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Depth distribution and ecological preferences of periphytic algae in Kenyir Lake, the largest tropical reservoir of Malaysia*

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Abstract We studied the depth distribution of periphyton, growing on inundated dead trees in Kenyir Lake, Malaysia in June 1995. The algal floral composition and structure manifested changes down the depth gradient in terms of species richness, abundance, diversity and cell density. In regression analysis, all these algal attributes were negatively correlated with the depth gradients at $P<0.05$. In terms of species richness, the bacillariophytes showed dominance over the cyanophytes and chlorophytes; whereas with respect to standing crop, the cyanophytes showed dominance over the bacillariophytes and chlorophytes. The chlorophyll *a* was higher at the mid and bottom-depths than the surface-depth in both the downstream and upstream sites, which showed that vertical productivity or biomass accumulation was greater in low light irradiance. The product-moment correlation analysis showed that conductivity, turbidity, dissolved oxygen, reactive phosphate and ammonium-nitrogen were highly correlated with the algal assemblage data. However, photosynthetic active radiation (PAR) showed poor correlation with the community data. These observations have cast some light on the autoecological characteristics, habitat preferences and environmental responses of tropical periphytic communities.

Keyword: depth; periphytic algae; tropical; large reservoir; Kenyir Lake; community structure; biomass

1 INTRODUCTION

Classically, limnological studies have focused on pelagic habitats and few studies have been made on water column profiling of autotrophs, either phytoplankton or periphyton, with relation to their biodiversity, community structure and primary productivity in freshwater bodies. Vertical distribution of periphytic algae in freshwater bodies from temperate regions have been extensively studied (e.g. Loeb et al., 1981, Wulff et al., 2005, Cantonati et al., 2009) compared to their tropical counterparts.

Kenyir Lake or Tasik Kenyir (Fig.1) is an artificial lake located in the state of Terengganu in northeast Malaysia created in 1985 by the damming of the Terengganu River to create the Sultan Mahmud Power Station. The depth profile study of Kenyir Lake is important in various ways. This is the largest reservoir not only in Malaysia but also in Southeast Asia. The mean-depth of Kenyir Lake is of 37 m. Periphyton, being autotrophs, are part of the trophic structure of an aquatic ecosystem. Understanding of the depth distribution of microflora and their productivity is crucial for proper management of reservoirs, but as of yet, they remain unexplored in Southeast Asia, particularly in Malaysia. Depth profile studies of periphyton are also linked with biomonitoring, and biodiversity studies. Nutrient cycling, primary production, lake metabolism are also directly linked with the autotrophic dynamics of waterbodies. Theoretical limnology, focusing on light attenuation and photochemistry study, also requires the study of depth profile (e.g. Nakano et al., 2006). For Kenyir Lake, being a large-deep reservoir, understanding of its vertical profiling with periphyton and their ecological preferences is

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important for developing sustainable fisheries in the context of overall lake management.

The objectives of the present study are firstly to investigate species composition, structure, diversity, ecological preferences, distribution patterns and biomass variations of periphytic algae down the depth gradient, and secondly to determine environmental descriptors that may have influence or impact on the periphytic assemblages in the water column.

2 MATERIALS AND METHODS

2.1 Description of the lake and sampling sites

Kenyir Lake is located between latitudes 4°40′N to 5°15′N and longitudes 102°32′E to 102°55′E in the state of Terengganu, the east coast of Peninsular Malaysia (Fig.1). This reservoir was created in 1986 to generate hydroelectric power and impounded two main rivers, River Terengganu and River Terengan (Furtado et al., 1977). The lake is very irregularly shaped and dendritic in nature. Its total water surface area is 36.900 h, with a mean-depth of 37 m and Top Water Level (TWL) of 145 m above mean sea level.

2.2 Sampling procedure

Innumerable trees, now dead, were flooded by the impoundment. Periphyton have grown on their submersed surfaces to a depth of 10 m. Periphyton samples were taken from two sites, Dam side (Site 1) and Petang River (Site 2), representing downstream and upstream habitats of the lake, respectively. The description of lake and sampling sites are detailed in Rouf et al. (2008). Periphytic algae were collected from three depth levels by SCUBA (Self-contained Underwater Breathing Apparatus) diving on a single occasion in June, 1995. These depths were 0.5 m (surface), 5 m (middle) and 10 m (bottom) at the Dam side and 0.5 m (surface), 2.5 m (middle) and 5 m (bottom) at the Petang River. For the purpose of statistical analysis, each standing dead tree was considered as one sampling unit, and from each depth at least three sub-samples were taken to make one composite sample.

All samples were preserved in formalin acetic acid Alcohol (FAA) solution for taxonomical study and in 90% Acetone saturated with Magnesium carbonate for chlorophyll measurement. Chlorophyll *a* was determined using the trichromatic equation method (APHA, 1989) after overnight extraction at 4°C temperature.

