

Research Article

Identifying functional groups of phytoplankton using data from three lakes of different trophic state

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Abstract. There is tremendous diversity in species of phytoplankton. Yet one may expect some degree of commonality in the response of similar species to similar conditions. Functional groups are those sets of species that respond similarly to environmental conditions because they have similar properties. The identification of such functional groups can assist model-based prediction of the abundance of phytoplankton as a function of time, space, and environmental conditions. Functional groups can also assist limnologists in the analysis and presentation of field data. We identified functional groups of phytoplankton using a combination of prior knowledge (based on taxonomic divisions and measurable properties) and statistical cluster analysis of long-term, species-level data from three Swiss lakes of different trophic state. For this task, we used the taxonomic division as the basic unit of analysis. Each taxonomic group was subdivided into several further groups by analysing the occurrence pattern of each species of the group

and grouping together species with similar patterns. The reasons for the occurrence pattern for each species within a group were then analysed based on the main properties of the species. The results of this analysis were used to merge groups that had similar occurrence for similar reasons across taxonomic boundaries. Groups with different occurrence patterns but similar properties were also merged. This led to suggestions for functional groups at multiple levels of aggregation. The resulting groups were used in a subsequent study for modelling phytoplankton in the three lakes used for this analysis. The general methodology of combining prior knowledge on properties with empirical evidence on occurrence should be useful for finding functional groups of phytoplankton in other lakes as well. Comparisons of studies across lakes can then contribute to the identification of universal functional groups of phytoplankton applicable to a broad class of waters.

Key words. Phytoplankton; functional groups; lake modelling.

Introduction

Phytoplankton grow under a wide variety of conditions. However, the characteristic responses of different species to similar conditions can differ significantly due to distinct abilities to obtain competitive advantage of certain situations. Since the trophogenic layer of a lake is always open to each invading species,

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Table 1. Overview of groupings used in a selection of published lake models.

Taxonomic Groupings	
<p>CE-QUAL-W2 (modified by Bowen and Hieronymus 2003)</p> <ul style="list-style-type: none"> ● dinoflagellates and diatoms ● chlorophytes and cryptophytes ● blue-green algae <p>LakeWeb-Model (Hakanson and Bouilon 2003, Hakanson 2004)</p> <ul style="list-style-type: none"> ● phytoplankton ● bacterioplankton ● benthic algae <p>Frisk et al. 1999</p> <ul style="list-style-type: none"> ● diatoms ● cyanobacteria <p>Kristov et al. 1999</p> <ul style="list-style-type: none"> ● diatoms: <i>Asterionella</i>, <i>Stephanodiscus</i> ● <i>Anabena</i> ● <i>Ceratium/Microcystis</i> group <p>SALMO (Benndorf and Recknagel 1982)</p> <p>Two of the following groups can be selected :</p> <ul style="list-style-type: none"> ● microplanktic diatoms: <i>Asterionella formosa</i> ● green algae and nanoplanktic diatoms: <i>Scendesmus quadricula</i> and <i>Cyclotella meneghiniana</i> ● blue-green algae: <i>Planktothrix redekei</i> <p>The properties and parameters for those groups are obtained from measurements and knowledge about the key species.</p>	<p>MINLAKE (Riley and Stefan 1988)</p> <ul style="list-style-type: none"> ● diatoms ● green algae ● blue-green algae <p>Phytoplankton groups have different rates of photosynthesis, respiration, settling, zooplankton grazing and nutrient requirements.</p> <p>Gragani et al. 1999</p> <ul style="list-style-type: none"> ● filamentous cyanobacteria of the <i>Oscillatoria</i> (<i>Planktothrix</i>) type ● green algae <p>DYRESM water quality (Hamilton and Schladow 1997)</p> <ul style="list-style-type: none"> ● cyanobacteria ● diatoms ● chlorophytes and other species <p>Glumso model (Jorgensen 1976, modified by Salomonsen and Jensen 1996)</p> <ul style="list-style-type: none"> ● chlorophytes ● diatoms <p>CAEDYM v2 (Romero et al. 2004)</p> <ul style="list-style-type: none"> ● Dinoflagellates ● Freshwater Cyanobacteria ● Marine/estuarine Cyanobacteria ● Chlorophytes ● Cryptophytes ● Marine/estuarine diatoms ● Freshwater diatoms
Nutrient-based Groupings	Property-based Groupings
<p>Roelke (2000)</p> <ul style="list-style-type: none"> ● P-specialist ● N-specialist ● intermediate group ● ciliates, microflagellates, bacteria 	<p>PROTECH (Reynolds and Irish 1997, Elliott et al. 1999a, Elliott et al. 1999b, Elliott et al. 2000, Reynolds et al. 2001)</p> <p>Eight out of 18 phytoplankton species can be chosen. Growth rate and light and temperature dependence are calculated from surface area, volume, and maximum dimension.</p> <ul style="list-style-type: none"> ● motility ● diatom (yes/no) ● grazed (yes/no) ● nitrogen fixer (yes/no)

the community of plankton is not fixed by historical dominance of certain species and each niche can be occupied by different forms. While this diversity is fascinating, it makes model-based prediction of phytoplankton response to changes in external influences extremely difficult. Models that treat phytoplankton as one component, with single, fixed values of parameters, cannot describe the variability observed in nature. Yet, it would be impossible to model each of the hundreds of species and strains that occur in any one water body individually.

To contend with the diversity of phytoplankton, modellers have often sought to identify functional groups of species that can be expected to have some degree of commonality in their response to similar conditions (Table 1). In many studies, this has involved splitting species along taxonomic lines (Bowen and Hieronymus, 2003; Riley and Stefan, 1988), and the division of dinoflagellates and diatoms from green algae and cyanobacteria is sometimes used (see

Table 1). Some models have handled selected species separately because of their importance in the water body being studied (e.g., Kristov et al., 1999). Others have used property-based groupings. PROTECH is notable in this regard (Reynolds and Irish, 1997; Elliott et al., 1999a; Elliott et al., 1999b; Elliott et al., 2000; Reynolds et al., 2001). Up to eight species can be selected. The properties of these species are then used to calculate the growth rates and their light and temperature dependencies. Roelke (2000) defined groups according to their ability to exploit particular nutrients, specifically differentiating between N and P specialists.

