

Phytoplankton community structure and succession in the water column of Lake Naivasha, Kenya: a shallow tropical lake

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Key words: succession, cyanobacteria, diatom, Aulacoseira

Abstract

Lake Naivasha is a shallow freshwater lake in the Rift Valley of Kenya. Since the 1980s, when the lake showed a seasonal shift between diatom and cyanobacterial dominance it has become moderately eutrophic. Its algal assemblage is now dominated by a persistent *Aulacoseira italica* population both numerically and in terms of contribution to overall primary production. Algal and cyanobacterial counts were used to derive Simpson's diversity, succession rate and total community succession, focusing on the 10 most numerically abundant taxa. 170 species were identified, 43 of which were in common with the 143 found in 1979–80, before the increase in trophic state. Most diatoms are indicators of moderate to high nutrient conditions. There is little horizontal or vertical variation in successional processes throughout the lake and although the absolute abundance of cells varies widely, proportional composition is relatively stable. In Crescent Island lagoon, the only regularly stratified site, hypolimnetic succession rates are lower than those in the epilimnion. Overall, community composition is controlled by mixing (and hence light regime) and nutrient availability. With 'endless summer' conditions and full mixing, there is a successional pattern of 'muted seasonality' adapted to physical instability and environmental stability.

Introduction

Lake Naivasha, in common with many tropical African lakes, experiences fluctuating water-levels which influence its area and productivity (Harper, 1991). It also shows continually changing limnology through rainfall fluctuations in the catchment (Vincent et al., 1979). Its limnology and productivity may also be affected by human intervention in the form of lakeside agriculture through papyrus clearance, drainage and application of fertilisers (Johnson et al., 1998) coupled with the effects of species introductions (Harper, 1991). These changes affect the aquatic plant ecology in terms of macrophyte species and distribution and phytoplankton biomass (Harper, 1992). Due to nutrient inputs, Lake Naivasha can now also be considered moderately eutrophic (Harper et al., 1993). Before eutrophication in the 1980s it exhibited lower but more seasonally variable biomass compared with temperate lakes, with a seasonal shift between diatoms and cyanobacteria (Kalff & Watson, 1986). This paper examines the planktonic community and the degree of succession which now occurs.

In general, tropical lakes show cyanobacterial dominance during droughts and falling water levels, and diatom dominance during periods of inflow and mixing (Harris & Baxter, 1996). Rapid monsoon dilution may affect community structure as physicochemical conditions are rapidly changed. The work of Lewis (1978) on Lake Lanao in the Philippines gives a clear description of how a small number of chemical and physical factors may control succession in a deeper, stratified seasonal lake. The succession from dominance by diatoms and cryptomonads to chlorophytes, followed by cyanobacteria and finally dinoflagellates was seen to be promoted by increased sunlight availability, reduced nutrient availability and greater water-column stability.

Site description

Lake Naivasha is a shallow freshwater lake situated in warm and semi-arid conditions in the eastern Rift Valley of Kenya, lying within an enclosed basin at an altitude of approximately 1890 m. Rainfall is bimodal with peaks during April and October but shows interannual irregularity and an annual evapotranspiration rate which exceeds local rainfall (Harper et al., 1995). Regular sampling sites on Lake Naivasha (Fig. 1) were chosen to provide a range of potential influences on light regime and resulting conditions.

The sample sites were as follows:

- 1. Crescent Island Lagoon a deep (ca. 18 m) almost completely enclosed sub-basin.
- 2. Malewa River inflow a shallow (ca. 2 m) turbid area where the River Malewa enters Lake Naivasha.
- 3. Rema Island an inshore area about 4 m deep away from any inflow.
- 4. Open Water the central area of the lake which is well mixed with less shore effects than the rest of the lake. It is about 5 m deep.
- 5. Hippo Point A well-mixed inshore site, about 6 m deep.
- 6. Oloidien Bay a well-mixed bay average depth 3 m with little agriculture or horticulture nearby, and furthest the main sediment input from the River Malewa.

The final four sites – RI, OW, HP and Bay – are used as replicates of the 'Main lake'.

Methods

Samples were taken from 4/12/97 to 21/10/98, at depths of 0, 1, 3 and 7 m using a 1.5-1 messengeractivated Institute of Oceanographic Sciences (IOS) sampler. This was used to over-fill sample bottles to prevent trapping of air. Water samples were passed through a 200- μ m screen in the laboratory, and then all algal and cyanobacterial taxa were identified to species where possible with a compound microscope at ×400 magnification. Counts were made to genus level in most cases as identification of all individuals to species was often impossible and/or excessively time-consuming. Two taxa were grouped more broadly



Figure 1. Map of Lake Naivasha with sampling sites and 1991 depth contours (m). From Hickley et al. (2002).

