The periodicity of phytoplankton in Lake Constance (Bodensee) in comparison to other deep lakes of central Europe

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Abstract

Phytoplankton periodicity has been fairly regular during the years 1979 to 1982 in Lake Constance. Algal mass growth starts with the vernal onset of stratification; Cryptophyceae and small centric diatoms are the dominant algae of the spring bloom. In June grazing by zooplankton leads to a 'clear-water phase' dominated by Cryptophyceae. Algal summer growth starts under nutrient-saturated conditions with a dominance of *Cryptomonas* spp. and *Pandorina morum*. Depletion of soluble reactive phosphorus is followed by a dominance of pennate and filamentous centric diatoms, which are replaced by *Ceratium hirundinella* when dissolved silicate becomes depleted. Under calm conditions there is a diverse late-summer plankton dominated by Cyanophyceae and *Dinobryon* spp.; more turbulent conditions and silicon resupply enable a second summer diatom growth phase in August. The autumnal development leads from a *Mougeotia* – desmid assemblage to a diatom plankton in late autumn and winter.

Inter-lake comparison of algal seasonality includes in ascending order of P-richness Königsee, Attersee, Walensee, Lake Lucerne, Lago Maggiore, Ammersee, Lake Zürich, Lake Geneva, Lake Constance. The oligotrophic lakes have one or two annual maxima of biomass; after the vernal maximum there is a slowly developing summer depression and sometimes a second maximum in autumn. The more eutrophic lakes have an additional maximum in summer. The number of floristically determined successional stages increases with increasing eutrophy, from three in Königsee and Attersee to eight in Lake Geneva and Lake Constance.

Introduction

It is the aim of this contribution to present a comparison of the phytoplankton seasonality in deep central European lakes of considerable size. All are characterized by basins with steep sides, small littoral zones, and a development of mainly pelagic communities. Unfortunately heterogeneity and incompleteness of available data make an equal treatment of all lakes impossible. Therefore, in the first section the periodicity of phytoplankton in Lake Constance is given in greater detail. This lake has been thoroughly studied from 1979 to 1982 by the working group of the Deutsche Forschungsgemeinschaft – sponsored project 'Carbon cycle in

Lake Constance' (Leader: M. Tilzer). The most important physical and chemical environmental variables (Stabel & Tilzer, 1981), the primary productivity (Tilzer, 1984), the seasonality of the phytoplankton (Sommer 1981a, b), of the zooplankton (W. Geller, in prep.) and sedimentation (H. H. Stabel, in prep.) have been studied at weekly intervals. In the second section a comparison with other central European lakes is attempted. The data are taken from literature and from unpublished lists (Zürichsee, Walensee, by courtesy of U. Zimmermann). Less frequent sampling and absence of background data on physical and chemical conditions and zooplankton make it inevitable in some cases to explain developments in those lakes

by analogy with Lake Constance. For example, the June minimum of algal biomass in Lake of Geneva has been interpreted as a grazing-induced clear-water phase in spite of absence of zooplankton data, because phytoplankton data are nearly identical to those from Lake Constance for the respective phase.

Inter-lake comparison needs some degree of abstraction from actual data. Here, the main abstraction is the deduction of a 'main sequence' in the succession of phytoplankton (Margalef, 1978). This concept is based on the experience that in a stratified body of water nutrients are successively depleted, interactions with higher trophic levels increase and non-motile algae replaced by motile or buoyant ones. Partial destratification or erosion of the thermocline by weather-induced mixing may lead to re-capitulation of earlier successional stages ('reversions' sensu Reynolds, 1980). In contrast to temporary reversions the autumnal erosion of stratification is a regular event and belongs to the 'main sequence'. An experimental demonstration for the distinction between the 'main sequence' and 'reversions' has been provided by destratification experiments (Reynolds, Wiseman, Godfrey & Butterwick, 1983).

Lake Constance (Bodensee)

Lake Constance (500 km² surface area, maximum depth 250 m, mean depth 100 m) is a warm-monomictic lake. The process of rapid eutrophication was stopped in the late 70's (Elster, 1982). At present the overturn concentrations of total phosphorus are about $100 \ \mu g \cdot l^{-1}$. Seasonality and stratification of nutrients and temperatures are available from Stabel & Tilzer (1981), and details on the counting method and further information on phytoplankton seasonality from Sommer (1981a, b). Phytoplankton species composition throughout the whole text refers to biomass, measured as cell volume.