It is not easy to decide which of the functional group approaches might be suitable for a certain water body. Additionally, functional groups defined for one water body might not be suitable for another, especially when the species composition is different. Therefore, it remains an open question as to how functional groups can be best defined for modelling.

Are taxonomic divisions appropriate? Should groupings be based on morphological properties? How can historical species-specific abundance data be used in this effort?

The goal of this paper is to address these questions and to find a suitable approach for dividing the phytoplankton of three Swiss lakes of different trophic state into functional groups.

Conceptual approaches of dividing phytoplankton into functional groups

Taxonomic groups

Taxonomic groups are often assumed to represent functional groups. Taxonomic classification of phytoplankton is based on pigment and cell wall composition, locomotory system, and general morphological and physiological structure.

The main taxonomic groups of phytoplankton in the set of lakes we consider in this paper are:

- CYANOPHYTA (blue-green algae) (1)
- HETEROKONTOPHYTA
 - o Chrysophyceae (golden(-brown) algae) (2)
 - o Bacillariophyceae / Diatomeae (diatoms) (3)
- DINOPHYTA (dinoflagellates) (4)
- CRYPTOPHYTA (cryptomonads) (5)
- CHLOROPHYTA
 - o Chlorophyceae (green algae) (6)
 - o Conjugatophyceae (conjugate algae) (7)

The taxonomic approach has the advantage that nearly all species can be assigned uniquely to a group. Thus, the resulting groups are mutually exclusive and contain the major portion of the total biomass (groups above: about 90 % of the total biomass for the lakes investigated in this study). However, while there are many commonalities among individual species within a taxonomic group, there can also be wide variety in the key properties determining their behaviour. Also, organisms from different taxonomic groups often evolved similar traits, suggesting that dividing species along strictly taxonomic lines alone may not be the most effective strategy for constructing functional groups.

Life strategy-based groups

Besides taxonomic groupings, there are also approaches to classifying species according to their life strategy. Divisions based on life strategy are promising because of their attempt to assemble phytoplankton species into a limited number of groups with similar behaviour.

A well-known example is the r-K concept (MacArthur and Wilson, 1967) that divides species into fast

growing r-species, and K-species that are competitive for other reasons (e.g., less edible). The r-species tend to occur in the early stages of succession and K-species in later stages.

Another classification based on ecological strategies, referred to as the C-S-R concept, is also well known (Grime, 1977). This concept was adapted for phytoplankton by Reynolds (Reynolds, 1988; Reynolds, 1997). It divides species into ruderals (R-Strategists), competitive (C-Strategists) and stress tolerant (S-Strategists) species. This classification was later extended by introducing an intermediate C-S group.

Life strategy-based approaches are appealing from a conceptual point of view. However, there are practical difficulties with the application of this approach for mechanistic modelling. Sometimes, it is difficult to assign a species to a certain group. The concepts describe a continuum between extremes and therefore it is difficult to delineate fixed boundaries between groups. The life-strategy-based groups do not cover all aspects that have been shown to be important in phytoplankton response (e.g., motility, silica requirement). Therefore, additional properties are sometimes employed for grouping (e.g., Lewis et al., 2002)

Property-based groups

Among the examples of using properties to form functional groups of phytoplankton species, Weithoff (2003) suggested drawing conclusions about environmental response based on six properties (functional traits): size, shape, nitrogen fixation potential, demand for silica, phagotrophy, and motility. This selection is based on the criterion of easy measurability. Some of these properties are directly relevant for determining response, while others are recommended because they are assumed to be determinants of other, more important traits, such as edibility, sedimentation velocity, and growth rate. However, there are also other important properties, such as affinity for phosphate, and temperature and light dependence, which probably cannot be derived from these simple properties.

Reynolds (1980) introduced another classification system by assigning 14 phytoplankton associations to sets of environmental conditions. This approach was extended to 31 associations by Reynolds et al. (2002). These groups are characterized by representative species.

An approach that combines physiological properties with ecological traits was suggested by König (2006). These groups were developed for two reservoirs in Germany, *a priori* knowledge from many other lakes and a comprehensive literature review. They are an extension of the functional groups already imple-

Table 2. Summary of important lake characteristics

	Walensee	Lake Zürich	Greifensee
Catchment area (km ²)	1061	1829	163
Meters above sea level (m)	419	406	435
Surface area (km ²)	24	67	8.5
Maximum depth (m)	151	136	32
Average depth (m)	105	49	18
Volume (10 ⁶ m ³)	2530	3300	150
Discharge (m ³ /s)	55	90	4
Retention time (y)	1.4	1.2	1.1
Average SRP concentration during turnover (µgP L ⁻¹)	~ 2–5	~ 25–40	~ 60–100

mented in the lake model SALMO (Benndorf and Recknagel, 1982). Taxonomic groups are split into subgroups using properties such as size, motility, capability of N-fixation, and whether they are filamentous. For each group, all properties that may be necessary for modelling are analyzed and a description of the properties is given. These properties include maximum growth rate, optimum temperature, minimum temperature, half saturation concentrations for light, phosphate and silica (K_I -value, K_P -value, K_{Si} -value), capability of N-fixation, sedimentation velocity, edibility, and motility.

Methods

As described above, various conceptual approaches for dividing phytoplankton into functional groups have been attempted. However, it is still not easy to decide which functional groups should be used for a particular water body and some of them are difficult to apply for modelling purposes. For this reason, it is important to search for empirical evidence of functional groups in measured phytoplankton data. This can be done by identifying groups of species that show similar occurrence patterns and then using biological knowledge to infer the most important properties defining these occurrence groups. We will develop such an approach and apply it to major taxonomic groups. We hope to obtain an empirical indication of the properties along which the taxonomic groups should be split and then possibly aggregated into functional groups across taxonomic lines. The properties associated with the functional groups will also allow us to suggest group memberships for species not present in the examined data-set.

Data and site description

We used data from three Swiss lakes in our analysis: Walensee (oligotrophic), Lake Zürich (mesotrophic), and Greifensee (eutrophic) (Table 2). Lake Zürich is divided into two basins by a natural dam. In this study, only the lower basin of Lake Zürich was

considered and will henceforth be referred to only as Lake Zürich.

