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Ecology of Phytoplankton in Tropical Waters: Introduction to the Topic and Ecosystem Changes from Sri Lanka

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Abstract: Some aspects of ecology of phytoplankton in four distinct types of standing water bodies were diagnosed using the outcome of a long-term study conducted in Sri Lankan reservoirs on species composition and richness, temporal and seasonal patterns in relation to environmental variables. Nearly 150 taxa belonging to nine taxonomic groups were identified of which some have been reported in previous studies. The numerical analysis of the overall species lists shows that the taxonomic composition, species richness and sequential periodicity varies largely among different types of environments with higher resemblance for water bodies located at comparable eco-regions with similar morphological, hydraulic, hydro-chemical and trophic features. Relative abundance and species spectrum can be used to classify the water bodies into oligo-mesotrophic (large and deep canyon-shaped, newly built hydropower reservoirs), meso-eutrophic (dry zone irrigation tanks) and eutrophic-heterotrophic (urban water bodies) which show distinct annual trophic alteration influenced by monsoonal rainfall. Unlike in temperate regions, they exhibit non-rhythmic successional episodes, some prefer specific chemical environment and some taxa become more stable when essential nutrients are in surplus. The numerical dominance or biomass is not regulated by grazing but a large amount of phytoplankton biomass is lost during water release from the euphotic zone.

Key words: Tropical phytoplankton, pantropical, species richness, seasonality, Sri Lanka.

Introduction

Phytoplankton is a key component of the aquatic (microbial) food web in temperate and tropical oceanic and athalassic waters reflecting the trophic status of the environment. In shallow inland waters in the humid tropics, they play an additionally important role in the pelagic food web as a direct and important source of food for commonly found seston-feeding fish (Hofer & Schiemer, 1983). Pico-phytoplankton (<2µm) play an important role to sustain aquatic (microbial) food webs in the ocean (Fenchel, 1988) and pelagic zones of the large inland lakes (Stockner & Poter, 1987) through a microbial loop. Phytoplankton taxa vary in distribution and they disperse through wind, oceanic currents, migratory birds etc. Majority of them are cosmopolitan. Phytoplankton communities in tropical lakes and reservoirs represent summer communities of temperate lakes with a large number of tropical taxa including pantropical and regional endemic elements (Vyvermann, 1996). Although there is a large diversity of standing water bodies in the tropical latitude resulting from climatic and geomorphologic heterogeneity, detailed phytoplankton investigations are rare on their spatial and temporal distribution, growth and survival, loss patterns, periodicity and changes in species composition in relation to environmental variables (Talling, 1966, 1986; Lewis, 1973, 1978; Ganf, 1974, Kalff & Watson, 1986;

Biswas,1978; Henry et al., 1984; Ramberg, 1987; Mukankomeje et al., 1993; Branco & Senna, 1994). Very few studies have addressed phytoplankton composition and their temporal changes under eutrophic conditions (Sugunan, 1980; Kannan & Job, 1980; Zafar, 1986; Osborne, 1991; Alvarez-Cobelas & Jacobsen, 1992). The accepted phenomenon is that temporal variability of phytoplankton in tropics are driven by seasonal rainfall and mixing, but diel patterns in shallow water bodies and long-term stable types with sudden shifts are poorly understood.

In small ponds and reservoirs in monsoon Asia, phytoplankton minimum can be characteristic during the wash-out and elevated turbidity in the wet months (Sugunan, 1980; Kannan & Job, 1980; Fatimah et al., 1984; Khondker & Parveen, 1993). Lewis (1996) suggested a progressive decline in phytoplankton diversity towards the tropics. On the contrary, extremely high diversity of phytoplankton has been shown for floodplain lakes in Papua New Guinea (Vyvermann, 1996). Phytoplankton communities in very large lakes are mainly dominated by non-motile species (Lewis, 1978; Carney et al., 1987; Talling, 1986). Species sequences have been reported during the early development of man-made lakes (van de Heide, 1973; Matsumara-Tundisi et al., 1991; Branco & Senna, 1996). However, dissimilarity in species composition and diversity of phytoplankton even in adjoining reservoirs occurs (Silva & Wijeyaratne, 1999).