The seasonal periodicity of phytoplankton species composition followed with slight deviations the same general pattern (Fig. 1) during the whole period of study (1979–1982).

(1) During winter a long period of deep circulation and low light intensities lead to extremely low algal densities.

(2) Mass growth of algae starts with the onset of thermal stratification in April/May. High nutrient availability and low grazing pressure gives rise to an assemblage of rapidly growing, nanoplankton species dominated by *Rhodomonas lens, R. minuta, Cryptomonas ovata* and small centric diatoms, mainly *Stephanodiscus hantzschii*. All these algae are heavily grazed by Cladoceran filter-feeders.

(3) Increased zooplankton grazing leads to a dramatic decrease of phytoplankton densities in early June. The scarce phytoplankton of this 'clear-water phase' (Lampert & Schober, 1978) is dominated by *Cryptomonas ovata* and *Rhodomonas minuta*.

(4) Towards the end of the clear-water phase shortage of food leads to a decline of zooplankton abundance. Algal biomass rises again. As long as nutrients are not yet depleted, *Cryptomonas ovata, C. rostratiformis* and *Pandorina morum* are the dominant algae.

(5) When soluble reactive phosphorus becomes depleted in July algal dominance shifts to the large and poorly grazed diatoms *Asterionella formosa, Fragilaria crotonensis, Stephanodiscus binderanus, Melosira granulata*. Current competition research has shown by continuous culture experiments that several species of net-planktonic diatoms tend to outcompete all other taxa if P is in short supply and rich silicate supply prevents Si-limitation (Tilman, 1977; Tilman, Kilham & Kilham, 1982; Sommer, 1983).

(6) When silicate is depleted (Sommer & Stabel, 1983) the diatoms are replaced by a dominance of *Ceratium hirundinella* (mid-August).

(7) In some years the *Ceratium*-stage is followed by a diverse phytoplankton dominated by the heterocystous blue-green algae *Anabaena flos-aquae, A. planctonica, A. spiroides, Aphanizomenon flos-aquae* and the Chrysophyceae *Dinobryon sociale* and *D. divergens*. There were some deviations from this scheme of summer succession. Upwelling of phosphate gave rise to short growth pulses of Cryptophyceae and upwelling of silicate led to a second summer diatom stage, which then replaced the Cyanophyceae-*Dinobryon* assemblage. The development of the Cyanophyceae-*Dinobryon* assemblage is considered the 'main sequence' of algal succession, whereas the late summer pulses of diatoms and Cryptophyceae are classified as reversions.
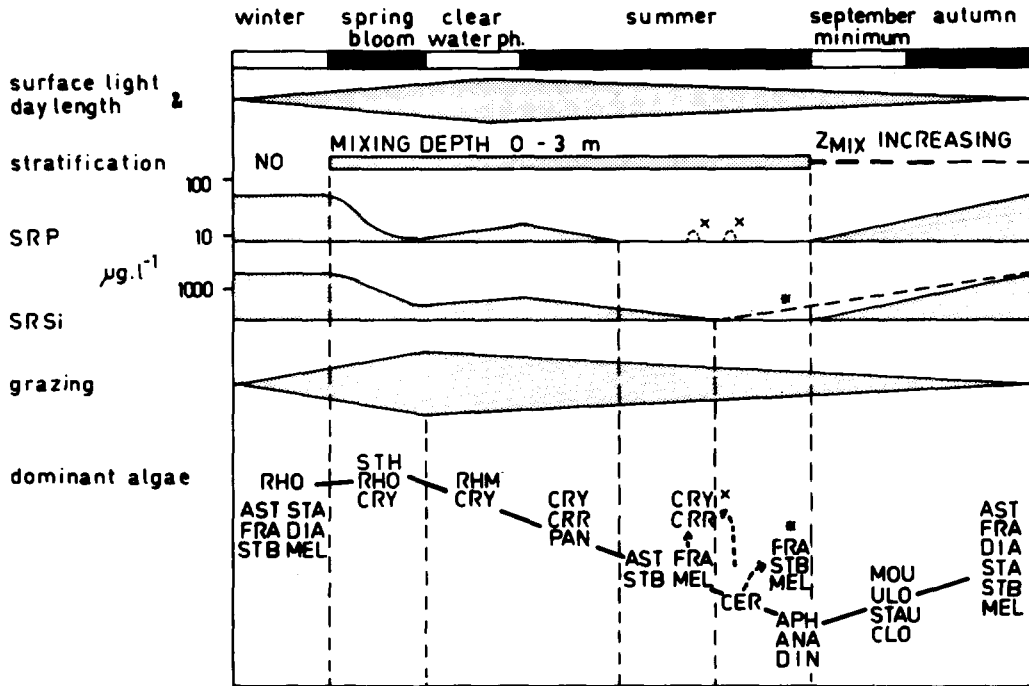
Fig. 1. Scheme of phytoplankton seasonality and of temporal evolution of environmental parameters in Lake Constance. Units for environmental variables except P and Si are arbitrary. The x-axis is out of scale temporally and rather reflects the number of successional stages than time.