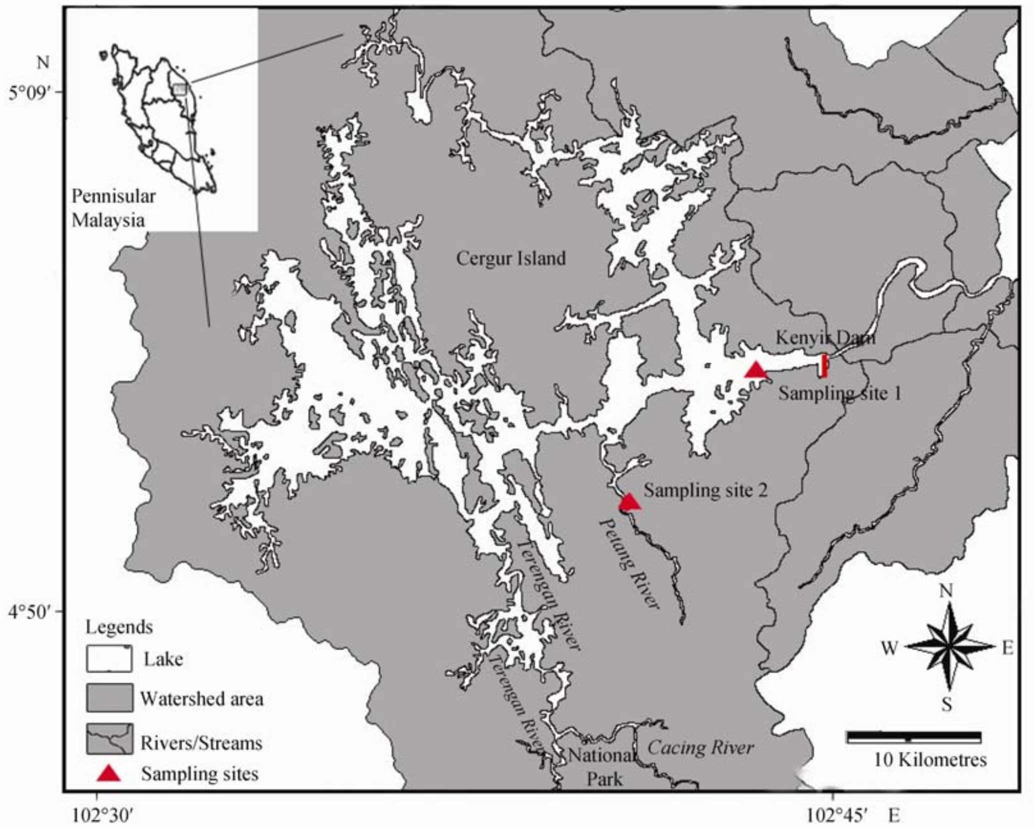


Fig.1 Map of Kenyir Lake showing location of the two sampling sites

Site 1: The dam side; Site 2: Petang River

In the periphytic assemblages, cyanophytes were mostly of filamentous type. The filaments (trichomes) were counted under the microscope; and later converted to cell number by multiplying with the respective *multiplication factor*, which is the average cell number per filament for each individual species or taxon determined by cell counts of at least 7–11 of filaments of the concerned species/taxon. The abundance of diatom taxa was calculated based on the monthly mean value of standing crop (cell density). Calculation of algal cell density per unit area of substrate was done by following APHA (1989).

2.2.1 Water samples

Water samples were collected in acid-washed 1 L polyethylene bottles. In the field, water chemistry data, such as pH, dissolved oxygen and secchi transparency were collected between 12.00 noon and 2.30 pm. Temperature, pH, conductivity and dissolved oxygen levels were measured by HYDROLAB Instrument (Microsonde model). Total dissolved solids (TDS) and turbidity were measured by hand-held TDS and Turbidity metres (DREL/2000) (Hach, 1993). Light was measured by a light meter (LI-COR, model Li-189) with an underwater quantum sensor. All these instruments were calibrated for their corresponding parameters during sampling. For all other chemical analysis, standard methods and procedures outlined in APHA (1989), Golterman et al. (1978) and Mackereth et al. (1978) were followed.

2.2.2 Identification of algae and numerical analysis

Algae were routinely examined and counted with a Nikon research microscope (OPTIPHOT) using ×40 and ×100 magnifications with oil immersion field objective lenses. For identification, reference books and works of Pascher (1913b), Desikachary (1959), Prowse (1962), Patrick et al. (1966), Whiteford et al. (1973), Mizuno (1978), Ho (1979), Geitler (1985), Bourrelly (1981, 1985, 1990) and Yamagishi et al. (1991) were followed. Diatom nomenclature was updated in accordance with Round et al. (1990). Simple regression, product-moment correlation (Zar, 1984), species richness, abundance, Shannon-Wiener diversity index (H'), Pileuo's evenness and Jaccard similarity index (J') (Ludwig et al., 1988) were deduced for the community and environmental data.

3 RESULTS

The collected algal mats were approximately 1 mm thick with a thin cover of polysaccharide matrix on the top. The mats of the bottom-depth were more fragmented, loose and sparsely distributed on the tree trunks than those of the surface and mid-depth. Over all depths, a total of 177 periphytic algal taxa were found: diatoms (comprising 98 taxa), cynaphotes (61), chlorophytes (13), and dinoflagellates (5) (Appendix 1). In depth-wise distribution at the Dam side, 67 taxa were found at both the 0.5 and 5 m depths and 45 taxa at 10 m. In the Petang River, the total number of taxa found at each depth was 79, 64 and 37 at 0.5 m, 2.5 m and 5 m, respectively (Table 1).

Cyanophytes: The number of cyanophytes did not vary significantly between surface and mid-depths, but declined to one-fourth and one-third at the bottom-depth at the Sites 1 and 2, respectively (Table 1). All the cyanophyte taxa were filamentous except *Chroococcus* sp.; *Microcystis* sp.; *Synechococcus leptosira*; and *Gloeocapsa* sp.. Some taxa also showed depth exclusiveness. For example, *Anabaena torlusa* and *Anabaena variabilis* were found exclusively at 0.5 m depth. *Oscillatoria acuta* and *Oscillatoria amphigranulata*, *Camptylonema indicum*,

Table 1 Changes in species number and cell density of the periphytic algae found on standing dead trees at the three depth levels in June 1995 (*n*=7)

Depth level (m)	Number of taxa				Cell density*			
	Cyanop. (±SE)	Bacillario. (±SE)	Chloro. (±SE)	Whole assemb. (±SE)	Cyano. (±SE)	Bacillario. (±SE)	Chloro. (±SE)	Whole assemb. (±SE)
Dam side								
0.5	26 (2.10)	36 (1.87)	5 (0.35)	67 (3.7)	5 563 (137)	682 (58)	65 (7)	6 336 (147)
5	26 (2.76)	33 (2.14)	8 (0.75)	67 (3.9)	4 337 (158)	1 046 (95)	45 (7.5)	5 428 (152)
10	5 (1.3)	38 (2.39)	2 (0.12)	45 (2.58)	1 126 (95)	1 230 (115)	24 (5.3)	2 380 (110)
Petang River								
0.5	26 (2.3)	49 (1.74)	4 (0.33)	79 (3.6)	5 020 (174)	669 (70)	188 (24)	5 877 (125)
2.5	23 (2.5)	38 (1.89)	3 (0.35)	64 (3.2)	4 535 (185)	1 553 (115)	121 (12)	6 209 (134)
5	8 (0.86)	26 (1.78)	3 (0.54)	37 (2.8)	1 325 (85)	762 (96)	100 (8)	2 188 (110)

*cell numbers /mm^2 substrate

Pseudoscytonema malayense; *Scytonema multiramosa* and *Aulosira simplex* were confined to 5 m depth only. At the 10 m depth, only five taxa, viz. *Anabaena cylindrica*, *Haplosiphon* sp. *Lyngbya perelegans*, *Scytonema* sp. and *Tolypothrix* sp., were encountered.