Phytoplankton taxonomy in Sri Lanka is fairly known (West & West, 1902; Apstein, 1907, 1910; Holsinger, 1955; Rott, 1983; Rott & Lenzenwerger, 1994; Rott et al., in press), and further attempts have also been made to understand the role of monsoon-bound seasonal hydrology on their abundance (Silva, 2004; Rott et al. in press) but long-term changes, growth and survival and succession under monsoon-bound seasonal eco-hydrology are unknown to a greater extent. The composition and relative abundance of common taxa of phytoplankton in man-made lakes in Sri Lanka were examined for a period of six consecutive years together with related environmental variables amidst outbreaks of several cyanobacteria blooms. Here, the results were examined in relation to relevant literature to highlight some aspects of phytoplankton ecology influenced by monsoon-bound seasonal eco-hydrology in tropical waters. Attempts are made to identify the most important functional species groups of phytoplankton and key variables for shaping of phytoplankton species composition along with the ecosystems heterogeneity.

Materials and Methods

The island of Sri Lanka (6º-10º N and 80º-82º E) is an extension of the Indian peninsula located on the Indo-Australian plate. Sri Lanka experiences monsoon weather and there are two distinct monsoon driven rainy seasons, the southwest or summer monsoon (May-Sep.) and the northeast or winter monsoon (Dec.-Feb.). The island is also influenced by atmospheric depressions that form in the Southwest Bay of Bengal and the Southeast Arabian Sea. However, an orographic rainfall prevails in the central highlands and the northeast monsoon brings heavy rains which is fairly widespread. Sri Lanka has no natural lakes and all inland water bodies are essentially man-made reservoirs constructed primarily for irrigation and hydropower generation. Radially draining rivers empty into the Indian Ocean through either riverine or basin estuaries. Coastal zone is also characterized with fringe mangroves, sand dunes, salterns and coastal lagoons. The built environment and the aquatic habitats in the coastal belt of the island was severely affected on 26th December 2004 by the tsunami tidal waves triggered by an earthquake of 9.0 Richter Index which had the epicentre northeast of Sumatra island.

Phytoplankton samples were collected from most of the inland water bodies throughout the island except the north and northeast since 1998 to 2004 randomly mainly under low and high water levels using 10 µm net hauls integrated over the near-surface layers (down to 5 m) and a water sampler. In addition, time series samples were collected for two consecutive years (1998-2000) from three reservoirs; an elongated canyon shaped and deep hydropower reservoir with steep slopes (Victoria) which is located in the central uplands and moderately deep hydropower cum irrigation reservoir (Udawalawe) and an irrigation reservoir (Minnieriya) which are located at the southern foothills of the mountains and close to the eastern lowland, respectively (Figure 1). All samples were immediately fixed with 2% neutralized formalin for laboratory identification under a research microscope (Olympus BX 51, magnifications up to 400 times). Reservoir ecosystems were also examined for basic environmental variables such as water level, water chemistry and chlorophyll-a (Silva & Gamlath, 2000; Silva & Schiemer, 2000). Detail taxonomic analysis was carried out at the Institute of Botany, University of Innsbruck, Austria (Rott et al., 2001, Rott et al., in press).

Results

***Phytoplankton Ecology*:** The phytoplankton in pelagic waters includes representatives of several groups of algae and bacteria, as well as the ineffective stages of certain actinomycetes and fungi. The aquatic habitats inhabited by phytoplankton are obviously heterogeneous. Temporal changes in mean temperature, irradiance, hydraulic throughput and nutrient availability are among the more obvious variables which determine their abundance. Diel changes in temperature/density stratification in tropical standing water bodies can have large effects on the vertical distribution of gas-vacuole possessing blue green algae with varying positive and negative buoyancy (Ganf, 1974). Vertical redistribution of populations with diel cycles can also result from active migration of flagellated phytoplankton (e.g., Euglenophytes, Dinoflagellates, Chrysophytes). Day-to-day variations of wind speed are positively related to the abundance, especially of diatoms (de Lima et al., 1983). The water input may influence the phytoplankton standing stocks by deepening the water column and reducing the underwater light penetration through introduced silt, by wash out effect in basins of short retention time and more favourably injecting nutrients. Vertical segregation of limiting space is less apparent in well mixing shallow water bodies and phytoplankton are mainly confined to the mixed layers in deep standing water bodies. This is mainly determined by underwater light climate rather than the thermal/density stratification. Therefore it is very unlikely that discontinuous vertical distribution of phytoplankton occurs under such conditions, which are different from temperate lakes and reservoirs (Harris & Smith, 1977). Annual variation of component species is rarely known for more than two years in tropical waters, so the regularity or otherwise of annual cycles is not well established (Talling & Lemoalle, 1998). Seasonal changes in species composition that differ by time-shifts, growth and loss rates, and inoculum level give rise to patterns of species succession. More uniform environmental gradients reduce temporal changes of phytoplankton and result in smaller species richness although environmental variability has a considerable impact upon phytoplankton ecology. However, geographical position and low latitude has no major influence on phytoplankton diversity and species richness (Rott et al., in press).