Species code:

ANA: *Anabaena* spp. APH: *Aphanizomenon flos-aquae*, AST: *Asterionella formosa*, CER: *Ceratium hirundinella*, CLO: *Closterium aciculare*, CRR: *Cryptomonas rostratiformis*, CRY: *Cryptomonas ovata*, DIA: *Diatoma elongatum*, DIN: *Dinobryon* spp., FRA: *Fragilaria crotonensis*, MEL: *Melosira granulata*, MOU: *Mougeotia thylespora*, PAN: *Pandorina morum*, RHO: *Rhodomonas* spp., RHM: *Rh. minuta*, STA: *Stephanodiscus astraea*, STB: *Stephanodiscus binderanus*, STH: *Stephanodiscus hantzschii*, STAU: *Staurastrum cingulum*, ULO: *Ulothrix subtilissima*.

(8) After an early autumn (September or early October) minimum of biomass, which is probably caused by deterioration of the light climate (decreasing day length, increasing mixing depth), phytoplankton is mainly composed of the filamentous Conjugatophyceae *Mougeotia thylespora,* the desmids *Staurastrum cingulum, Closterium aciculare* and the filamentous Chlorophyceae *Ulothrix subtilissima.* Deeper mixing provides rich nutrient supply.

(9) In late autumn (November, December), when mixing depth further increases (>30 m) and light and temperature decrease, the green algae are replaced by diatoms, largely the same species as in summer; additionally *Stephanodiscus astraea* and *Diatoma elongatum* can be important.

The development from the onset of the spring-bloom till the Cyanophyceae-*Dinobryon* phase in

August represents the process of autogenic succession, where the main selective environmental variables are a consequence of the previous activities of planktonic organisms. For example, ambient nutrient concentrations become controlled by phytoplankton consumption and recycling through zooplankton grazing and excretion; water transparency becomes controlled by phytoplankton densities; high densities of food-algae give rise to increased zooplankton fecundity and, in return, zooplankton grazing becomes a selective factor for phytoplankton. Selection for a high maximum growth rate ('r-selection'; e.g. at the start of the vernal growth phase) is replaced by selection for growth under low nutrient conditions (either by high uptake affinity or by storage capacity) and by selection for loss resistance. Resistance against grazing is usually achieved by large cell- or colony-

4

size, resistance against sinking by being a flagellate or by being buoyant (Cyanophyceae). These various adaptations are commonly lumped together under the ambiguous term 'K-selection' (Sommer, 1981a). The autumnal development is characterized by alleviation of competition and increased selection by physical factors (light, temperature).

Inter-lake-comparison

The comparison is restricted to the alpine and pre-alpine region of central Europe (Fig. 2). The lakes considered are in ascending order of eutrophy:

