Ammonium–Nitrogen were consistently low, indicating low levels of Nitrogen (Fig. 3). Additionally, cyanobacterial blooms, particularly of the non-nitrogen fixing genera (such as *Microcystis*) are strongly influenced by turbulence, with high levels of turbulence preventing the formation of blooms (Dokulil and Teubner 2000; Reynolds 1987). We observed that turbulence varied on a daily basis during the high water period and mornings seemingly had a greater inflow of water. The duration and intensity of turbulence was not measured in this study, but it was clear that turbulence was low. The turbulence of the region is moderated by the underlying geomorphology of the haors with levees and shallow water areas further reducing the force of incoming water (Geisen et al. 2000). The resulting water columns were consequently quite stable, with periodic breaks of moderate turbulence. This allowed the bloom-forming *Microcystis* to dominate since relatively stable water columns with periods of water mixing promote their growth (An and Jones 2000; Dokulil and Teubner 2000).

The periodic dominance of *Melosira* in tropical freshwater ecosystems is also widespread (Miyajima et al. 1994), and high densities of *Melosira* from June to August and low diversity of the members of Bacillariophyceae in the following months in our study corresponds with findings of Islam (1969) and Islam and Paul (1978). High densities of *Melosira* have been linked to high silicate levels coupled with moderate to high levels of turbulence (Miyajima et al. 1994; Bormans and Condie 1998). The intermittent turbulence observed in the Tanguar Haor, particularly during the high water period could have been responsible for allowing high densities of *Melosira* to occur between July and August, followed by declines in abundance as the turbulence decreased with the receding water levels. The conditions however were more suitable for *Microcystis*, preventing *Melosira* from becoming totally dominant.

The dominance of *Microcystis* may suppress other genera (Zohary et al. 1996), and we observed that most of the Cyanophyceae, some Chlorophyceae (*Ulothrix*, *Mougeotia* and *Cosmarium*), some Bacillariophyceae (*Nitzschia* and *Amphora*) and one Dinophyceae (*Ceratium*) showed significant increases during the low water period (Table 2). Relatively lower densities of *Microcystis* in combination with changes in the physical conditions during the low water period may have promoted the growth of other genera that were otherwise out-competed.

This study is among the few that takes a close look at phytoplankton communities in relation to the seasonal flooding and physicochemical variables in a shallow wetland complex in Bangladesh. Plankton communities were dominated by *Microcystis* and to lesser extent *Melosira*. Physicochemical variables collectively varied across the four sampling periods although this was not necessarily evident when considering the variables independently. Diversity of phytoplankton also varied with the seasons, and we suggest the blooms of *Microcystis* could be responsible for suppressing the growth of other genera. Whereas the study is based only on six month's data, it shows trends in phytoplankton dynamics that are important in attaining a better understanding of tropical floodplain ecosystems in the region. Further studies are urgently needed to assess year-to-year variation in phytoplankton in such wetland complexes in the northeastern Haor Basin. The entire region is of critical importance for wintering birds, aquatic wildlife, and freshwater fisheries and the degradation and loss of such wetlands is an important problem. Understanding the ecology of Tanguar Haor is crucial to developing a more comprehensive management plan, particularly in relation to the existing fisheries that are so closely linked with the physicochemical variables, the phytoplankton and the annual flood cycle.

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