Long-term changes in nutrient supply to tropical standing water bodies represent a very large scale (decades to millennia) shift in the balance and spectra of resources to which phytoplankton abundance and species composition are known to respond. Such changes occur naturally, at different rates, in either direction and have a variety of causes. Relatively dramatic increase in the amount of nutrients reaching lakes and reservoirs in the recent decade, especially in the developing countries and attendant changes in their trophic status have served to focus a great deal of attention to the problem of nutrient enrichment or eutrophication. However, trophic evolution may be influenced by other factors, such as extensive changes in sediment accumulation and their relative contribution to the nutrient pool. Further, the relative enrichment of tropical water bodies has been a direct consequence of socio-cultural advances made by growing human populations (Silva, 2004). Nevertheless, it triggers to increase the average algal standing crop (with attendant decrease in transparency and hypolimnetic oxygen), the size of individual maxima compounded by the shift in species dominance with toxigenic species/strains towards more conservative, persistence forms (e.g. many cyanobacteria) and the consequent loss of amenity that generate concern about eutrophication of lakes and reservoirs.

In natural waters, there are many environmental variables to which growth rates of autotrophs might respond (e.g., temperature, light intensity, periodicity and nutrient availability). Temperature and light may not be limiting phytoplankton growth to a great extent in tropical waters; however, nutrients are more likely to be critical throughout the growth phase. Marked seasonal shifts in the temperate region are generally accepted to influence the sequence in variation of phytoplankton species with each able to grow and perhaps to dominate the phytoplankton assemblage. Although periodic changes in dominant species (the seasonal succession) has been investigated and described for a large number of temperate water bodies (Reynolds, 1986), this aspect is poorly understood for tropical waters. Further, seasonal succession of phytoplankton species in tropical water appears to present no order as established in temperate ones (e.g., Diatoms → Cryptomonas → various green algae → Cyanobacteria → Dinoflagellates) partly driven by physical changes, grazing, allelopathy, depletion of critical nutrient etc., but evidently there are more successional episodes in tropical waters resulting from mixing events which renew nutrients and increases turbulence while decreasing transparency (Lewis, 1996). Species sequences are also to be expected during the early development of man-made lakes (Biswas, 1978; van der Heide, 1973).

There is no sufficient circumstantial evidence to show that the environmental variables such as increasing temperature or stability, decreasing frequency of light fluctuations, and decreasing nutrient availability control phytoplankton growth periodicity in tropical waters. However they exhibit evolutionary adaptations to avoid unfavourable environmental conditions by experiencing a resting phase (perennation) as common in dinoflagellates and producing asexual spores or akinetes in the case of many species of filamentous cyanophytes. Physiological and behavioural flexibility of *Microcystis* evidently accommodate to environmental stresses better than most particularly fast growing species. Tropical species, also with high growth rate, can respond quickly to the availability of environmental resources but do not or cannot maintain their maximum densities for a long time and on the other hand species with lower growth rate and slower response are adapted to tolerate a long period of resource stress. The former may be recognized colonizing opportunistic r-selected, to latter with constant allochthonus equilibrium or k-selected species (Kilham & Kilham, 1980). The overwhelming dominance of *Microcystis* in the dielly mixed Lake George, Uganda throughout most of the year and the evidence for inability of any other species to compete with (Ganf, 1974), it is also an instance for a k-strategist in an ecologically stable environment. Genus *Microcystis* is an excellent example of an extreme k-selected phytoplanker in the tropics (Silva, 2004; Rott et al., in press).