(flagellates, cyanobacteria), as the aim was a broad overview of planktonic succession rather than an indepth study of community structure. Previous work, albeit on British rivers (Hawkes, 1979), has shown that generic groupings can clarify otherwise complex community changes by reducing the number of groups requiring monitoring. This reduces complexity due to species-specific environmental requirements, although the species forming a group must show broadly similar characteristics to avoid oversimplification. Counting was undertaken using an eyepiece graticule and sedimentation chamber with a Zeiss Axiovert 100 inverted microscope (Zeiss, Germany). Cells were identified and counted along random transects covering 200 whole graticule areas. Cells were counted which were wholly within the area or touching the right or bottom edge. A multiplication factor then gave counts ml⁻¹ Flagellates and cyanobacteria form two broad functional groups. The most important groups (those which form 10% or more of total cell numbers at any time) were considered separately to identify any succession for a given sample site. Cyanobacteria were counted as numbers of colonies. Some species were



Date

Figure 2. Main lake algal succession4/12/97–21/10/98.

present in such small numbers that they did not feature in analysis of succession.

Proportion of total count

Simpson's Diversity scores were calculated for all samples counted and analyses performed between sites and depths to investigate both horizontal and vertical spatial variation in the algal community. The index (Simpson, 1949) was

$$D = \Sigma P_i^2,$$

where P_i is the proportional numerical abundance of each species *i*.

To measure community change, estimates of succession rate were calculated (Jassby & Goldman, 1974; Lewis, 1976). These integrate changes in biomass or abundance over time through summation of such changes for each species as a proportion of the whole community. The Jassby & Goldman (1974) succession rate (R_s) was

$$R_{\rm s} = \sqrt{\{\Sigma ({\rm d}c_i/{\rm d}t)^2\}},$$

where

$$c_i(t) = b_i(t) / \sqrt{\{\Sigma b_i(t)^2\}}$$

and

$$b_i(t)$$

is the numerical abundance of species i at time t with n possible species.

Jassby-Goldman measurements do not include directional aspects of succession, therefore using the above equations but weighting all species equally gives the formula derived by Lewis (1976):

$$R_{\rm s} = \Sigma i \frac{|\{b_i(t_1)/B(t_1)\} - \{b_i(t_2)/B(t_2)\}|}{(t_2 - t_1)},$$

where $b_i(t)$ is the abundance of species *i* at time *t* and B(t) is the size of the community at time *t*.

Results

The 170 identified species (and eight identified to genus only) are listed in the Appendix. The taxa most abundant were; *Ankyra, Aulacoseira*, cyanobacteria, *Ceratium, Chlorella, Cocconeis*, flagellates, *Navicula, Scenedesmus* and *Synedra* (Fig. 2). This shows *Aulacoseira* dominance in main lake surface water for

Table 1. Succession rate profiles for site CI

Depth (m)	12/12– 6/1	6/1– 16/1	17/4– 12/5	3/10– 13/10	Mean
0	0.055	0.062	0.035	0.076	0.057
1		0.066	0.022	0.018	0.035
3	0.052	0.067		0.011	0.043
7	0.027	0.040	0.027	0.029	0.031



Figure 3. Regression of succession against time.

most of the sampling period, although early in this period *Scenedesmus* was more important whilst other taxa contributed variably to the algal assemblage.

Succession rate

Figure 3 illustrates the weak relationship ($r^2 = 0.092$) and non-significant correlation ($C_p = 0.304$, df = 40, p > 0.05) between total succession values (S-total) and period. For site CI, a profile of S-total values was developed (Fig. 4), showing that community fluctuations were greater at the surface than deeper in the water column. This is also clearly illustrated by successional rate (Table 1) indicating that surface fluctuations were not only greater in magnitude, but also occured more rapidly, than those lower down the water column.

Table 2. Mean planktonic diversity values

Site	Mean diversity	Site	Mean diversity
Main, surface	0.55	CI, 1 m	0.48
MR, surface	0.64	CI, 3 m	0.44
CI, surface	0.62	CI, 7 m	0.42



Mean S-total

Figure 4. Profiles of total succession for Crescent island lagoon (CI).