Königssee (Siebeck, 1982, Germany, year of study: 1978/79, 5 μg $P_{TOT} \cdot l^{-1}$ during spring overturn), Attersee (Müller, 1979, Austria, 1977–1979, 5 μg $P_{TOT} \cdot l^{-1}$), Walensee (U. Zimmermann, unpubl. data, Switzerland, 1981, 20 μg $P_{TOT} \cdot l^{-1}$), Vierwaldstätter See/Lake of Lucerne (Bloesch, 1974, Switzerland, 1969/70, 20 μg $P_{TOT} \cdot l^{-1}$), Lago Maggiore (Ruggiu et al., 1980, Switzerland/Italy, 1979/80, 45 μg $P_{TOT} \cdot l^{-1}$), Ammersee (Steinberg, 1980, Germany, 1976, 55 μg $P_{TOT} \cdot l^{-1}$), Zürichsee (U. Zimmermann, unpubl. data, Switzerland, 1979–1981, 75 μg $P_{TOT} \cdot l^{-1}$), Lac Leman/Lake of Geneva (Druart & Revaclier, 1979–1981, Switzerland/France, 80 μg $P_{TOT} \cdot l^{-1}$), Bodensee/Lake Constance (Germany/Switzerland/Austria, 1979–1982, 100 μg $P_{TOT} \cdot l^{-1}$). More detailed chemical and biological infor-
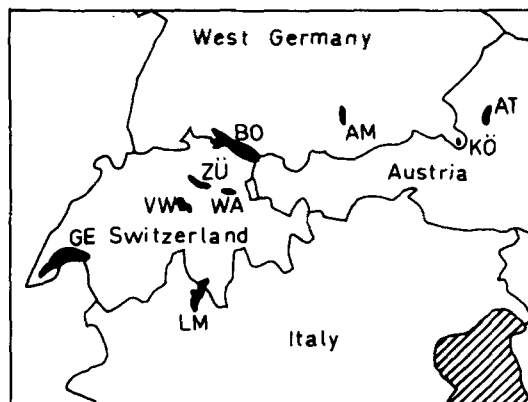

Fig. 2. Geographical distribution of the lakes included in the study. For lake code see Table 1.

mation may be obtained from the original literature; morphometric data are given in Table 1.

The seasonal development of algal biomass of the 9 lakes is compared in Fig. 3. As far as data are available, the general pattern of the annual biomass curves does not vary greatly from year to year. The selection for Fig. 3 was made in favour of the years with highest sampling frequency and/or best information on environmental background data. In all of the lakes except for Lago Maggiore where insufficient sampling frequency hinders interpretation, algal mass growth does not start before the onset of thermal stratification. During the years of study Zürichsee and Lac Leman stratified remarka-

Table 1. Morphometric data of the lakes included in the present study.

| Lake	surface area (km²)	maximum depth (m)	mean depth (m)	retention time (y)
Königssee (KÖ)	5.2	190	98	2.3
Attersee (AT)	46	171	84	7
Walensee (WA)	24	145	100	1.4
Vierwaldstätter See (VW) (Lake Lucerne)	114	214	104	1.8
Lago Maggiore (LM)	212	370	177	4
Ammersee (AM)	48	83	38	2.5
Zürichsee (ZÜ) (Lake Zürich)	65	136	51	1.4
Lac Leman (GE) (Lake Geneva)	582	310	153	12
Bodensee* (BO) (Lake Constance)	500	252	100	4

*) without 'Untersee'
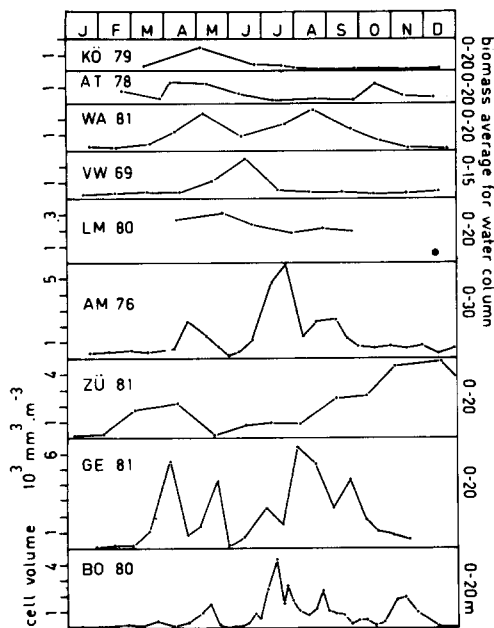
Fig. 3. Seasonality of phytoplankton biomass in 9 Central European lakes, arranged in ascending order of eutrophy. For lake code see Table 1.

bly earlier than the other lakes. Minor peaks of biomass may occur during calm periods of the homothermic phase although the general biomass trend during overturn is downward. This pattern seems to distinguish deep lakes from shallow ones, where the vernal bloom commonly starts immediately after ice-break (see for example the lower part of Lake Constance – 'Untersee', Bürgi, 1977). In oligotrophic lakes there is either a unimodal (Königssee, Vierwaldstätter See) or a bimodal (Attersee, Walensee) annual development of phytoplankton. The bimodal pattern has also been observed in the oligotrophic phase of Bodensee (Grim, 1939).