Phytoplankton in standing waters are lost from the suspension due to mortality caused by resources or some other physiological limitations, or by infected diseases, attacked by parasites (bacteria, virus or fungi), or grazing by phytoplanktivorous predators and filter feeders. They also sink throughout the water column since they are heavier than the water and unable to restore their position by swing or regulating buoyancy except in flagellates and some colony forming cyanobacteria (e.g., *Microcystis*) respectively. Intrinsic sinking rate is pronounced under some environmental conditions such as long-term chronic nutrient deficiencies, especially dissolved silicate in the case of diatom populations (Smadya, 1970; Lehman, 1979). Grazing by herbivorous animals (protozoa, rotifers, micro-crustaceans and fish) inhabiting the same water mass deplete the standing stocks and may have profound effects on their dynamics and population ecology. However, available data sometimes conflict with broadly spread preconception that grazing regulates the phytoplankton assemblage. Some tropical taxa (e.g., Cyanobacteria and Dinoflagellates) are well known to secrete a variety of chemical substances for defensive purposes which are toxic to other organisms including fish and mammals.

The composition of phytoplankton communities and the relative abundance of component species undergo continuous changes on a varying scale. Although the spatial and temporal distribution of phytoplankton are concurrent with environmental variables in different types of water bodies of diverse morphology and trophic status, progress in understanding and prediction has been very slow even in the case of temperate waters (Reynolds, 1986). Certainly, there are still no widely accepted explanations either of mechanisms that derive seasonal increase and declining of phytoplankton or of the factors that adjust long-term floristic changes. However, in recent years highly enriched (hypereutrophic) ponds and lakes in the tropics, seasonal succession and changes in community composition have been attributed to anthropogenic eutrophication. Studies on Lake Lanao, the Philippines show particularly how well tropical phytoplankton can respond to seasonal changes in mixing and light climate (Lewis, 1973, 1978). Situations were quite different in the African Rift Valley lakes with incomplete seasonal stratification (meromixis), where species composition and periodicity are primarily regulated by nutrient limitation especially with respect to nitrogen deficit (Talling, 1966). Lake George in Uganda, a shallow equatorial lake with more regular diel alteration, stable micro stratification and holomixis, presents an extreme case of environmental selectivity that apparently favours one of the strongest k-strategist, *Microcystis* (Ganf, 1974). Although many freshwater phytoplankton are generally cosmopolitan in geographic distribution, there are marked differences among the major taxonomic groups in tropical and temperate waters. These dissimilarities are not necessarily attributable solely to temperature or latitude (Reynolds, 1986). Centric diatoms, especially *Melosira* and *Cylcotella* are relatively more abundant than pinnate species in the tropics, among the Dinoflagellates, *Peridinium* species tend to replace the genus *Ceratium* towards the equator. *Staurastrum* spp, common desmids with 8-12 and 20 arms tend to replace 4-6 armed forms of temperate ones. Cyanobacteria are generally more abundant in tropical lakes and reservoirs and *Spirulina* is another common genus found in shallow nutrient rich saline lakes in the tropics.

***Perennial reservoirs*:** Man-made perennial water bodies in Sri Lanka are primarily of four categories according to their geographical location, morphology, seasonal hydrology and present catchment use. A majority of shallow lowland reservoirs belong to the ancient category with relatively large area/volume ratio. They start filling with the onset of the second inter-monsoonal rains (Oct.-Nov.), and reach full supply level towards the end of the northeast monsoon (Dec.-Feb.). Although, they retain water till April, water releases progressively through surface outflow for downstream irrigation and reach the lowest level towards Aug.-Sep. As a consequence of seasonality in input and output and water storage, renewal rates exhibit strong seasonal differences with marked annual drawdown. In contrast, newly built, canyon shaped deep highland reservoirs, located in the wet/ intermediate zones, with relatively small area, volume ratios, receive water during both monsoons. Since they release water through bottom outlets right through the year for hydropower generation, the water level becomes relatively low from April through September. The third category, a few number of small urban water bodies with small watersheds located in major cities, shows variable hydrological patterns depending on their major uses and local rainfall pattern. Most of them have been subjected to high anthropogenic pressures and environmental variables which are tied up with hygienic and economic conditions of the riparian communities. In addition, a couple of small reservoirs constructed also for irrigation and located in the highest elevation (>1500 m amsl) experience a relatively narrow annual temperature range with a wide diel range but they also undergo a dry phase from January to April.