CI diversity

MR diversity



Figure 5. Simpson's Diversity, 4/12/97-21/10/98.

Diversity

Figure 5 shows Simpson's diversity over time for all sites. Table 2 shows mean values for a number of sites and depths. Site CI is investigated in profile due to its temporarily stratified nature (Hubble, 2000), whilst MR and Main sites are fully mixed (Hubble, 2000), showing no significant vertical variation.

All sites show a similar pattern of temporal diversity change, with troughs in January 1998 when



Figure 6. Phytoplankton community composition at Crescent Island lagoon (site CI).

there was almost total domination by an abundant population of *Aulacoseira*. Diversity was however similar between sites, with an overall mean of 0.60, and maxima generally occurring when *Aulacoseira* densities were relatively low.

There are no significant differences in diversity between sites, suggesting that the processes affecting diversity act equally throughout the lake. Sites CI and Main lake are not significantly correlated, and regression is closest between sites MR and Main lake, possibly due to the different hydrological regime found at site CI. Figure 6 shows depth profiles of community composition at site CI. The percentage composition of main taxa in the main lake correlates with that at site CI at all depths (p < 0.001). Although absolute abundance of taxa may vary, proportional community structure is therefore closely linked both vertically and between sites.

Aulacoseira formed approximately 50% of the surface community and 70% at a depth of 7 m. 'Other main taxa' (those which are sometimes dominant or sub-dominant) formed 10-20% of the community, with the remaining groups in small, fairly equal proportions. Comparing Fig. 5 with Fig. 7, community succession, shows that low diversity periods equated to high Aulacoseira periods as this genus comprised over 90% of the algal community at times. Such periods occurred during January and October 1998, whilst high diversity - low Aulacoseira periods are seen during December 1997 and April-May 1998. Vertical differences at site CI (Tables 2 and 3) show that hypolimnetic diversity is lower than that in the epilimnion, probably due to the more physically stressed conditions caused primarily by light attenuation. The

most significant differences are between 0m and the other depths although diversity reduced with depth as *Aulacoseira* dominance increased.

Discussion

Comparison with the 170 species and eight genera identified during this study and the 143 taxa identified by Kalff & Watson (1986) during 1979-80 shows 43 species common to both studies. No relationship was found between species abundance and algal biomass, the latter used as a measure of lake trophy in the earlier study. More species have been found in this study than by Kalff & Watson (loc cit), but it is important to note that species richness may be underestimated even for large samples of a speciose community (Lande, 1996). This is because in natural assemblages, increased competition amongst individuals in a community can lead to competitive exclusion. Thus as the density of individuals increases, richness does not increase with sample size as much as expected (Goldberg & Esterbrook, 1998) as seen in dense Ceratium populations in Lake Naivasha (Hubble, 2000). Cox (1996) gives details of diatom species' environmental requirements. Of the 47 diatom species identified with known environmental requirements, 35 are either widespread or found in waters of moderate to enriched electrolyte or nutrient conditions (eutrophic). Of the remainder, 5 indicate moderate electrolyte or nutrient conditions (mesotrophic) and 7 indicate low to moderate electrolyte or nutrient conditions (oligotrophic). The oligotrophic species such as Fragilaria capucina were rarely found, and only in small numbers. Oligotrophic conditions probably no longer exist following the water level decline between 1980 and 1987, which allowed land to be cultivated with subsequent inundation of that land (Harper et al., 1993), hence such populations may be merely relicts, although F. capucina is known to exist as a number of ecological races.

Overall succession from diatoms and cryptomonads to chlorophytes, cyanobacteria and finally dinoflagellates may be largely controlled by a small number of key factors (Lewis, 1979) and promoted by high insolation, reduced nutrient availability and reduced mixing. Work at Lake Kinneret, Israel (Pollingher 1981) also indicates that low sinking rates and high nutrient availability are favourable as diversity increased during mixed and high nutrient periods, whilst it was minimal during periods of strong physical, chemical and biological stress. This indicates that in

Table 3. Site CI diversity comparison between sampling depths

Cp (prob)	r^2 (one-tailed probability)				
	CI 0 m	CI 1 m	CI 3 m	CI 7 m	
CI 0 m		0.736 (0.029)	0.576 (0.035)	0.564 (0.021)	
CI 1 m	0.858 (0.01)		0.946 (0.045)	0.876 (0.078)	
CI 3 m	0.759 (0.05)	0.972 (<0.001)		0.888 (0.387)	
CI 7 m	0.751 (0.05)	0.936 (<0.001)	0.942 (0.01)		

df = 5 for comparisons with CI 3 m; df = 6 for other comparisons.