In the Dam side, 14, 18 and 3 cyanophyte genera were encountered at the 0.5, 5 and 10 m depths, respectively. At the 0.5 m depth, *Anabaena* and *Lyngbya* were represented by four taxa each followed by *Phormidium* and *Oscillatoria* (two taxa each); and *Stigonema* and *Scytonema* (two taxa each). At the 5 m depth, *Lyngbya* were comprised of four taxa followed by *Scytonema* (three taxa), *Aulosira*, *Anabaena* and *Oscillatoria* (two taxa each). *Westiella* sp. and *Wollea saceta* were confined exclusively to the 5 m depth.

In the Petang River, a total of 16 cyanophyte genera were encountered each at the surface and middle depths whereas the bottom depth contained only five taxa. Among them, *Lyngbya* was represented by 6 taxa followed by *Phormidium* (four taxa) and *Anabaena* (three taxa). The remaining 13 genera were each comprised of one taxon. The bottom depth taxa were *Lyngbya*, *Phormidium*, *Anabaena* two taxa each; and *Scytonema* and *Schizothrix* one taxon each.

Bacillariophytes: The species richness of the bacillariophytes was almost static along the depths in the Dam side, whereas it gradually declined from upper to lower depths in the Petang River. Here, the number of taxa at the bottom-depth (5 m) was nearly half that of the surface-depth (0.5 m). The cell density varied with depth, gradually increasing from the surface to the bottom depths in the Dam side, while in the Petang River, the mid-depth possessed the highest cell density (Table 1).

In terms of genera, bacillariophytes did not vary widely with depth, however, their species composition varied in the Dam side. Here, 15 genera were found at both the 0.5 m and the 5 m depths and 14 at the bottom (10 m) depth. At the surface-depth (0.5 m), *Navicula* was comprised of seven taxa, followed by *Pinnularia* (four taxa), *Amphora*, *Cymbella*, *Eunotia*, *Frustulia*, *Gomphonema* (three taxa each) and *Achnanthes*, *Neidium* (two taxa each). At the middle-depth (5 m), the genus containing highest number of taxa shifted to *Pinnularia*, with seven taxa, followed by *Gomphonema* and *Eunotia* (four taxa each), *Frustulia*, *Navicula* (three taxa each) and *Cymbella* (two taxa). *Stauroneis pusilla* was exclusively found at the mid-depth in both the sites. At the bottom depth (10 m), *Eunotia* possessed highest number of taxa (seven) followed by *Navicula* and *Pinnularia* (six taxa each), and *Frustulia* and *Gomphonema* (3 taxa each).

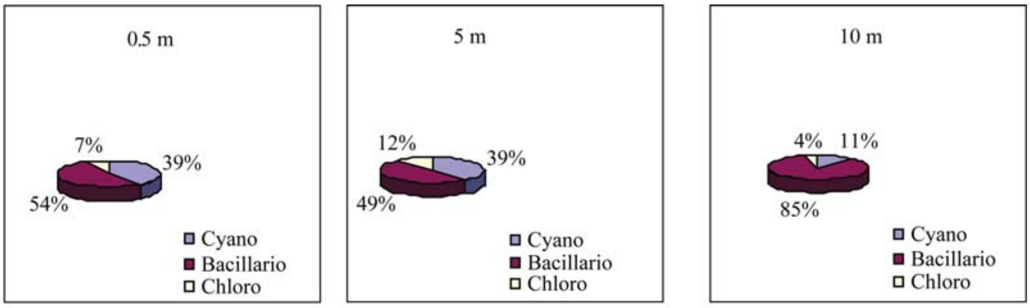
In the Petang River (Site 2), the total numbers of genera were 17, 16 and 11 at the 0.5 m, 2.5 m and 5 m depths, respectively. Like the Dam side, the taxa comprising each genus varied widely. At the surface-depth, *Pinnularia* had seven taxa, followed by *Eunotia* and *Cymbella* (6 each). At the middle-depth, *Navicula* comprised six taxa followed by *Cymbella* and *Achnanthes* (5 taxa each) and *Pinnularia* (three taxa). The taxa composition at the bottom depth was similar to that of the middle-depth. At the bottom depth (5 m), *Cymbella* and *Achnanthes* contained five taxa each followed by *Navicula* and *Gomphonema* (three taxa each) then *Eunotia* and *Pinnularia* (2 taxa each).

Chlorophytes: Chlorophyta was a minor group in terms of both species richness and standing crop (cell density) in this reservoir. Any trends of variation in their vertical distribution were also negligible due to their poor presence. This class constituted only 5%–6% of the total taxa and 1%–3% of the total standing crop of the whole assemblage.

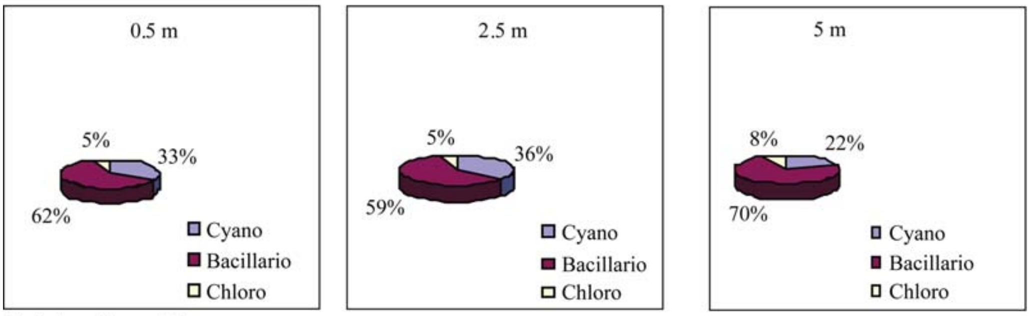
In terms of species richness, diatoms (bacillariophytes) dominated (ranging from 49 to 85% of all species) followed by cyanophytes (ranging from 11% to 39%) and chlorophytes (ranging from 4% to 12%) (Fig.2). The Jaccard similarity indices showed low similarity of floral composition between the depths: the maximum similarity was found to be only 35% (Table 2).