Species richness: A total of 146 taxa belonging to nine major classes were identified from the Sri Lankan water bodies during the study (Table 1) of which Chlorophytes (28%), Zygnemaphytes (24%) and Cyanophytes (23%) represented the highest numbers of taxa compared to Diatomophytes (16%). Other five groups (Chrysophytes, Cryptophytes, Dinophytes, Euglenophytes and Xanthophytes) that are found less than 4% are of minor contribution to species richness. Of Cyanophytes, the genus *Microcystis* represented the highest number of species richness whereas the highest number of taxa of Chlorophytes was represented by the genus *Coelastrum.* Surprisingly, the genus *Staurastrum* of Zygnemaphytes was represented by 19 species. However, species richness in Sri Lankan reservoirs was relatively small compared to natural lakes located at similar latitudes (Vyverman, 1996; Rott et al., in press). This may be ascribed to unavailability of truly lacustrine habitats. Of the 34 genera of cyanobacteria, a majority were found in three types of water bodies except in high mountain reservoirs. This is perhaps resulted in a low number of samples examined from those reservoirs. Species richness of diatoms, green algae and desmids was low in both eutrophic urban water bodies and the small reservoirs located at highest elevation. Some of the diatoms found occasionally in small numbers could be either sessile or benthic forms, and may not be truly planktonic (e.g., *Cymbella*, *Gyrosigma*, *Navicula*, *Surirella*, *Tabellaria*). The highest number of desmids, particularly the genus *Staurastrum*, were found in newly built hydropower reservoirs (Rott et al., in press) and a few of them also colonized irrigation reservoirs during high water level.

In addition, several common diatom taxa (mainly centric forms) were found in all four types of water bodies and dominated at many instances with chain forming centric diatom, *Aulacoseira granulata*. A pinnate diatom, the genus *Synedra* was commonly found and numerically abundant in some irrigation reservoirs situated in the Kala Oya basin. A new species of centric diatoms of the genus *Urosolenia* (a freshwater counterpart of the genus *Rhizosolenia*) described by Rott et al. (in press) was uncommon and infrequent. Dinoflagellates were represented by a few taxa and one species of the genus *Peridiniopsis* was dominant in several samples collected from some dry zone reservoirs. Only two taxa (genus *Cryptomonas* and genus *Rhodomonas*) represented the Cryptophytes whereas one species of each genus, *Centritractus Isthmochloron* and *Pseudostaurastrum* and two species of the genus *Goniochloris* of Xanthophytes were found in small numbers only from dry zone irrigation tanks and hydropower reservoirs. There were only two species of the genus *Mallomonas* of Chrysophytes in very low numbers but with a wide spatial distribution. In contrast, Euglenophytes were present with several taxa particularly from eutrophic waters. A taxa of the genus *Xanthidium*, a unicellular desmid was common and numerically dominant only in the small high mountain reservoirs.

***Community and size structure*:** The results of long-term seasonal studies conducted in two irrigation reservoirs, Minneriya and Udawalawe located in the northeast, and southern dry zones respectively, the largest and the deepest hydropower reservoir (Victoria) and an urban water body (Kandy Lake), located 510 m amsl at the heart of the second largest city are discussed here to highlight some aspects of phytoplankton ecology in Sri Lanka. In Minneriya the phytoplankton assemblage was dominated by unicellular centric diatoms (*Stephanodiscus neoastraea* and *Cyclotella pseudostelligera*), and small colony forming Cyanophytes during high water level (Jan.-Feb.). The phytoplankton growth increased progressively with decreasing water level (Apr-Sep) while replacing *C. pseudostelligera* by a chain-forming centric diatom, *Aulacoseira granulata* as subdominant and an increase of several filamentous Cyanophytes from variable size classes. This moderate shift in the species composition resulted in reshaping the size spectrum of the phytoplankton assemblage from the smaller to the larger size classes (see Rott et al., in press).