Monthly profiles of physical, chemical and biological variables for Lake Zürich and Walensee for the years 1972–1999 were obtained from the Water Supply Authority of Zürich (WVZ). For Greifensee, monthly to weekly depth integrated measurements (mixed samples from 0–20 m depth) for the years 1985–2000 (1987–2002 for biological data) were obtained from the Limnology Department of Eawag (Dübendorf, Switzerland). Phytoplankton and zooplankton concentration data consist of counts of 100 to 140 different species. Biovolumes were calculated by multiplying the counts of each species by the typical volume of one cell or individual of this species. Volume was then converted to wet mass using the density of water.

The analysis was performed for the years 1988–1999 because data from all lakes were available for this period and most of the relevant environmental conditions remained relatively stable. The most important environmental conditions for the growth of phytoplankton are light intensity, mixing depth, temperature and nutrient concentrations (phosphate, silica, nitrate, ammonium). These conditions are described briefly for the three lakes in the following paragraphs. Further details on lake characteristics and methods of data collection are provided by Mieleitner and Reichert (2006).

Lake Zürich

This lake is monomictic: it is usually thermally stratified during summer and mixes during winter. In most winters, the lake is mixed completely but in some winters mixing depth only reaches 60 to 100 m because the winter is too warm or the winds are not strong enough to mix the lake completely. Lake Zürich is protected by hills, therefore only weak winds reach the lake surface. Winter stratification or even ice cover occur only if the winter is extremely cold. In March, the temperature at the lake surface starts to increase and stratification builds. Each year, a clear division of the water body into epilimnion, metalimnion, and

hypolimnion is present from April/May until September or October. The temperature in the epilimnion reaches 20 to 25 °C during the summer (July and August), and the depth of the thermocline is between 5 and 10 meters, increasing during autumn (from December to February) (Zimmermann et al., 1993; Bossard et al., 2001). Small variations occur from year to year, but there have not been significant exceptions during the study period. Phosphate concentrations during spring turnover are between 25 and 40 µgP/L. In summer, phosphate in the epilimnion is depleted to 1 µgP/L or undetectable concentrations. Phosphate is the limiting nutrient for plankton growth during summer. Silica concentrations are usually between 2000 and 3000 µgSiO₂/L during turnover. During stratification, silica is reduced to between 200 and 400 µg SiO₂/L, sometimes approaching the limiting concentration of 120 µg SiO₂/L (according to Reynolds et al., 2001). Nitrogen never appears to be limiting in Lake Zürich.

Greifensee

Greifensee is a dimictic lake. The temperature and mixing regime of Greifensee is similar to that of Lake Zürich. Greifensee is also not exposed to strong winds and has a stable metalimnion with a strong temperature gradient from April/May until September/October. The surface temperature usually reaches 20 to 25 °C during two or three months in summer. Because the lake is much shallower than Lake Zürich, it is mixed completely each winter. Phosphate concentration during turnover changed significantly during the study period. From 1988 to 1991, values were around 100 µgP/L but have since decreased to about 60 µgP/L. In summer, as in Lake Zürich, phosphate is depleted to 1 µgP/L or undetectable concentrations in the epilimnion and limits plankton growth. Silica concentrations during turnover are similar to those in Lake Zürich. During stratification, silica is depleted to concentrations between 200 and 1000 µgSiO₂/L, sometimes reaching the limiting concentration of 120 µg SiO₂/L. In Greifensee, nitrogen is never limiting.

Walensee

Walensee is monomictic. It has a small surface area to volume ratio. Therefore, air temperatures in winter seldom cool the lake to temperatures lower than 5 °C and the lake has never frozen. Walensee is exposed to strong winds throughout the year. Therefore, when the surface of the lake is warmed during the spring and stratification initiates, the strong winds mix the surface water precluding a strong temperature gradient. Throughout the summer, a stable metalimnion cannot establish in Walensee. The deep mixing during the

stratified period leads to an exchange of temperature/heat and nutrients over a thicker water layer than in the other lakes. Therefore, surface temperatures are generally lower. Temperatures during the summer months are often around 20 °C or below. Also, nutrients can be exchanged with the hypolimnion throughout the summer (Zimmermann et al., 1993). In Walensee, phosphate concentrations are much lower than in the other lakes. During turnover they only reach 2 to 5 µgP/L. Silica concentrations remain between 1000 and 2000 µgSiO₂/L throughout the year. Only rarely are they depleted during summer and never to limiting concentrations. Nitrogen is apparently never limiting in Walensee.

Algorithm

We applied the following procedure for defining functional groups:

1. Start with a classification of relevant species into the most important taxonomic groups.
2. Apply occurrence-based clustering techniques to available data on the most abundant species (see below for details) to identify characteristic, occurrence-based sub-groups of taxonomic groups.
3. Identify response-related properties that characterize the groups identified in the previous step using biological knowledge.
4. Assign less abundant species to the groups according to their taxonomy and their properties to obtain a classification that contains the major portion of the total biomass.
5. Aggregate the groups identified in the previous step across taxonomic boundaries by merging groups with similar behaviour and similar reasons for this behaviour. Groups with different behaviour are also merged if they have similar properties.

The rationale and specific methods employed in step 2 were as follows:

Species that have a similar response to environmental conditions might be expected to occur jointly at certain times of the year. Therefore, identification of groups of such species amounts to looking for sets of species with similar relative abundance patterns. We used relative abundance to compare patterns of occurrence, rather than absolute abundance, as the latter can vary strongly between species. To identify sets of species with similar occurrence patterns, we used statistical cluster analysis.