Species abundance

Cyanophyta: The species abundance at different depths varied considerably. In the Dam side, the dominant cyanophyte taxa at the 0.5 m depth, in order of abundance, were: *Schizothrix lamyi*, *Anabaena cylindrica*, *Oscillatoria splendida*, *Microcoleus* sp., *Lyngbya perelegans*, *Scytonema fremyii*, *Lyngbya porphyrosiphonis*, *Stigonema minutum*, and *Fischrella moniliformis* (Fig.3). These nine taxa contributed 80% of total cyanophyte cells. At the mid-depth (5 m), dominance shifted, the dominant taxa being *Scytonema multiramosa*, *Lyngbya perelegans*, *Haplosiphon* sp. *Lyngbya* sp., *Anabaena cylindrica*, *Schizothrix lamyi*, *Microcoleus* sp., *Aulosira bombayensis* and *Lyngbya porphyrosiphonis*. At the 10 m depth, only five taxa were encountered: *Anabaena cylindrica*, *Haplosiphon* sp. *Lyngbya perelegans*, *Scytonema* sp.



A. The Dam side station



B. Petang River station

Fig.2 Compositional proportions of algae on natural substrates at different depths in June, 1995

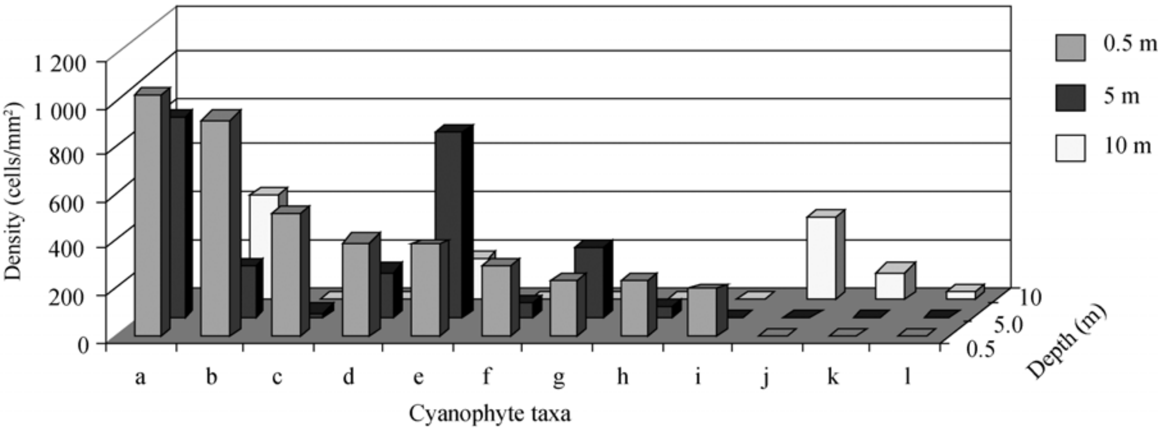


Fig.3 Variation of abundance with depth of the dominant cyanophytes found on natural substrates at the Dam side station

Legend: a. *Schizothirx lamyi*; b. *Anabaena cylindrical*; c. *Oscillatoria splendida*; d. *Microcoleus* sp; e. *Lyngbya perelegans*; f. *Scytonema fremyi*; g. *Lyngbya porphyrosiphonis*; h. *Stigonema minutum*; i. *Fischrella moniliformis*

Table 2 Jaccard Similarity Indices (C_j) comparing floral assemblages between depths

Station	Floral group	Surface-depth versus mid depth	Mid-depth versus bottom-depth	Bottom-depth versus surface-depth
Dam side station	Cyanophytes	0.35	0.27	0.25
	Bacillariophytes	0.31	0.31	0.16
Petang River station	Cyanophytes	0.32	0.25	0.15
	Bacillariophytes	0.31	0.11	0.05

and *Tolypothrix* sp. In the Petang River, the most abundant cyanophyte taxa were *Oscillatoria splendida*, *Anabaena cylindrica*, *Haplosiphon* sp., *Schizothrix brauni*(?), *Phormidium purpurescence*, *Fischerella moniliformis*, *Anabaena circinalis* and *Scytonema* sp. at the 0.5 and 2.5 m depths, while *Anabaena cylindrical*, *Phormidium purpurescence* and *Phormidium corium* were found at the 5 m depth.

Bacillariophyta: Bacillariophytes also showed variations in abundance with depth. At the Dam side, at 0.5 m depth, the dominant taxa were *Frustulia saxonica*, *Frustulia rhomboides*, *Encyonema gracilis*, *Fragilaria construens*, *Navicula cryptocephala*, *Frustulia vulgaris*, *Gomphonema longiceps*, *Pinnularia parva*, *Neidium productum*, *Eunotia lunaris* and *Navicula radiosa*. They comprised 70% of the total diatom cell count at this depth. At the 5 m depth, dominance shifted to *Navicula cryptocephala*, *Tabellaria fenestrata*, *Fragilaria construens*, *Frustulia saxonica*, *Encyonema gracile*, *Pleurosigma elongatum*, *Achnanthes linearis*, *Gomphonema gracile*, *Gomphonema parvulum*, and *Navicula radiosa*. The dominance again shifted at the 10 m depth, the representative taxa being *Navicula cryptocephala*, *Navicula radiosa*, *Fragilaria construens*, *Eunotia lunaris*, *Eunotia sudetica*, *Eunotia monodon*, *Eunotia praerupta*, *Nitzschia rhomboides*, *Tabellaria fenestrata*, *Eunotia major v. indica*, and *Gomphonema parvulum*.

In the Petang River, the dominant taxa at the surface-depth (0.5 m) were *Encyonema gracilis*, *Cymbella minuta*, *Navicula radiosa*, *Cymbella ventricosa*, *Gomphonema longiceps*, *Navicula feuerborni*, *Gyrosigma* sp., *Frustulia rhomboides*, *Pleurosigma elongatum*, *Gomphonema parvulum* and *Navicula gracilis* (Fig.4). At the mid-depth, the dominance shifted to *Navicula radiosa*, *Gyrosigma* sp., *Gomphonema parvulum*, *Navicula gracilis*, *Navicula feuerborni*, *Neidium affinis*, *Achnanthes inflata*, *Achnanthes tropica*, *Fragilaria construens* and *Gomphonema gracile*. At the bottom depth, the dominance again shifted to *Achnanthes crenulata*, *Achnanthes inflata*, *Achnanthes linearis*, *Achnanthes tropica*, *Cocconeis placentula*, *Cyclotella kuetzingiana*, *Cymbella ehrenbergii*, *Cymbella turgida*, *Cymbella javanica*, *Cymbella tumida*, and *Cymbella ventricosa*.