Table 1: Phytoplankton taxa list

Phytoplankton			*Reservoir Type*			
Group: *Cyanophyceae (Cyanobacteria)*	GD	N	A	B	C	D
Genus: Anabaena .		2			r	
Anabaenopsis		2	r	r	r	
Aphanothece		1	r		r	
Aphanizomenon	t/wt	2	r	f	r	R
Aphanocapsa	c	1	r	r	r	
Chroococcus	t/wt	2	f	f	f	R
Coelomoron	t	1	r	r		
Coelosphaerium.		1	r	r	r	
Cyanodictyon	c	1	f	ff	f	
Cylindrospermopsis	t/wt	1	r	r	ff	
Dactylococcopsis		1	r	r		
Gloeotrichia		1		r		
Lemmermaniella		1	r	f		
Lyngbya		2	r	r	r	R
Merismopedia	t/wt	3	f	f	f	F
Microcystis	t/wt	5	ff	f	ff	F
Oscillatoria	wt	1	r	r	r	R
Planktolyngbya	t/wt	2	r	r	f	R
Pseudoanabaena		1	r		r	
Snowella		1	r	r		
Spirulina	t	2	r		ff	
Group: *Diatomophyceae (Diatoms)*						
Genus: Aulacoseira	t	1	f	f	f	F
Cyclotella	t/wt	3	f	f	r	R
Cymbella		1	r	r	r	
Fragilaria		1	r	r		
Gyrosigma		1	r			
Navicula		2	r		r	
Pinnularia		2	r		r	
Rhizosolenia		1	r	r		
Stephanodiscus			f	r	f	R
Surirella		1	r	r		
Synedra		1	f	r	f	R
Tabellaria		1	r	r		
Urosolenia	t	1	r	r	r	
Group: *Chrysophycea*						
Genus: Mallomonas		3	r	r	r	R
Group: *Cryptophyceae*						
Genus: Cryptomonas		1		r		
Rhodomonas		1	f	f		
Group: *Xanthophyceae*						
Genus: Centritractus		1	r	r		
Goniochloris		2	r	r		
Isthmochloron		1	r	r		
Pseudostaurastrum		1	r	r		
Group: *Dinophyceae*						
Genus:Gymnodinium		1	r		r	
Peridiniopsis	c	2	r		r	
Peridinium	c	2	r	r/f	r	R

(contd.)

Table 1 (contd.)

Group: *Chlorophyceae (Greens)*						
Genus: Ankistrodesmus	t	2	r	r	r	R
Botryococcus		1	r	f	r	R
Chlamydomonas		1	r	r		
Coelastrum	t/wt	5	r/f	r	r	
Ceonococcus		1	r	r		
Crucigenia		1		r		
Crucigeniella	t	1	r	r		
Dictyosphaerium	t	2	r	r	r	
Elakatothrix		1	r	r		
Franceia		1	r	r		
Golenkinia		1	r			
Kirchneriella	t	2	r		r	
Koliella		1			r	
Lagerheimia	t/wt	1	r	r		
Monoraphidium		4	r	r	r	
Nephrocytium		1		r		
Oocystis		2	r	r	r	R
Pediastrum	c	3	f	f	f	F
Scenedesmus		4	r	r	r	R
Sorastrum		1		r		
Tetraedron	c	2	r	r	r	R
Tetrastrum	c	2	r			
Treubaria		1		r		
Group: *Zygnemaphyceae (Desmids)*						
Genus: Closterium		4	r	r	f	R
Cosmarium		5	r/f	r	f	R
Euastrum	t	1		r		
Micrasterias		1		r		
Mougeotia		1	r		r	
Staurastrum	t/wt	19	r	f		R
Staurodesmus		3	r	r		
Xanthidium		1			F	
Group: *Euglenophyceae*						
Genus: Euglena		2	r	r	f	R
Trachelomonas		2	r	r		
Phacus		2	r		f	
Total Number of Taxa		**146**				

GD, geographic distribution; N, number of taxa; A, dry zone irrigation reservoirs; B, deep hydropower reservoirs; C, urban lakes; D, high mountain reservoirs; t, tropical ; w/t, warm temperate; c, cosmopolitan; f, frequent; ff, very frequent; r, rare.

In the case of Udawalawe there were two distinct phases, the water level was low during Jan.-Feb 1999 and the colony forming Cyanophyte, *Cyanodictyon imperfectum* was the most frequent with a small Dinoflagellate and Cryptophytes as sub-dominants. The water level decreased a great deal during Jan-Feb in the following year, and the phytoplankton assemblage was dominated by *A. granulata* with a Chlorophyte, *Pediastrum simplex* as a sub-dominant species causing a strong shift in size spectrum from the small to the largest size class. The water level was extremely low during Aug-Sept. and both filamentous and colony-forming cyanobacteria dominated the phytoplankton assemblage. In Victoria reservoir, with the highest species diversity mainly three taxonomic groups, desmids (especially Staurastrum), Cyanophytes and Chlorophytes dominated during high water level (Jan-Feb) in 1999. A shift towards a high density of *A. granulata* was observed until August with *M. aeruginosa* as sub-dominant. The size spectrum in this reservoir showed in both situations a clear maximum with the largest size class and a moderate with the smallest size class.