Cluster analysis is a method for grouping a collection of objects into subsets or “clusters” that are similar to one another according to a specified similarity (or dissimilarity) metric (Hastie et al., 2001). We used hierarchical cluster analysis, which

yields a hierarchy of possible groupings so that any number of similar groups can be selected, depending on the level of complexity desired. A key consideration in the application of cluster analysis is the choice of the distance metric used to compare the objects being clustered. The definition of this metric can only come from application-specific considerations (Hastie et al., 2001). For our analysis, we defined the distance metric in the following way:

- a) For each water body, species-specific biomass measurements during the years 1988–1999 were indexed using the day of the year (i.e., 1 through 366) as the time variable for measured abundance data, rather than the actual date. This served to aggregate the data of several years into one collective year. This was done because it became apparent that species composition varied significantly across years, and that some species that typically occur at a certain time of year do not occur together every year.
- b) The single species abundance data from the collective year were smoothed over time for each lake using the LOESS algorithm (Chambers and Hastie, 1991; Cleveland and Devlin, 1988; Cleveland and Grosse, 1991) of the statistical software package S-PLUS (<http://www.insightful.com>). This serves to smooth the measured abundance values in a manner that accounts for their temporal proximity to adjacent values. (We used LOESS parameter values of: span = 0.65, polynomial degree = 2.)
- c) The data of multiple water bodies compiled in this way were concatenated by appending the data from the collective years of each water body one after the other. For example, for our lakes, Walensee comprised rows 1–366, Lake Zürich rows 367–742, and Greifensee rows 743–1108. This was done to allow us to analyze the behaviour of the species in all three water bodies jointly.
- d) The resulting smoothed daily values in abundance of each species were normalized by dividing by the summed abundance for that species over the collective years. This served to focus the analysis on similarities in the temporal pattern of relative abundance, rather than on similarities in the magnitude of abundance.
- e) A hierarchical cluster analysis was performed on the smoothed daily data using the difference in normalized abundance across all 3×366 days.
- f) The cluster analysis was performed on each taxonomic group separately to split each taxonomic group into several subgroups.

Several cluster algorithms are available with the statistical software package S-PLUS. We used the algorithm AGNES, an agglomerative method which constructs a hierarchy of clusters (Struyf et al., 1997). Each observation starts as a small cluster by itself. The two most similar clusters are then combined. This continues until only one cluster remains containing all the observations. We used the Euclidean distance (total sum of squared deviations) as the measure of dissimilarity, and Ward's method for fusion so that the criterion for combining clusters was the smallest possible increase in the sum of squared deviations (Kaufman and Rousseeuw, 1990).

Results

For our analyses, we only considered species that contributed more than 0.1% to the total biomass in the years 1988–1999. Together, these species comprised 87, 86, and 92% of the total biomass in Walensee, Lake Zürich, and Greifensee, respectively. In total, 33 species were included in the analysis (Table 3).

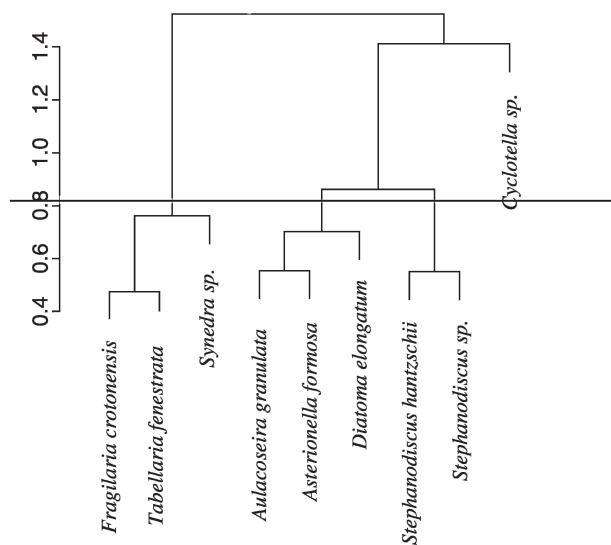
In terms of contribution to total biomass, the dominant species in oligotrophic Walensee and mesotrophic Lake Zürich were similar. The exception is *Planktothrix rubescens*, which is the dominant species in Lake Zürich but is found only in low abundance in Walensee. The major species in the eutrophic Greifensee are somewhat different from the other two. In particular, there is a larger contribution of green algae and mucilaginous blue-green algae.

Division of each taxonomic group into occurrence groups

In the following sections, we describe for each taxonomic group the division into subgroups based on the cluster analysis occurrence patterns. Possible reasons for the observed patterns are proposed, however, some open questions remain. In cases where the reasons for the same occurrence patterns were clearly different, the group was split into subgroups. Due to space constraints, we cannot show the cluster trees and plots for all taxonomic groups, but the tree and plots of the groups found for diatoms are shown as an example (Figure 1 and Figure 2). For each taxonomic group, the level of group division was chosen to separate all important patterns. Table 4 gives an overview of the division of all taxonomic groups and the species and occurrence patterns of each subgroup.

Table 3. Species included in the analysis and their biomass contribution in the three study lakes. The given biomass contributions (% bm) are the contributions of the species to the total biomass in the years 1988–1999.