CI 7m



100%

80%

60%

40%

20%

0%

12/12

6/1

16/1 17/4 12/5





21/10

3/10

Date

early succession, low sinking rates and high nutrient availability favour low SA:V species (e.g. *Aulacoseira*) whereas nutrient depletion and low turbulence favour high SA:V species (e.g., *Microcystis*) which can scavenge scarce nutrients. The favouring of diatoms is seen both from palaeolimnology (Richardson & of persistent assen

can scavenge scarce nutrients. The favouring of diatoms is seen both from palaeolimnology (Richardson &
Richardson, 1972) and more recently (Melack, 1979,
Kalff & Watson, 1986) in Lake Naivasha where there
was an almost permanent early successional state.
Lind (1968) stated that Lake Naivasha was dominated by *Aulacoseira ambigua* but no explanation of
phytoplankton periodicity was made, although for the
Sasumua and Ruiru reservoirs in Kenya it was considered to be controlled by rainfall. *Aulacoseira* is
now the most important algal genus, both numeric-Naivasha
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between
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due to tw
1. There
the successional state.

ally and in terms of its contribution to overall primary productivity (Hubble, 2000). Melack (1979) separated phytoplankton seasonal-

ity in tropical lakes into three broad categories. The most common pattern is that of pronounced seasonal fluctuations corresponding with differences due to rains, rivers or mixing. This was seen in Lake Oloidien and sometimes Crescent Island lagoon where mixing was predominant with minimal river inflow. Developing this idea, a second pattern consists of 'muted seasonality' due to the presence of buffer fringes, perennial rivers and sufficient internal recycling of nutrients. Diel variations are thus greater than longer-term changes, as conditions of 'endless summer' are found (Kilham & Kilham, 1990); this pattern is seen in Lake Naivasha. This means that as the same phytoplankton assemblages can persist for many days, species must be adapted to the full range of environmental variation. Phytoplankton communities may therefore experience both physical instability due to the mixed state of the water column and environmental stability as this mixing provides a certain light regime and prevents sedimentation loss. This form of 'continuous disturbance' is paralleled in ecosystems such as continually grazed grasslands where succession may be considered a function of 'vital attributes' (Noble & Slatyer, 1980). Around its persistent assemblages, Lake Naivasha did show wide short-term community variations such as temporary Chlorella dominance and wind-driven concentrations of Ceratium (Hubble, 2000). These occurred despite rapid physical and chemical turnover, and the idea that brevity of the mixing period may restrict species fluctuations (Ganf & Horne, 1975). The dominant or 'central' form of the assemblage however remained stable. This form of seasonality is contrary to the first

pattern where there is seasonal succession because species composition changes as conditions change, with species better adapted to the new conditions becoming dominant. A final pattern, not seen in Lake Naivasha, is that of 'multiple stable points' in the form of persistent assemblages with occasional abrupt shifts between them.

Hypolimnetic succession rates are also notably lower and less variable than those of surface waters due to two main factors:

- 1. There is greater physical stability found below the surface as the largely wind-driven mixing processes have a smaller effect deeper in the water column. In the temporarily stratified Crescent Island lagoon, diversity is however significantly correlated between samples from 0 and 7 m, suggesting that there is only partial separation.
- 2. There is reduced productivity below the optimal photosynthetic depth of approximately 0.5– 0.75 m, and therefore community fluctuations are slowed by the reduced rates of cellular division, and overall lower numbers of algal cells.

Such rates of succession (as well as indices of ecosystem stability) change as succession progresses as the resulting increased order leads to system predictability and pre-adaptation. There are changes in phytoplankton community structure; however, no stages are seen which correlate with nutrient levels. Lake Naivasha is moderately eutrophic and shows diatom dominance with dinoflagellate and cyanobacterial subdominance. It therefore fits with the mesotrophic stage expected in temperate waters as many phytoplanktonic species are found across a range of latitudes. Considerable fluctuations in nutrient levels were measured (Hubble, 2000), but as the pattern of temperate oligotrophic–eutrophic succession is not seen, they are not large enough to constitute a change in trophic state.