Table 2: Morphometric and some physical, chemical and trophic ranges of four types of water bodies

Parameter	Reservoir Type A	B	C	D
Elevation (m)	80-100	400-1200	0-510	>1500
Reservoir Area (ha)	180-6280	375-2350	18-110	15-57
Catchment (km^2)	6-900	121-560	10-102	
Maximum Depth (m)	6.5-37	78-102	2.5-13	12.5-16
Capacity (Mm^3)	15-570	173-860	0.3-2.5	0.2-0.4
Temperature (°C)	27.0-32.0	26.1-29.0	24.5-32.5	21.4-28.2
EC (μS cm^{-1})	60-760	30-60	300-	14-46
pH	7.32-8.35	7.09-7.89	7.42-8.86	6.78-7.68
Secchi Depth (m)	40-280	90-300	25-125	205-210
Total-P (μg l^{-1})	20-45	15-35	24-110	10.6-26.6
Nitrate-N-P (μg l^{-1})	60-124	36-102	36-880	46-280
Diss. Silica (mg l^{-1})	0.24-4.46	0.24-1.32	0.26-6.08	0.24-1.24
HCO^-_3 (mg l^{-1})	56-248	34-52	122-460	25-46
SO_4^-(mg l^{-1})	1.22-8.86	0.42-2.14	2.24-8.64	0.24-1.24
Cl^- (mg l^{-1})	4.26-18.2	3.64-4.58	2.46-3.48	
Na^+ (mg l^{-1})	4.26-12.4	2.34-6.84	1.24-2.46	
K^+ (mg l^{-1})	1.24-2.84	0.82-2.02	0.81-1.24	
Ca^{++} (mg l^{-1})	8.42-16.82	3.06-6.82	1.82-4.68	
Mg^{++} (mg l^{-1})	3.45-7.42	1.28-2.48	1.02-1.28	
Chl-a (μg l^{-1})	15-65	5.6-16	50-150	12.4-24

In Kandy Lake, from September 1996 to January 1997, *A. granulata* dominated the species assemblage with *P. simplex* as the sub-dominant species. *Merismopedia punctata* was a common Cyanophyte during this period but registered in relatively low numbers. *M. aeruginosa*, although present, was recorded in small numbers with the other minor taxa. *A. granulata* decreased considerably during dry weather (Feb-May) in 1997 while *P. simplex* became the dominant taxa. *A. granulata* increased again towards the wet season and progressively decreased during Feb-Mar 1998. The abundance of *P. simplex* was suppressed by a colony forming cyanophyte, *M. punctata* and registered as the sub-dominant taxa between May and July, 1998. *M. aeruginosa* succeeded as the sub-dominant species in August 1998. The abundance of *M. aeruginosa* and the other species decreased again during the rainy season (Nov-Jan) in 1998. In March 1999, towards the beginning of the southwest monsoonal rain, *M. aeruginosa* appeared as a thick bloom. The surface scum disappeared gradually but *M. aeruginosa* was retained as the dominant species since then. In the following inter-monsoonal rain (Oct-Dec) in 1999, *A. granulata* and *P. simplex* re-appeared in the Lake in moderate numbers but did not re-establish. *P. simplex* remained in small numbers and the abundance of other Cyanophytes such as *M. wesenbergii*, *M. incerta*, *Chroococcus*, *Coelosphaerium* and *Anabaenopsis* species increased progressively in the phytoplankton assemble. This resulted in a complete shift of phytoplankton species assemblage dominated by *A. granulata*, *P. simplex* and *M. punctata* during pre-blooming to species mainly dominated by Cyanophytes after blooming.