Walensee		Lake Zürich		Greifensee	
species	% bm	species	% bm	species	% bm
<i>Fragilaria crotonensis</i>	21.52	<i>Planktothrix rubescens</i>	33.81	<i>Cryptomonas sp.</i>	16.79
<i>Tabellaria fenestrata</i>	11.72	<i>Fragilaria crotonensis</i>	9.09	<i>Chlamydomonas sp.</i>	12.11
<i>Stephanodiscus hantzschii</i>	8.96	<i>Monas sp.</i>	4.91	<i>Microcystis sp.</i>	8.54
<i>Dinobryon sp.</i>	7.28	<i>Stephanodiscus hantzschii</i>	4.55	<i>Rhodomonas sp.</i>	4.77
<i>Rhodomonas sp.</i>	7.10	<i>Cryptomonas sp.</i>	4.38	<i>Cyclotella sp.</i>	3.91
<i>Asterionella formosa</i>	4.29	<i>Tabellaria fenestrata</i>	3.59	<i>Asterionella formosa</i>	3.66
<i>Ceratium hirundinella</i>	3.82	<i>Aulacoseira granulata</i>	3.45	<i>Dictyosphaerium sp.</i>	3.61
<i>Cryptomonas sp.</i>	3.62	<i>Rhodomonas sp.</i>	2.56	<i>Eutetramorus fottii</i>	3.54
<i>Monas sp.</i>	2.61	<i>Asterionella formosa</i>	2.54	<i>Fragilaria crotonensis</i>	3.47
<i>Erkenia subaequiciliata</i>	2.16	<i>Gymnodinium helveticum</i>	2.27	<i>Aphanothece sp.</i>	3.27
<i>Peridinium sp.</i>	2.14	<i>Dinobryon sp.</i>	2.12	<i>Merismopedia sp.</i>	2.81
<i>Aulacoseira granulata</i>	1.87	<i>Ceratium hirundinella</i>	2.05	<i>Tabellaria fenestrata</i>	2.79
<i>Synedra sp.</i>	1.62	<i>Synedra sp.</i>	1.96	<i>Ochromonas sp.</i>	2.02
<i>Pandorina morum</i>	1.60	<i>Stephanodiscus sp.</i>	1.63	<i>Stephanodiscus hantzschii</i>	1.92
<i>Stephanodiscus sp.</i>	1.50	<i>Peridinium sp.</i>	1.60	<i>Aulacoseira granulata</i>	1.91
<i>Gymnodinium helveticum</i>	1.46	<i>Erkenia subaequiciliata</i>	1.31	<i>Stephanodiscus sp.</i>	1.89
<i>Diatoma elongatum</i>	1.40	<i>Pandorina morum</i>	1.06	<i>Anabaena sp.</i>	1.82
<i>Microcystis sp.</i>	1.35	<i>Aphanizomenon flos-aquae</i>	0.88	<i>Ceratium hirundinella</i>	1.65
<i>Cyclotella sp.</i>	0.53	<i>Microcystis sp.</i>	0.82	<i>Katablepharis sp.</i>	1.52
<i>Katablepharis sp.</i>	0.19	<i>Diatoma elongatum</i>	0.81	<i>Oocystis sp.</i>	1.48
<i>Planktothrix rubescens</i>	0.07	<i>Katablepharis sp.</i>	0.34	<i>Gomphosphaeria lacustris</i>	1.37
<i>Ochromonas sp.</i>	0.06	<i>Cyclotella sp.</i>	0.19	<i>Pandorina morum</i>	1.35
<i>Oocystis sp.</i>	0.06	<i>Ochromonas sp.</i>	0.10	<i>Aphanizomenon flos-aquae</i>	1.30
<i>Aphanothece sp.</i>	0.05	<i>Oocystis sp.</i>	0.08	<i>Gymnodinium helveticum</i>	1.27
<i>Aphanocapsa sp.</i>	0.04	<i>Aphanocapsa sp.</i>	0.08	<i>Aphanocapsa sp.</i>	1.05
<i>Chlamydomonas sp.</i>	0.01	<i>Chlamydomonas sp.</i>	0.06	<i>Salpingoeca sp.</i>	1.00
<i>Aphanizomenon flos-aquae</i>	0.00	<i>Aphanothece sp.</i>	0.04	<i>Dinobryon sp.</i>	0.56
<i>Dictyosphaerium sp.</i>	0.00	<i>Dictyosphaerium sp.</i>	0.03	<i>Diatoma elongatum</i>	0.10
<i>Merismopedia sp.</i>	0.00	<i>Merismopedia sp.</i>	0.00	<i>Peridinium sp.</i>	0.06
<i>Salpingoeca sp.</i>	0.00	<i>Anabaena sp.</i>	0.00	<i>Synedra sp.</i>	0.03
<i>Anabaena sp.</i>	0.00	<i>Salpingoeca sp.</i>	0.00	<i>Planktothrix rubescens</i>	0.02
<i>Eutetramorus fottii</i>	0.00	<i>Eutetramorus fottii</i>	0.00	<i>Monas sp.</i>	0.00
<i>Gomphosphaeria lacustris</i>	0.00	<i>Gomphosphaeria lacustris</i>	0.00	<i>Erkenia subaequiciliata</i>	0.00

**Figure 1.** The cluster tree and cut level for diatoms. The length of the branches is proportional to the distance between species.

Cyanophyta (blue-green algae)

Occurrence

Based on the cluster analysis, blue-green algae were split into two groups: one group with occurrence in summer in Greifensee and one group with occurrence in winter and summer in Lake Zürich and Greifensee. In Walensee, the concentrations of blue-green algae are always so low that they can be neglected.

Species, properties, interpretation

The **first group** (occurrence in summer in Greifensee) consists mainly of mucilaginous blue-green algae. During the study period (1988–1999), the mucilaginous forms *Microcystis sp.*, *Aphanothece sp.*, *Snowella* (Syn *Gomphosphaeria*) *lacustris*, *Merismopedia sp.*, *Aphanocapsa sp.*, occurred regularly in summer and autumn each year in Greifensee. In Lake Zürich, these were at much lower concentrations and did not occur regularly. The filamentous form *Anabaena sp.* occurred in summer in some years in Greifensee and Lake Zürich (*blue.1*, A1) (Table 4).

This group is dominated by mucilaginous colonial forms. The species of this group have a low sinking

Table 4. Taxonomic groups and division into subgroups. The lakes are abbreviated as W (Walensee), Z (Lake Zürich) and G (Greifensee).

Taxonomic Group	Subgroup	Time of occurrence	Species
1. Cyanophyta (blue-green algae)	A1 (blue.1)	G: summer/autumn	<i>Microcystis sp.</i> , <i>Aphanothece sp.</i> , <i>Gomphosphaeria lacustris</i> (<i>Snovella lacustris</i>), <i>Merismopedia sp.</i> , <i>Aphanocapsa sp.</i> , <i>Anabena sp.</i>
	A2 (blue.2)	Z: winter and summer	<i>Planktothrix rubescens</i>
	A3 (blue.3)	Z: winter and summer G: winter and summer	<i>Aphanizomenon flos-aquae</i>
2. Chrysophyceae (golden-brown algae)	A4 (chrys.1)	W: all year Z: all year	<i>Monas sp.</i> , <i>Erkenia subaequiciliata</i>
	A5 (chrys.2)	G: all year	<i>Ochromonas sp.</i> <i>Salpingoeca sp.</i>
	A6 (chrys.3)	W: summer Z: summer G: summer	<i>Dinobryon sp.</i>
3. Diatomeae (diatoms)	A7 (diat.1)	W: spring and summer Z: spring G: spring	<i>Stephanodiscus sp.</i> , <i>Stephanodiscus hantzschii</i>
	A8 (diat.2)	G: spring	<i>Cyclotella sp.</i>
	A9 (diat.3)	W: spring Z: spring and winter G: spring and autumn	<i>Aulacoseira granulata</i> , <i>Diatoma elongatum</i> , <i>Asterionella formosa</i>
	A10 (diat.4)	W: all year Z: summer G: all year	<i>Fragilaria crotonensis</i> , <i>Tabellaria fenestrata</i> , <i>Synedra sp.</i>
4. Dinophyta (dinoflagellates)	A11 (dino.1)	W: spring and summer Z: spring and summer G: spring	<i>Gymnodinium helveticum</i>
	A12 (dino.2)	W: summer Z: summer G: summer	<i>Ceratium hirundinella</i> , <i>Peridinium sp.</i>
5. Cryptophyta (cryptomonads)	A13 (crypt.1)	W: all year Z: all year G: spring and summer	<i>Cryptomonas sp.</i> , <i>Rhodomonas sp.</i> , <i>Katablepharis sp.</i>
6. Chlorophyceae (green algae)	A14 (green.1)	G: spring and summer	<i>Dictyosphaerium sp.</i> , <i>Chlamydomonas sp.</i>
	A15 (green.2)	G: summer	<i>Oocystis sp.</i> , <i>Eutetramorus fottii</i>
	A16 (green.3)	W: all year Z: summer G: spring	<i>Pandorina morum</i>