The decline after the vernal maximum is slow and leads to an extended summer depression. Only in Walensee do elevated levels of biomass persist through summer, probably because the unusually high mixing depth (10–20 m) of this lake guarantees better nutrient supply. In the richer lakes (Ammersee, Zürichsee, Lac Leman, Bodensee) the vernal bloom collapses rapidly, probably because of excessive grazing. A decrease in the rate of cell-division because of nutrient limitation or low trans-

parency of the water at the height of the spring-bloom might augment the effect of grazing. After the clear water phase there is a pronounced summer maximum in three cases (Ammersee, Lac Leman, Bodensee) and a less pronounced autumnal maximum. In Zürichsee the annual peak of biomass is reached in late autumn. Although the conclusion might be biased by differences in sampling frequency, it seems obvious that the rapidity and the amplitude of biomass fluctuations increase with increasing eutrophy. The ratios of minimum to maximum biomass range from 1:10 in Attersee and Vierwaldstätter See to 1:250 in Bodensee.

An attempt has been made to deduce successional stages in the same manner as for Lake Constance and to relate them to available data on the environmental conditions (Fig. 4). Seven phases were distinguished. The spring bloom was realized in in all lakes, the clear water phase only in the eutrophic lakes. A summer growth phase with high ambient concentrations (SRP >5 μg l^{-1}) of phosphate only occured in Ammersee, Zürichsee, Lac Leman, Bodensee. A summer phase, where phosphate was depleted, but silicate still available at high concentrations ($\sim 1\,000$ μg Si l^{-1} in Bodensee) occurred in all lakes. A subsequent phase of silicate depletion (<200 μg Si l^{-1}) in summer was found in Vierwaldstätter See, Lago Maggiore, Ammersee, Lac Leman, Bodensee, and questionably in Zürichsee. Combined nitrogen was found to be depleted only in Vierwaldstätter See, Ammersee and Lac Leman. Autumn was characterized by increasing mixing depths in all lakes.

Floristic comparison is restricted to dominant algae. At the present state of our knowledge, where we do not know the exact physiological properties and environmental requirements of most species, it is not appropriate to make inter-lake comparisons at the species level. Furthermore, stochastic variability of environmental variables may influence the abundance of species with very similar physiological properties to such a great extent that no regularity will be found at the species level. Therefore, it seems useful to combine species in groups of ecologically equivalent species ('functional units'): i.e. (large) planktonic diatoms, small centric diatoms, Cryptophyceae, Chlorophyceae, Conjugatophyceae (in all cases *Mougeotia* sp. combined with several desmids), and heterocystous Cyanophytes. Species are only mentioned if they have a characteristic dis-

tribution or if they are the only important species representing their taxonomic group.

The species composition of the vernal maximum is characterized by a trend to replace the net-planktonic diatoms by small centric diatoms and Cryptophyceae with increasing phosphate richness. This finding agrees with experimental studies of Tilman, Kilham & Kilham (1982), who found that species of *Asterionella, Synedra* and *Fragilaria* are better competitors for P than small Centrales. In eutrophic lakes where P is not limiting during early spring, the higher maximum growth rate makes nanoplanktic algae such as small Centrales and *Rhodomonas* dominant. *Oscillatoria rubescens* is an important contributor to the spring bloom in the medium range (Lago Maggiore, Ammersee). The clear-water phase is uniformly dominated by Cryptophyceae, which are also important contributors to summer minima in oligotrophic lakes and to phosphate-rich phases during summer in the eutrophic lakes. The combination of phosphate depletion and high silicate concentrations nearly always gives rise to a dominance of net-planktonic diatoms (only exception: Attersee). After their collapse because of silicate deficiency Conjugatophyceae dominate in Vierwaldstätter See and Lago Maggiore, *Ceratium hirundinella* in Ammersee, Lac Leman, Bodensee. Heterocystous Cyanophyceae are typical for nitrate deficiency. In autumn in nearly all lakes the net planktonic diatoms are important (exception: Vierwaldstätter See), and in Lago Maggiore, Ammersee, Zürichsee they are combined with *Oscillatoria rubescens.* Before this phase the most eutrophic lakes have a non-diatom, early-autumn stage.