Functional species groups: Irrespective of the type of water bodies, phytoplankton species composition showed marked temporal changes. Numerical abundance was low during the peak of rainy season and high during dry season with a noticeable sequential change in species composition. The predominant taxonomic group (in terms of numerical abundance) were the diatoms during the dry season in lowland reservoirs, whereas desmids and cyanobacteria were predominant in deep hydropower reservoirs. *Microcystis*, a potential k-strategist (Reynolds, 1986) dominates eutrophic urban water bodies with high concentrations of nitrogen whereas *Cylindrospermopsis*, a nitrogen fixer, a potential r-strategist with a highly flexible ecological niche (Reynolds et al., 2002) was dominant during low water periods in an urban lake with relatively low nitrogen concentration. *Microcystis* and *Spirulina* co-exist in an urban lake influenced by tidal fluxes which is located in the heart of the capital city, Colombo. Dinoflagellates, particularly the genus *Peridiniopsis*, were dominant occasionally in dry zone irrigation reservoirs during low water level. Altogether, six functional species groups were found in the four types of water bodies comprising the following: filamentous nitrogen fixing cyanobacteria (*C. raciborski*), small colony forming cyanobacteria not forming surface scums (*Merismopedia* and *Cyanodictyon*), potential r-strategists; non-nitrogen fixing *Microcystis* (k-strategist); small centric diatom, *Cyclotella* (r-strategists) and a large centric diatom, *A. granulata* (k-strategist). Unicellular desmids, especially the genus *Staurastrum*, were rich in deep hydropower reservoirs characteristic with soft and low pH. Shift in functional groups were always linked either with dilution or enrichment.

Discussion

The environmental variables in Sri Lankan standing water bodies are strongly influenced by the seasonal changes of monsoon driven or orographic rainfall and elevation. The highest rainfall in Sri Lanka occurs during the winter monsoon from November until January, whereas the summer months (June to September) are normally dry. However, the rainfall pattern in southeast Asia (and the total rainfall for a rainy season) is variable (Zubair, 2002), so that even within a short period of the investigation a considerable difference in phytoplankton could be found from year to year because of high water demand during dry periods. The temperature variation over time in the Sri Lankan reservoirs was not more than 5°C with a minimum in January. But diel range is significantly high and it increases with increasing altitude. This may have a pronounced influence on the diel variation of phytoplankton species composition especially in the vertical axis. Temporal variations of underwater light climate resulting from overcast sky and turbidity (planktonic and inorganic particles) were found frequently related to changes in phytoplankton quantities and growth. Variations in nutrient concentrations are in general related to changes in water level, flushing and phytoplankton growth. Although noticeable variations in both P- and N-compounds are common, the average nutrient level allow ranking the water bodies along a trophic gradient. Carbon supply is influenced by comparably low alkalinity with the lowest values in highland reservoirs and variations in pH from neutral or slightly acidic to highly alkaline (pH over 8.1) is also influenced by rainfall. Extreme variations of pH occur in the highly eutrophic urban water bodies and in the dry zone reservoirs it coincides with high and low water levels.

Three distinct trophic categories influenced mainly by rainfall—meso-eutrophic (dry zone reservoirs), oligo-mesotrophic (deep highland reservoirs) and eutrophic-hypertrophic (urban water bodies)—are established in Sri Lanka (Silva, 2004; Rott et al., in press). Besides, it seems that phytoplankton ecology is more influenced by the hydraulic balance, water chemistry and wind and temperature driven mixing processes rather than grazing. The comparison of phytoplankton structure indicates a pronounced gradient of complexity (species richness) positioned along a trophic gradient from the most eutrophic urban reservoirs to the oligo-mesotrophic deep highland reservoirs. Further, water chemistry, basin morphology, and water renewal influenced by natural and anthropogenic factors are important for both the selection of dominant taxa and the seasonal shifts of functional species groups.

Although in fact temperature variation in four types of water bodies are narrow as a potential environmental variable, when it couples with hydrological conditions and wind mixing with regular changes between rainy and dry season, these are sufficient enough to cause a shift in phytoplankton size and species structure (Rott et al., in press). Variability of species richness seems to be more related and much inclined to trophic status than to stability/variability pattern of the environment (Tolotti, 2002). The deep upland reservoirs are strongly influenced by monsoon wind. However, changes in pattern of phytoplankton are not so clear since these canyon shaped reservoirs are sheltered against wind and the monsoon intensity by surrounding hilly landscape (de Lima et al., 1983). In shallow reservoirs, diurnal variations are stronger than seasonal differences and hinder species succession resulting in phytoplankton stability (equilibrium) because of resuspension but large seasonal variations were apparent in all types of water bodies. These were strongly related to water level, water renewal and mixing pattern in contrast to the long-term stability and sudden shifts reported from specific shallow lakes in Africa (Melack, 1979). Apparently, the succession rate of phytoplankton in the shallow water bodies is lower than in the deep-water ones but the factors that drive this obvious disparity remain for future studies.

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