In summary, the lake is now dominated by *Aulaco-seira* following eutrophication, probably due to land use changes in the early 1980s. As well as the seasonal pattern of dominance, the species present have also largely changed since eutrophication began to occur, and most diatoms found are indicative of moderate to high nutrient levels. Large community fluctuations are seen but these are temporary with the community rapidly reverting to its *Aulacoseira*-dominated state. As the lake experiences the 'endless summer' conditions of the tropics and is well-mixed, there is strong spatial homogeneity in the phytoplankton community as its composition is controlled by light regime and nutrient availability. Changes in successional processes and

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Phylum Cyanophyta

Order Chroococcales (14 spp.) Aphanothece caldariorum Richter Aphanothece ellipsoidea Schröder Aphanothece nidulans Richter Chlorogloea microcystoides Geitler Chroococcus limneticus Lemmermann Chroococcus turgidus (Kützing) Nägeli Gloeothece rupestris (Lyngbye) Bornet Merismopedia convoluta Brébisson Merismopedia geminata Lagerstedt Merismopedia tenuissima Lemmermann Microcystis aeruginosa (Kützing) Kützing Microcystis biformis (A. Braun) Rabenhorst Microcystis viridis (A. Braun) Lemmermann

Order Nostocales (= Oscillatoriales) (11 spp.) Anabaena sphaerica Bornet & Flahault Anabaena spiroides (Lemmermann) Elenkin Anabaenopsis circularis (G.S. West) Müller Borzia trilocularis Cohn Lyngbya epiphytica Gardner Lyngbya muralis Kützing Lyngbya sp. Nostoc parmelioides Kützing Oscillatoria jenneri (Hassall) Kützing Oscillatoria sp. Spirulina subsalsa Oersted

Phylum Chrysophyta

Order Ochromonadales (2 spp.) Didymochrysis paradoxa Pascher Mallomonas leboimei Bourrelly

Order Chromulinales (7 spp.) Chromulina pyriformis Playfair Chrysococcus rufescens Skuja Chrysomonas ellipsoidea Skvortzov Chrysospora fenestrata Pascher Epicystis peridinearum Pascher Gloeochrysis pyrenigerum Pascher Ochromonas viridis Bourrelly

Phylum Bacillariophyta

Order Achnanthales (5 spp.) Achnanthes brevipes Agardh Achnanthes exigua Grunow Achnanthes inflata Kützing Achnanthes minutissima Kützing Diatomella hustedtii Manguin Order Coscinodiscales (6 spp.) Aulacoseira ambigua (Grunow) Simonsen Aulacoseira granulata (Ehrenberg) Simonsen Aulacoseira italica (Ehrenberg) Simonsen Cyclotella meneghiniana Kützing Cyclotella stelligera Cleve & Grunow Stephanodiscus neoastraea Håkannson & Hickel Order Diatomales (11 spp.) Cocconeis placentula Ehrenberg Diatoma ehrenbergii Kützing Diatoma tenuis Agardh Fragilaria capucina Desmazières Rhoicosphenia curvata (Kützing) Grunow Synedra acus Kützing Synedra berolinensis Lemmermann Synedra capitata Ehrenberg Synedra pulchella Kützing Synedra ulna (Nitzsch) Ehrenberg Synedra sp. Order Eunotiales (2 spp.) Eunotia denticula (Brébisson) Rabenhorst Eunotia monodon (Gregory) W.Smith Order Naviculales (45 spp.) Amphora communata Grunow Amphora ovalis Kützing Caloneis amphisbaena (Bory) Cleve Cymatopleura solea (Brébisson) W.Smith Cymbella lacustris (Agardh) Cleve Cymbella prostrata (Berkeley) Cleve Denticula pelagica Hustedt Denticula thermalis Kützing Diploneis didyma (Ehrenberg) Cleve Encyonema minutum (Hilse in Rabenhorst) D.G.Mann Encyonema prostratum (Berkeley) Kützing Epithemia turgida (Ehrenberg) Kützing Gomphonema acuminatum Ehrenberg Gomphonema augur Ehrenberg Gomphonema truncatum (= constrictum) Ehrenberg Gomphonema olivaceum (Hornemann) Brébisson Gyrosigma attenuatum (Kützing) Rabenhorst Navicula capitata Ehrenberg Navicula cryptocephala Kützing Navicula cuspidata Kützing Navicula gibbula Cleve Navicula lanceolata (C. Agardh) Kützing Navicula pygmaea Kützing Navicula protractoides Hustedt Navicula radiosa Kützing Navicula schoenfeldii Hustedt Navicula scutelloides W. Smith Navicula trivialis Lange-Bertalot