velocity. Some of them have gas vacuoles and are capable of vertical movement by buoyancy alteration. So they can perform a vertical migration to the surface during the day and to nutrient rich sub-surface waters during the night. Their ability to regulate their position is an advantage under stratified conditions. Under mixed conditions, buoyancy regulation is often ineffective at maintaining them at a certain depth. (Paerl, 1988). The affinity of this group to phosphate is rather low (high K_p) (Sommer, 1989), but can be compensated by vertical migration and the ability to store phosphorus internally when there is excess phosphate. Their light requirement is also high (high K_l). Therefore, they can grow only in summer when mixing depth is not too great. The growth in summer is also supported by their poor edibility and their low sinking velocity (Paerl, 1988).

The **second group** consists of the two species: *Planktothrix rubescens* and *Aphanizomenon flos-*

aquae. It is dominated by *P. rubescens* in Lake Zürich where it is the most abundant species. It can account for up to 89 % of the biomass and accounts for about 20 % of the biomass on average (Gammeter et al., 1997). It has its maximum biomass in winter. The reasons for the behaviour of *P. rubescens* in Lake Zürich were analyzed and described in several studies (Bossard et al., 2001; Walsby et al., 2001; Micheletti et al., 1998; Schanz, 1985; Anneville et al., 2004) and are well known. It can grow with very low light intensities and is inhibited by high light intensities. It can control its position in the water column with gas vacuoles and so positions itself in the metalimnion. In winter when the mixing depth increases, it still has an advantage because of its low light requirement and can continue to grow as long as the mixing depth is not too great.

Because of the significantly different properties of the two species in this group, it is further divided into

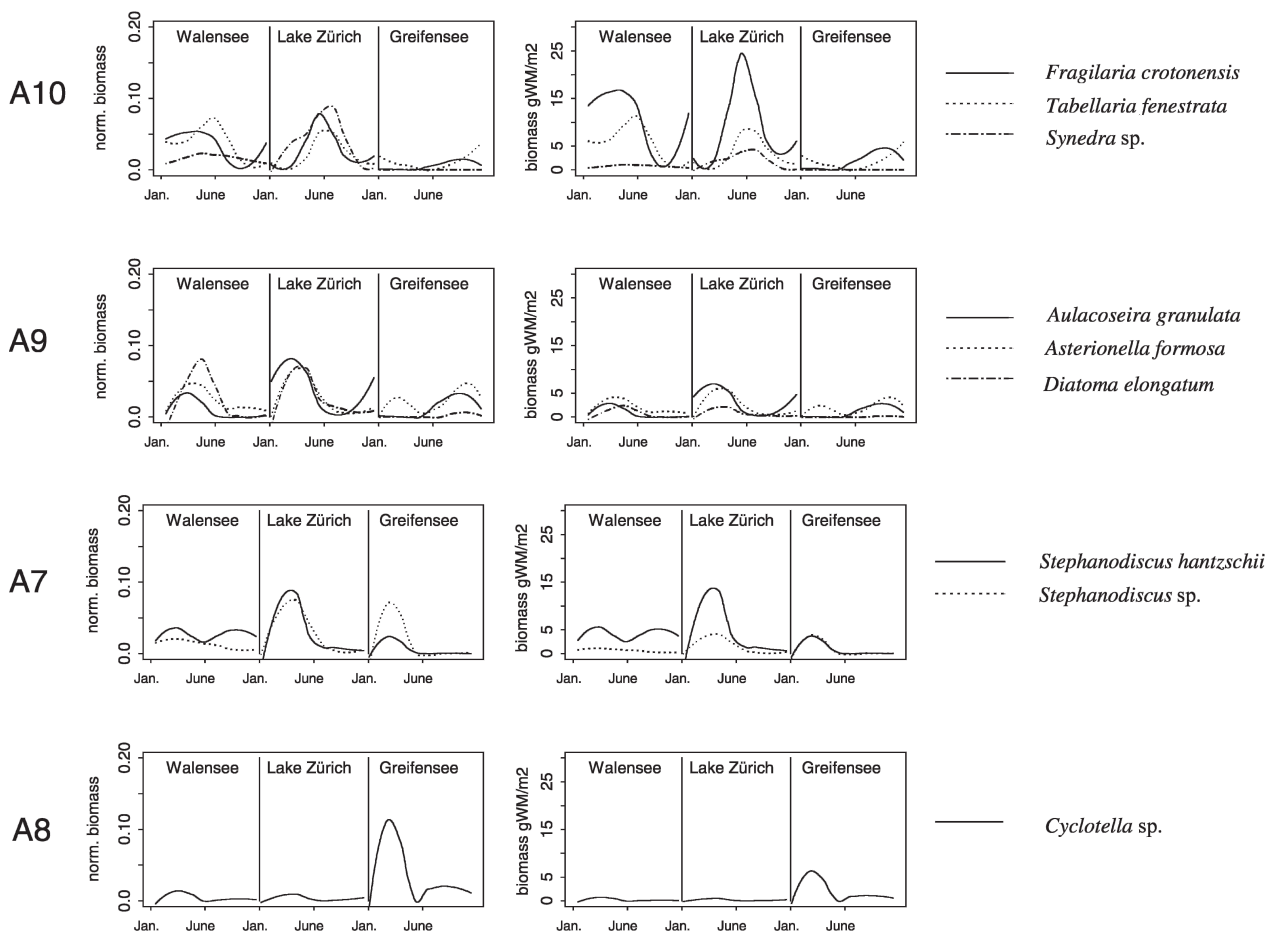


Figure 2. Seasonal pattern of the four groups identified in figure 1. Left: smoothed, normalized biomass; Right: smoothed, unnormalized biomass.

two groups: *Planktothrix rubescens* (blue.2, A2) and *Aphanizomenon flos-aquae* (blue.3, A3) (Table 4).