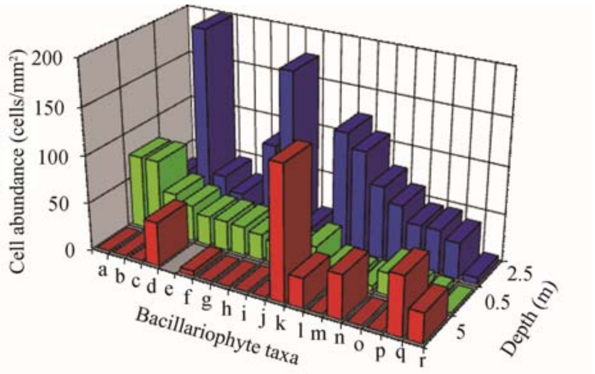


Fig.4 Variation with depth in species abundance of the dominant diatom taxa found on natural substrates at the Petang River station in June, 1995

In the figure the depth order is changed for the sake of better visualization. a. *Encyonema gracilis*; b. *Cymbella minuta*; c. *Navicula radiosa*; d. *Gomphonema gracile*; e. *Cymbella ventricosa*; f. *Gomphonema longiceps*; g. *Navicula feurborni*; h. *Gyrosigma* sp.; i. *Frustulia rhomboides*; j. *Pleurosigma elongatum*; k. *Gomphonema purvulum*; l. *Navicula gracile*; m. *Neidium affinis*; n. *Achnanthes inflata*; o. *Achnanthes tropica*; p. *Fragialria construens*; q. *Achnanthes crenulata*; r. *Coconeis placentula*

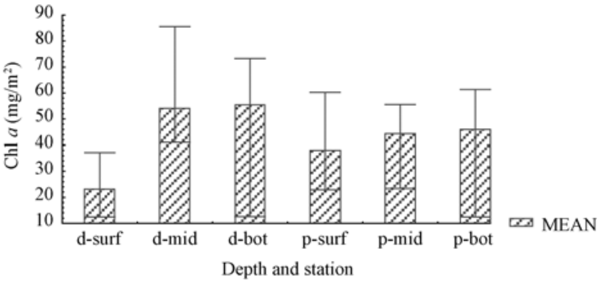


Fig.5 The variation in chlorophyll *a* concentration of the periphytic algae on standing dead trees at the different depths at the Dam side and Petang River stations, collected in June 1995

Legends: D = Dam side. P = Petang River. Bar = Standard deviation

Species diversity: As with taxa richness, the Shannon-Wiener diversity indices (H') of the assemblages decreased from upper to lower depths. The maximum H' value was 3.36. Classwise, diatoms were more diverse than cyanophytes and chlorophytes, the latter being marginalized in the whole assemblages (Table 3).

Chlorophyll *a* biomass: In both sites, chlorophyll *a* was found to be much higher at the mid and bottom depths than at the surface depth. Chlorophyll *a* varied widely at the bottom depth, ranging from 225.7 to 580 mg/m^2 at the Dam side and from 110 to 610 mg/m^2 in the Petang River (Fig.5).

Statistical analysis: Different algal attributes, such as species richness, diversity and cell density were regressed against the depth profile. All of the community attributes were found to be highly correlated with the depth gradient at $P<0.05$ level (Table 4).

Environmental parameters: A total of nine water chemistry and limnological parameters were measured down the depths (Table 5). pH ranged between 6.85 and 7.12, water temperature ranged between 29.05°C and 31.3°C. Conductivity ranged between 25 and 28 μS/cm. PAR ranged between 78.00 and 1 781 μmol/m^2 s in the Dam side, and between 112.78 and 526.3 μmol/m^2 s in the Petang River. Results of the product-moment correlation analysis between species number and cell density of periphytic algae on standing trees and environmental parameters are cited in Table 6.

Table 3 Number of taxa (*S*), species diversity (*H′*) and evenness (*J′*) of the periphyton assemblages at different depths in June, 1995 (*n*=7)

Depth (m)	Cyanophytes			Bacillariophytes			Chlorophytes			Whole assemblage		
	S	*H′*	*J′*	*S*	*H′*	*J′*	*S*	*H′*	*J′*.	*S*	*H′*	*J′*
St. 1: Dam side												
0.5	26	2.65	0.81	36	3.21	0.90	5	0.92	0.57	67	3.11	0.74
5	26	2.46	0.76	33	2.68	0.77	8	1.58	0.76	67	3.1	0.74
10	5	1.36	0.98	38	3.23	0.89	2	0.56	0.81	44	3.00	0.79
St. 2: Petang River												
0.5	26	2.6	0.80	49	3.36	0.86	4	0.82	0.59	79	3.13	0.71
2.5	23	2.5	0.82	38	3.11	0.85	5	0.97	0.62	64	2.95	0.74
5	8	1.69	0.87	26	2.99	0.92	3	0.65	0.64	37	2.67	0.75

Table 4 Results of the linear regression between the different algal attributes and the different depth levels (*n*=7; *P*<0.05)

Dependent variables	Independent variables	*r*	*Y*
Species Nos.- Dam	Different depth levels	-0.87	$y = 70.95-2.32x$
Species Nos.-PR	Different depth levels	-0.99	$y = 81.87-8.49x$
Total cell Nos.-Dam	Different depth levels	-0.96	$y = 6711-397x$
Total cell Nos.-PR	Different depth levels	-0.83	$y = 6640-748x$
Species diversity Dam	Different depth levels	0.91	$y = 3.125-0.011\ 1x$
Species diversity-PR	Different depth levels	0.99	$y = 3.15-0.093x$

Table 5 Ambient environmental data at the different water depths in June, 1995

Parameters	Depth level (Dam side)			Depth level (Petang River)		
	0.5 m	5 m	10 m	0.5 m	2.5 m	5 m
pH	7.12	7.20	7.10	6.70	7.00	6.85
Temperature (°C)	31.3	30.15	29.98	29.98	29.88	29.5
Conductivity (μS/cm)	26.4	25.00	26.7	26.00	26.00	28.00
DO (mg/L)	7.84	7.64	6.96	7.35	7.24	6.56
Turbidity (NTU)	1.45	1.46	1.51	1.30	1.32	1.34
Reactive phosphate (mg/L)	0.11	0.16	0.18	0.03	0.04	0.04
Ammonia-N (mg/L)	0.04	0.03	0.06	0.07	0.06	0.09
Nitrate-N (mg/L)	0.5	0.4	0.6	0.2	1.00	0.8
Nitrite-N (mg/L)	0.003	0.035	0.003	0.011	0.01	0.01
PAR (μmol/m^2 s)	1 781	338	78.20	526.3	242.3	112.78