Appendix 1. Continued

Navicula tuscula (Ehrenberg) Grunow Navicula sp. Neidium ampliatum (Ehrenberg) Krammer Nitzschia acicularis (Kützing) W. Smith Nitzschia amphibia Grunow Nitzschia fonticola Grunow Nitzschia linearis (Agardh) W. Smith Nitzschia palea (Kützing) W. Smith Nitzschia pusilla Grunow Nitzschia sp. Pinnularia maior Ehrenberg Pinnularia viridis (Nitzsch) Ehrenberg Rhopalodia gibba (Ehrenberg) O. Müller Stauroneis anceps Ehrenberg Surirella angusta Kützing Surirella linearis W. Smith Tryblionella apiculata Gregory

Phylum Chlorophyta

Order Volvocales (4 spp.) Chlamydomonas debaryana Gorosch Chlamydomonas ovalis Pascher Chlorotriangulum minutum Kufferath Dunaliella lateralis Pascher & Jahoda Order Chlorococcales (37 spp.) Acanthosphaera zachariasi (Geitler) Lemmermann Ankistrodesmus falcatus (Chodat) Lemmermann Ankistrodesmus gelifactum (Chodat) Bourrelly Ankyra ancora (G.M. Smith) Fott Ankyra judai (G.M. Smith) Fott Botryococcus braunii Kützing Botryosphaera sudetica (Lemmermann) Chodat Characium ornithocephalum A. Braun Chlorella miniata (Nägeli) Oltmanns Chlorella vulgaris Beijerinck Chlorococcum wimmeri (Rabenhorst) Starr Chodatella ciliata (Lagerheim) Lemmermann Chodatella quadriseta Lemmermann Coelastrum microsporum Nägeli Coelastrum reticulatum (Dangeard) Senn Crucigenia quadrata Morren Crucigenia tetrapedia (Korchikoff) Bourrelly Dictyosphaerum pulchellum Wood Euastropsis richteri (Schmidle) Lagerheim Micractinium pusillum (Lund) Fresenius Oocystidium ovale Korchikoff Oocystis lacustris Chodat Pediastrum boryanum Meyer Pediastrum clathratum (Schröder) Lemmermann Pediastrum duplex Meyer Pediastrum tetras (Corda) Rabenhorst Selenastrum bibraianum Reinsch Scenedesmus crassus Chodat Scenedesmus falcatus Chodat

Appendix 1. Continued

Scenedesmus flexuosus (Lemmermann) Ahlstrom Scenedesmus protuberans Fritsch & Rich Scenedesmus tenuispina Chodat Scenedesmus sp. Sphaerocystis schroeteri Chodat Tetraedron caudatum Lemmermann Tetraedron limneticum (Skuja) Borge Tetrastrum heteracanthum (Nordstedt) Chodat Order Oedogoniales (3 spp.) Oedogonium mammiferum Wittrock Oedogonium minus Wittrock Oedogonium sudanense Gautlièvre Order Desmidiales (11 spp.) Closterium acerosum (Schrank) Ehrenberg Closterium acutum Brébisson Closterium setaceum Grönblad Cosmarium depressum Riverdin Cosmarium meneghinii Brébisson Gonatozygon monotaenium De Bary Micrasterias tropica Nordstedt Pleurodiscus africanus Bourrelly Staurastrum lunatum Ralfs Staurastrum sebaldi Krieger & Bourrelly Staurodesmus dickei (Ralfs) Lillieroth Phylum Euglenophyta Order Euglenales (7 spp.) Euglena polymorpha Dangeard Euglena variabilis Klebs Euglena viridis Ehrenberg Phacus tortus (Lemmermann) Swirenko Scytomonas pusillus Stein Sphenomonas quadrangularis Stein Strombomonas gibberosa (Playfair) Deflandre Phylum Pyrrhophyta Order Prorocentrales (2 spp.)

Gymnodinium inversum Nygaard Gymnodinium sp. Order Peridiniales (4 spp.) Ceratium cornutum (Ehrenberg) Chapman & Bachmann Ceratium hirundinella (O.F. Müller) Schrank Peridiniopsis borgei Lemmermann Peridinium volzii Lemmermann Order Cryptomonadales (7 spp.) Chroomonas acuta Ütermohl Chroomonas minuta Skuja Chroomonas minuta Skuja Chroomonas marssonii Skuja Cryptomonas ovata Ehrenberg Cryptomonas tetrapyrenoidosa Skuja Tetragonidium verrucatum Pascher