Only a few species have a clearly restricted distribution. *Uroglena americana* and *Cyclotella bodanica* are restricted to the oligotrophic Königssee. In Bodensee *Cyclotella bodanica* had already disappeared in a very early stage of eutrophication (Geller, 1980). *Tabellaria fenestrata* (or *flocculosa* var. *asterionelloides*) is important only in Attersee, Walensee, and Vierwaldstätter See. The classic Central European indicator alga of eutrophication, *Oscillatoria rubescens,* is restricted to the medium P-range, and important only in Vierwaldstätter See, Lago Maggiore, Ammersee, and Zürichsee. The *Oscillatoria* population in Attersee is allochthonous (from Mondsee); in Lac Leman it exists, but not as a dominant alga. The decrease of *Oscillatoria*

rubescens at the upper end of the eutrophication scale can only be explained hypothetically: the commonly observed metalimnetic oversummering of this alga becomes impossible, when metalimnetic light intensities are too low due to attenuation by high epilimnetic biomasses. *Ceratium hirundinella,* although found in all lakes, is a dominant species only in the most productive lakes.

The number of successional stages seems to increase with ascending eutrophy, from three in Königssee, Attersee, Walensee to eight in Bodensee and Lac Leman. There seems to be a greater number of ecological niches along the time axis in more eutrophic lakes. There are several situations in eutrophic lakes which probably do not occur in oligotrophic waters: the sudden change from nutrient-rich to nutrient-poor conditions, depletion of silicate and of nitrate, and high plankton densities which make self-shading an important selection factor. Additionally the commonly observed shift from a zooplankton dominated by Copepoda to Cladocera, with much higher growth rates, probably increases the temporal variability of the grazing pressure. Abundant Cladoceran zooplankton seems to be a prerequisite for the development of pronounced mid-summer clear-water phases, at the beginning of which algal population declines of nearly one halving per day are quite common.

Concluding remarks

It was possible to arrange the nine lakes in a linear array of ascending phosphate richness, because they agree in several important features: they are deep, stratifying, Ca-rich lakes belonging to the same climatic region. The role of N in eutrophication of these lakes could not be evaluated, since N data were not always available. Except for episodic N-depletion, as shown in Fig. 4, the original authors considered their lakes rather to be P-limited systems. Future expansion of inter-lake comparison of algal seasonality will probably lead to multi-dimensional arrangements. In spite of several deficiencies of the available material, it seems obvious that phytoplankton succession is a regular process. Further investigation has to take care of sampling frequency – weekly intervals are recommended – and sufficient background data, especially on zooplankton.

Lake code	KÖ	AT	WA	VW	LM	AM	ZÜ	GE	BO
Overturn P-tot	5	5	20	20	45	55	75	80	100
Springbloom	U-D^{cv}	T	D$^?$	Cr-O-d	D-D-d	O-D-d	Cr-d	Cr-d	Gr-?
Clear Water	/	/	/	/	?	Cr	Cr	Cr	Cr
Summer P-rich Si-rich	/	/	/	/	?	D-D-Cr	H-Cr	Cr-Ch	Gr-?
Summer P-poor Si-rich	D-d-Cr	Cr	D-Cr	D^T	D	D	D-Cr	D	D
Summer P-poor Si-poor	/	/	/	Co	Co-O	Ce	?	Ce	Ce / H-Di
Summer NO3- Autumn poor	/	/	/	H	?	H	*?	H	/
Autumn	D^{cv}-d	D	D	O	O-D	O-D	H-O-Ce / O-D	Ce / D	Ce / D

Fig. 4. Seasonality of dominant algae in 9 Central European lakes. x-axis: lakes in ascending order of eutrophy. Y-axis: phases. A diagonal line indicates that the respective phase is not represented in the lake. Shading indicates elevated levels of biomass (>1000 mm^3 m^{-3}).

Algal code: Ce: *Ceratium,* Ch: Chlorophyceae, Co: Conjugatophyceae, Cr: Cryptophyceae, Cy: *Cyclotella bodanica* (if written as exponent: important among other diatoms). D: net planktonic diatoms, d: small centric diatoms, Di: *Dinobryon,* H: Heterocystous Cyanophyceae, O: *Oscillatoria rubescens,* T: *Tabellaria;* U: *Uroglena.*

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