Table 6 Results of the product-moment correlation analysis between species number and cell density of periphytic algae of standing trees and environmental parameters found at the different depth levels in the Dam side (*P*<0.05 level)

Variables	Cyano. taxa	Bacilla. taxa	Chloro. taxa	Cyano.-cell	Bacilla. cell	Chloro. cell	Whole assem. taxa	Whole assem. cell
pH	0.65	-0.62	0.90	0.43	0.00	0.20	0.50	0.47
Temperature(°C)	0.060	0.90	0.10	0.79	0.98	0.91	0.70	0.76
Conductivity(μS/cm)	-0.94	-0.50	-0.70	1.00	0.93	0.98	1.00	0.99
DO(mg/L)	0.98	0.40	0.70	1.00	0.88	0.96	1.00	1.00
Turbidity (NTU)	-0.99	0.34	0.80	0.99	0.85	0.94	1.00	1.00
Reactive phosphate (mg/L)	-0.72	0.82	0.30	0.88	1.00	0.97	0.80	0.85
Ammonia-N(mg/L)	0.94	0.14	1.00	0.82	0.50	0.67	0.90	0.85
Nitrate-N(mg/L)	-0.87	0.33	1.00	0.70	0.33	0.51	0.80	0.74
Nitrite-N(mg/L)	0.50	0.76	0.90	0.25	0.19	0.01	0.40	0.30
PAR(μmol/m^2 s)	0.62	0.89	0.10	0.81	0.98	0.92	0.70	0.77

4 DISCUSSION

This study has revealed some interesting characteristics and attributes of periphytic assemblages down the depth gradient of the Kenyir Reservoir, which has an average depth of 37 m and is a mesotrophic waterbody.

The euphotic zone in Kenyir Lake extends to 15 m depth while the lake littoral depth (Z) was found to be 19 m in June, 1995. The current study showed that periphytic algae did not grow beyond 10 m depth, at which the light irradiance was found to be 78 μmol/m^2 s. Perpihyton assemblages showed gradual reduction with depth in terms of both in species richness and abundance. The species composition also varied considerably, which was depicted by the Jaccard similarity indices (Table 2). The linear regression results (Table 4) showed that species richness, diversity, and standing crop (dependent variables) and the different depth levels (independent variables) were significantly correlated at the $P<0.05$ level. This signifies that the algal communities have their habitat or ecological preferences along the environmental gradients that are vertically stratified. In other words, they have their own niche occupancies being driven by their inherent autoecological characteristics or behavior. Depth related reduction of the algal assemblages in other large freshwater bodies have also been reported. For example, in Lake Michigan, shallow, mid and deep zones were differentiated on the basis of species composition, abundance and diversity (Stevenson et al., 1981). Another example is Lake Baikal, which showed zonation of benthic algal distribution with depth (Nozaki et al., 2002).

The inter-community composition showed that diatoms thrived better than blue-greens and greens down the depth gradient. In terms of species richness, diatoms dominated at all three depths. In the Dam side, their cell densities were higher at the deep and mid depths (though much lower than that of the cyanophyta at the surface). The situation was similar in the Petang River, with the exception that diatom cell density was highest at the mid-depth. In India, periphyton of submersed plant parts and of glass slides in deep water rice fields showed vertical variations where the bottom and surface levels were dominated by bacillariophytes and chlorophytes, respectively (Das et al., 1994). Poulickova et al. (2006) found that diatom species richness was higher at an oligotrophic site and that of cyanobacteria were often available in the eutrophic fish ponds. The species richness of diatoms may be linked to the trophic status of Kenyir Lake, it being a mesotrophic water body.

Some interesting information has also been revealed about the habitat or autoecological preferences of cyanophytes. *Schizothrix lamyi* showed a tendency to decline from surface to bottom depths. *Anabaena cylindrica* and *Scytonema fremyii* showed non-rhythmic or heterogeneous abundance in all three depths. *Oscillatoria splendida* was found in negligible amounts at the surface and mid depths. *Fishchrella moniliformis* was only present at the surface-depth. *Lyngbya porphyrosiphonis* was at almost equal abundance at the surface and mid depths, but was absent at the bottom-depth. The trend of *Stigonema minutum* was the same as *Oscillatoria splendida*, whereas *Haplosiphon* sp. and *Lyngbya perelegans* were more abundant at the mid-depth. The oligotrophic lake of Taupo in New Zealand showed three periphytic zones: surface (0–2 m), mid water (2–20 m) and deep (>20 m) where diatoms (*Aulacoseira granulata*, *Rhopalodia novaezealandiae*, *Epithemia sorex*, and *Fragilaria* spp.) dominated the deep assemblage, while cyanophytes, (*Tolypothrix tenuis* and *Mastogloia elliptica*) dominated the mid-depth and *Scytonema*, *Dichothrix*, and filamentous chlorophytes dominated the shallow zone (Hawes et al., 1994). This type of zonation was apparently absent in Kenyir Lake.

In this study, some diatom taxa also showed clear depth preferences. For example, *Gomphonema parvulum* gradually increased from surface to bottom depths, while *G. longiceps* showed the opposite trend to that of *G. parvulum*. It is pertinent to mention that *G. parvulum* was one of the most dominant taxa in the monsoon period (December) when the lake water in Kenyir shifted towards slightly acidic. In the dry period (June), when the lake water became more alkaline, its abundance declined considerably (Rouf, 1997). Another gomphonoid diatom, *Gomphonema gracile* did not show significant change down the depth gradient in the present study. *Cymbella gracilis* gradually decreased from the surface to the mid-depth and was absent at the bottom-depth. *Navicula radiosa* and *Gyrosigma* sp. were dominant in the mid-depth but absent in the bottom-depth, whereas *Navicula gracilis* was present in all the depths and was more dominant in the mid-depth. These phenomena show conspicuous ecological preferences for habitats by individual diatom taxa or species.