Aphanizomenon flos-aquae was investigated by Uehlinger (1980), who found that it rarely occurs between March and July but mostly occurs from August to October. Sometimes winter blooms also occur. This is in agreement with our findings. *A. flos-aquae* sometimes occurs in late summer and sometimes in winter in both Lake Zürich and Greifensee. In spring, it cannot grow because its growth rate is low at low temperatures and so it is overgrown by fast spring forms. In summer, it can grow relatively quickly despite the low nutrient concentrations because of its relatively low K_P -value. Also during summer, zooplankton concentrations are high and it profits from its poor edibility. Its low light requirement might play a role during the winter blooms.

Blue-green algae likely do not occur in Walensee because of low phosphate concentrations, low temperatures and deep mixing depth during the summer.

Chrysophyceae (golden-brown algae)

Occurrence

Chrysophyceae were divided into three clusters. One with occurrence during the whole year in Lake Zürich and Walensee (*chrys.1*, A4), a second with occurrence during the whole year in Greifensee (*chrys.2*, A5) and a third with occurrence in summer in all lakes (*chrys.3*, A6) (Table 4).

Species, properties, interpretation

The **first group** (*chrys.1*, A4) (occurrence during the whole year in Lake Zürich and Walensee) consists of the very small single celled algae *Monas* sp. and *Erkenia subaequiciliata*. They occurred regularly each year with several peaks per year.

The **second group** (*chrys.2*, A5) (occurrence during the whole year in Greifensee) also consists of small single cells: *Ochromonas* sp. and *Salpingoeca* sp. They also occurred each year with several peaks per year. The occurrence in spring of those two groups can be explained by their very high growth rate. The growth rate of this group is high enough that they can grow in

summer despite their good edibility. They only disappear if the zooplankton concentration is very high (e.g., during the clear water phase in Greifensee). Furthermore, these species have a very low K_P -value and are also phagotrophic, which supports their growth in summer when phosphate concentrations are low (Sandgren, 1988; Jones and Ilmavirta, 1988).

The **third group** (*chrys.3*, A6) (occurrence in summer in all lakes) consists of only one species: *Dinobryon* sp. During the study period it occurred regularly in summer in Walensee and Lake Zürich and Greifensee. In Walensee, it often had an additional peak in autumn. *Dinobryon* sp. is a large colony building species with medium growth rate. The growth in summer is due to the poor edibility and the very low K_P -value (Sandgren, 1988; Jones and Ilmavirta, 1988). It also occurs in Walensee because of its very low K_P -value.

Bacillariophyceae / Diatomeae (diatoms)

Occurrence

Diatoms were divided into four groups. A first group with occurrence in spring in all lakes (*diat.1*, A7), a second with occurrence in spring in Greifensee (*diat.2*, A8), a third with occurrence in spring in Walensee and Lake Zürich and spring and autumn in Greifensee (*diat.3*, A9), and a fourth with occurrence in summer in Lake Zürich and winter and spring in Walensee and Greifensee (*diat.4*, A10).

Species, properties, interpretation

The **first group** (*diat.1*, A7) (occurrence in spring in all lakes) consists of small centric diatoms (*Stephanodiscus* sp., *Stephanodiscus hantzschii*). They occur regularly in most years in Walensee, Lake Zürich and Greifensee. In Walensee, there is sometimes also a summer or autumn peak. The high growth rate and low light requirement (low K_I -value) of small centric diatoms supports growth in spring. The concentrations in summer are lower because of the good edibility of these species (Sommer, 1988).

The **second group** (*diat.2*, A8) (occurrence in spring in Greifensee) consists of the small centric diatoms *Cyclotella* sp. They formed a spring peak in Greifensee in most years, and seldom in Walensee and Lake Zürich. The reasons for the occurrence of the small centric diatoms in spring are the same as for the first group.

The **third group** (*diat.3*, A9) (occurrence in spring in Walensee and Lake Zürich, spring and autumn in Greifensee) consists of the large diatoms *Asterionella formosa*, *Aulacoseira granulata*, and *Diatoma elongatum*. The strategies and properties of large diatoms are described by Sommer (1988). Their disadvantages are a high sinking velocity and the dependence on an additional nutrient due to the siliceous frustule. Their

main advantage is their very low K_P -value, as shown in several studies (Holm and Armstrong, 1981; Sommer, 1983; Tilman and Kiesling, 1984). Other important properties of large diatoms are a medium growth rate, a low K_I -value, and poor edibility. The growth in spring is supported by the low K_I -value.

Sommer et al. (1986) also reported that large diatoms contribute to, and often dominate, the spring bloom, especially in oligotrophic lakes. The reasons for this are probably the low light requirement, the very low K_P -value and the tolerance for low temperatures. Sommer (1986) states that "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 et al. (1982), who found that species of *Asterionella*, *Synedra*, and *Fragilaria* are better competitors for P than small Centrales."

In summer these species can also grow because of their poor edibility and very low K_P -value.

The **fourth group** (*diat.4*, A10) (occurrence in summer in Lake Zürich and winter and spring in Walensee and Greifensee) is dominated by the two large diatoms *Fragilaria crotonensis* and *Tabellaria fenestrata*. Also *Synedra* sp. is part of this group. Like the previous group these large diatoms have a medium growth rate, a low K_I -value, very low K_P -value, high sedimentation velocity, and a poor edibility. These properties explain the occurrence in summer, which is supported by the very low K_P -value and a poor edibility. In Walensee these large diatoms also occur in spring, where they can compete because of their very low K_P -value and low light requirement similar to the large diatoms of group three.

Fragilaria is different from other large diatoms. It has a higher optimum temperature and a higher K_I - and K_P -value (König, 2006).