Some interesting trends in genera-wise diatom distribution were also revealed in this study. In the

Dam side, at the surface-depth (0.5 m), the dominant genus in terms of species number was *Navicula*, whereas in the mid-depth the dominance shifted to *Pinnularia*, and at the 10 m (bottom depth), to *Eunotia*. *Navicula* is a eurytopic genus; *Pinnularia* and *Eunotia* are mostly acidophilic genera. The trend of decreasing pH with depth coincided with this depth distribution. However, in Petang River, the surface-depth was dominated by *Pinnularia* and *Gomphonema* and the deeper two depths by *Navicula*, *Cymbella* and *Achnanthes*. The light irradiance was less in Petang River, being only one-third to that of the Dam side (Table 5). This would probably have some effect on depth distribution of diatoms. Diatoms have shown conspicuous depth preferences in other studies also. They migrate in response to changes in ambient microhabitat to find their preferred environment. For example, in an experiment in Lake McCnaughy, a large reservoir in Nebraska, USA, diatoms responded consistently to switching with manipulation of clay tiles. Out of the 32 most common taxa, 26 showed significant upper (10) or lower (16) depth choices (Hoagland et al., 1990). In another experiment, Mitbavkar et al. (2004) demonstrated that irradiance has a greater role than tide in controlling microscale migration of diatoms. In the temperate environment of Finland, Wulff et al. (2005) found that in the sediment of a microtidal fjord, pelagic forms of diatoms inhabit the deeper locations, while epipelic and epipsammic forms inhabit the shallower sites.

Many important environmental parameters, such as turbidity, dissolved oxygen, conductivity, reactive phosphate levels and ammonium-nitrogen levels have contributory effects on the depth distribution and growth of periphyton in the Kenyir Lake (Table 6). However PAR showed poor relationship with the whole assemblage data. Wulff et al. (2005) found that light is not the only important environmental factor but rather a combination of temperature, salinity and light explain 57% of the diatom taxa variation in redundancy analysis (RDA). However, Hoagland et al. (1990) found that light regime and wave disturbance were the main controlling factors for vertical zonation of freshwater epilithic algae.

Cells adapted to high light intensity have lower chlorophyll *a* content per cell than those adapted to low light intensities (Wetzel, 1983) Vertical patterns of primary production in Kenyir corroborated this phenomenon. The ecological effects of light and temperature on the photosynthesis and the growth of algae are inseparable because of interrelationships between metabolism and light saturation. Generally, the intensity of light required to saturate algal photosynthesis increases as water temperature increases. In Kenyir, in the Dam side, the light-irradiance levels were 1 781, 338 and 78 μmol/m^2 s at 0.5 m, 5 m and 10 m depths, respectively (Table 5). Here, the chlorophyll *a* at the mid and bottom depths was more than double that of the surface-depth. In Petang River, light-irradiance values were almost half those of the Dam side being 569.3; 287 and 183 μmol/m^2 s at 0.5 m, 2.5 m and 5 m depths, respectively (Table 9). The chlorophyll *a* values at the mid and bottom depths were slightly higher than that of the surface depth. Nutrients are locked up in the hypolimnion due to thermal stratification in Kenyir Lake (Yusoff et al., 1994). This might also have an impact on primary production in the Dam side.

Horizontal heterogeneity in lakes may also have some effects on vertical distribution or heterogeneity of algal assemblages. Tilzer (1990) emphasized that spatially variable inputs of energy from the overlying atmosphere, in the forms of irradiance and kinetic energy, as well as differences in atmospheric pressure, can cause significant horizontal heterogeneity in large lakes. The Dam side and Petang River sampling sites are, respectively, typical representatives of lentic and lotic habitats in a reservoir ecosystem (Thornton et al., 1990). Petang River (Site 2) is a shallow, narrowed water-channel shaded by the tropical rainforest. The water was more turbid and irradiance was also less than that of the Dam side. The Dam side site is in the main basin of the reservoir with a wide open pelagic zone and with a steep littoral area. These physiogeographic differences may have contributory effects on periphytic algal assemblages.

5 CONCLUSION

In this study, periphytic algae showed significant differences in their depth distribution, which reflects on their niche or habitat preferences down the water column. It was also evident that vertical productivity or biomass accumulation was greater in low light-irradiance. However, depth related trends or distribution patterns of periphytic assemblages warrant further, more extensive (both vertically and horizontally) studies in the reservoir. This information may be immensely helpful in developing sustainable fisheries and for overall lake management particularly in the context of apprehended vulnerability of aquatic ecosystems due to climate changes.

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APPENDIX-1

List of periphytic algae found at all depths in both the Dam side and the Petang River sites in Kenyir Lake, Malaysia in June 1995

CYANOPHYTES (61 taxa)	
Anabaena circinalis	Rabenh
Anabaena cylindrica	Lemmermann
Anabaena elliptica	Lemmermann
Anabaena gelatinicola	Ghosh (after Ghosh)
Anabaena torulosa	(Carm) Lagerh. ex. Born et Flah
Anabaena variabilis	Kütz
Anabaenopsis elenkinii	Miller
Aphanizomenon flos-aquae	Ralfs
Aulosira bombayensis	Gonzalves
Aulosira simplex	Bharadw
Calothrix fusca	(Kutx) B and F
Camptylonema indicum	Schmidle
Chroococcus sp.	Nag
Dasygloea amporpha	Thwaites
Dichothrix sp.	Zanard
Fischerella moniliformis	Fre'my
Gloeocapsa sp.	Kütz
Haplosiphon intricatus	West, W. & G. S.
Haplosiphon sp..	Nag
Lyngbya allorgei	Fre'my
Lyngbya contorta	Lemm.
Lyngbya lagerheimii	(Mobius) Gom.
Lyngbya mesotricha	Skuja
Lyngbya mucicola	Lemm.
Lyngbya perelegans	Lemm.
Lyngbya porphyrosiphonis	Fre'my
Lyngbya sp.	Ag.
Microchaete elongate	Fre'my
Microchaete tenera	Thuret
Microcoleus lacustris	(Rabenh.) Farlow
Microcystis sp.	Kütz
Nodularia sp.	Mertens
Nostoc calcicola (?)	Breb. (after Fre'my)
Oscillatoria acuta	Bruhl and Biswas
Oscillatoria amphigranulata	Van Goor
Oscillatoria sp.	Pollini
Oscillatoria splendida	Grev
Phormidium calcicola	Gardner
Phormidium corium	(Ag.) Gom.
Phormidium mucicola	Hub.- Pest. and
Phormidium mucosum	Gardner
Phormidium purpurscens	Kütz.
Phormidium valderianum (?)	(Delp.) Gom.
Pseudoananbaena sp.	Koppe
Pseudoscytonema malayense	Biswas
Rivularia sp.	(Roth) Ag.
Schizothrix braunii	(A. Br.) Gomont
Schizothrix lamyi	Gomont
Scytonema fremii	Nom.nov.
Scytonema malayiyensis	Bharadw
Scytonema mulitiramosum	Gardner
Scytonema myochrous	(Dillw). Ag.
Scytonema sp.	Ag.
Stigonema mesentericum	Geitler
Stigonema minutum	Agardth
Stigonema panniforme	(Ag) Born. et Flah.
Synechococcus leptosira	Nageli
Synechococcus sp.	Nag
Tolypothrix sp.	Kutz
Westiella sp.	Borzi
Wollea saceta	Born. et Flah
DIATOMS (98 taxa)	
Achnanthes crenulata	Grunow
Achnanthes inflate	Kuetzing (Grunow)
Achnanthes linearies	W. Smith
Achnanthes microcephala (?)	(Kuetzing) Grunow
Achnanthes minutissima	Kützing
Achnanthes wolterckii	Hustedt
Acnanthes tropica	Hustedt
Amphipleura sp.	Kuetzing
Amphora angusta	(Gregory) P.T. Cleve
Amphora bitumida	Prowse

To be continued

continued

Amphora coffaeiformis	C.A. Agardh
Amphora holsatica var. *malayana*	Prowse
Cocconeis placentula	Ehrenberg
Cyclotella kuetzingiana	Thwaites
Cymbella ehrenbergii	Kuetzing
Cymbella graciles	Rabenhorst (Cleve)
Cymbella javanica	Hustedt
Cymbella lanceoleta	(Ehrenberg) van Heurck
Cymbella microcephala	Grunow
Cymbella minuta	Hilse. ex. Rabenhorst
Cymbella parva	(W. Smith) Cleve
Cymbella prostrate	(Berkeley)
Cymbella turgida	Gregory
Cymbella ventricosa	Kützing
Desmogonium rabenhorstianum	Grunow
Diatomella sp.	Greville
Eunotia diodon	Ehrenberg
Eunotia diodon v. *minor*	
Eunotia lunaris	(Ehrenberg) Grunow
Eunotia lunaris v. *capitita*	Grunow
Eunotia major	Cleve
Eunotia major v. *indica*	Grunow
Eunotia monodon v. *constricta*	Ehrenberg
Eunotia monodon v. *undulata*	Hustedt
Eunotia pectinalis	Küetzing) Rabenhorst
Eunotia pectinalis v. *minor*	Rabenhorst
Eunotia praemonas	Cleave -Euler
Eunotia praemonas v. *tibertica*	Åke Berg
Eunotia praemonas v. *inflata*	Cleave
Eunotia praerupta	Ehrenberg
Eunotia sudecita	Muller
Fragilaria capucina	Desmazieres
Fragilaria construens	(Ehrenberg) Grunow
Fragilaria virescens	Ralfs
Frustruria vulgaris	(Thwaites) De Toni
Frusturia rhomboids	(Ehrenberg) De Toni
Frusturia saxonica	(Ehrenberg) De Toni
Gomphonema longiceps v. *subclavata*	Grunow
Gomphonema gracile	Ehrenberg
Gomphonema longiceps	Ehrenberg
Gomphonema parvulum	(Kuetzing) van Heurck
Gomphonema subtile	Ehrenberg
Gyrosigma balticum	(Ehrenberg) Rabenhorst
Gyrosigma distortum	(W. Smith) Cleve
Gyrosigma elongatum	W. Smith
Gyrosigma sp.	Hassal
Navicula cryptocephala	Kützing
Navicula cuspidate	Kützing
Navicula feurborni	Hustedt
Navicula gibbula?	Cleve, P. T
Navicula gracilis	Ehrenberg
Navicula miniscula	Grunow
Navicula pupula	Kützing
Navicula radiosa	Kützing
Navicula rhynocephala	Kützing
Navicula sp. (new-3 ?)	
Navicula subtilissima	Cleve
Navicula tornensis	Cleve
Navicula viridula v. *linearis*	Hustedt
Neidium affine amphirhynchus (?)	(Ehrenberg) Cleve
Neidium iridis	Ehrenb.
Neidium productum	(W. Smith) Cleve
Nitzschia scaloris	
Nitzschia vermicularis	Grunow
Pinnularia microstauron	(Ehrenberg) Cleve
Pinnularia appendicula	Agardth
Pinnularia biceps	Peterson
Pinnularia bogtensis	Grunow
Pinnularia brauni	Grunow
Pinnularia brevicostata	Cleve
Pinnularia microas v. *ambigua*	Meister
Pinnularia parva	(Gregory) Cleve
Pinnularia subsolaris	(Grunow) Cleve
Pinnularia tabellaria	Ehrenberg
Pinnularia tabellaria	Ehrenberg
Pinnularia trigoncephala	Cleve
Pinnularia viridis	(Nitzsch) Ehrenberg
Pleurosigma elongatum	W. Smith
Rhopalodia gibberula	(Ehrenberg) O.F.Muller
Staurneis pusila	Cleve
Stauroneis anceps	Ehrenberg
Stauroneis phoenicenteron	(Nitzsch) Ehrenberg
Stenopterobia intermedia	(Lewis) Fricke
Surirella tenera	Gregory
Synedra ulna	(Nitz.) Ehrenberg
Tabellaria fenestra	(Lyng.) Kützing
Tabellaria flocossa	(Roth) Kutzing
CHOLOROPHYTA (13 taxa)	
Crucigenia sp.	Morren
Euastrum sp.	*Ehrenb. ex Ralfs*
Gonatozygon sp.	*de Bary*
Mougeotia sp.	Agardh
Oedogonium sp.	Hirn
Penium sp.	Brébisson
Pleurotaenium sp.	Nägeli .
Spirogyra laxa	Kuetzing
Spondylosium sp.	Kützing
Staurastrum dejectum	Brébisson
Staurastrum glade	(Meyen) Ralfs
Staurastrum margaritaceum	(Ehrenb.) Ralfs ex Menegh
Zygogonium sp.	Kuetzing