Dinophyta (dinoflagellates)

Occurrence

Dinoflagellates were divided into two occurrence groups. One group with occurrence in spring and summer in all lakes (*dino.1*, A11) and one group with occurrence in summer in all lakes (*dino.2*, A12).

Species, properties, interpretation

The **first group** (*dino.1*, A11) (occurrence in spring and summer) consists of the species *Gymnodinium helveticum*. It had a clear spring bloom each year in all lakes and also occurred in summer in Walensee and Lake Zürich in most years. *Gymnodinium helveticum* is mixotrophic. Phagotrophy in *Gymnodinium helveticum* and other dinoflagellates is common. Colonial green algae, flagellates, and small diatoms have been

found inside *Gymnodinium helveticum* (Frey and Stoermer, 1980; Irish, 1979). In the lakes we studied, *Gymnodinium helveticum* is often not coloured. It feeds on small algae and particles. The peak in spring is probably because the concentration of their food (small algae) is high at this time.

The **second group** (*dino.2*, A12) (occurrence in summer in all lakes) consists of the species *Ceratium hirundinella* and *Peridinium* sp. Those species are large motile species. Due to their large size they cannot be grazed by filter-feeding zooplankton. They have a low specific growth rate and high half saturation constants for phosphate uptake (K_p). Due to their motility they have no sedimentation losses. Another advantage of the motility is that they can perform diel vertical migration: during the day they go to the surface layer and at night they move to nutrient rich sub-surface layers. Additionally, they are able to use inorganic as well as organic phosphorus and have the ability for storage of phosphorus. Despite their high K_p -value they can compete under conditions of nutrient depletion because of their ability of nutrient storage, vertical migration, and ability to use organic phosphorus (Pollinger et al., 1993; Pollinger, 1988; Heaney, 1988). Another important factor determining the occurrence pattern of dinoflagellates is their life cycle. Dinoflagellates can build non-motile cysts. These cysts can survive a long time in the sediment. In temperate zones, dinoflagellates often grow during the thermal stratification. Encystment occurs in autumn at the end of the stratification period and the cysts are overwintering forms. Temperature is reported to play an important role in the process of excystment and encystment. Excystment occurs when the temperature of the water increases (Pollinger et al., 1993; Pollinger, 1988; Heaney, 1988).

Ceratium hirundinella and *Peridinium* sp. tolerate a wide range of environmental conditions and occur at the same time each year relatively independent of nutrient availability.

Cryptophyta (cryptomonads)

Occurrence

Cryptomonads were not divided into subgroups. They occur during the whole year in all lakes. In Greifensee, they build an obvious spring peak and a smaller summer peak (*crypt.1*, A13).

Species, properties, interpretation

The species of this group are *Rhodomonas* sp., *Cryptomonas* sp., and *Katablepharis* sp.

The occurrence in spring can be explained by the very high growth rate of the species. In all lakes they also occur during summer, which indicates that their growth rate is high enough that they can build biomass

despite their good edibility (Klaveness, 1988; Jones and Ilmavirta, 1988). Only in Greifensee during the clear water stage when the zooplankton concentrations are very high is the concentration of cryptomonads low.

Chlorophyceae (green algae)

Occurrence

Green algae were divided into three groups based on their occurrence. One group with a spring peak and a weak summer peak only in Greifensee (*green.1*, A14), a second group with occurrence in summer only in Greifensee (*green.2*, A15) and a third group with occurrence throughout the year in all lakes (*green.3*, A16).

Species, properties, interpretation

The **first group** (*green.1*, A14) (occurrence in spring in Greifensee) consists of *Chlamydomonas* sp. and *Dictyosphaerium* sp.. *Chlamydomonas* sp. had a pronounced spring peak each year in Greifensee. In summer, it usually had one or two smaller peaks. The biomass of *Dictyosphaerium* sp. is comparably low. *Chlamydomonas* sp. contains small fast growing forms that could explain the occurrence in spring.

The **second group** (*green.2*, A15) (occurrence in summer in Greifensee) consists of the large, colonial non-motile species *Oocystis* sp. and *Eutetramorus fottii*. Large green algae have a high light requirement and relatively high K_p -values (Happey-Wood, 1988; Sommer, 1989; Tilman et al., 1982). Due to their large size and mucilage they are not easily grazed and have a low sinking velocity (Happey-Wood, 1988). The main reasons for the occurrence in summer of these species is the high light requirement and the poor edibility of the species. The low sinking velocity also supports growth in summer.

The **third group** (*green.3*, A16) (occurrence throughout the year in Lake Zürich and Walensee and spring in Greifensee) consists of *Pandorina morum*. *P. morum* is a large mucilaginous colonial species that is motile by flagella. It can sustain itself throughout the year, however, at very low concentrations. Its properties are similar to the former group. A possible reason why *P. morum* has a different occurrence pattern than the other large colonial green algae is its motility and ability for vertical movement.

Chlorophyceae only occur in very low concentrations in Walensee because they have a high phosphate requirement and the phosphate concentrations in Walensee are too low.

Green algae have high optimum temperatures and are not able to grow at very low temperatures. This prevents their growth in spring and supports their growth in summer (König, 2006; Butterwick, 2005).

Table 5. Summary of the properties of the 16 occurrence groups. The following abbreviations are used: $k_{gro,max}$: specific growth rate, K_I and K_P : half saturation constants for light and phosphate, Si req.: requirement for silica, v_{sed} : sedimentation velocity, N_{fix} : ability to fix nitrogen. Key properties are printed in bold.

Group	Name	$k_{gro,max}$	edibility	K_I -value	K_P -value	Si req.	v_{sed}	motility	N_{fix}
A1, blue.1	mucilaginous blue green algae	medium	low	high	high	no	very low	some gas vacuoles	most no
A2, blue.2	<i>Planktothrix rubescens</i>	low	very low	very low	low	no	0	gas vacuoles	no
A3, blue.3	<i>Aphanizomenon flos-aquae</i>	low	very low	low	low	no	0	gas vacuoles	yes
A4, chrys.1	small chrysophyceae	very high	high	low	low	no	0	yes	no
A5, chrys.2	small chrysophyceae	very high	high	low	low	no	0	yes	no
A6, chrys.3	large chrysophyceae (<i>Dinobryon</i>)	medium	low	medium	low	low	0	yes	no
A7, diat.1	small diatoms	high	high	low	medium	yes	medium	no	no
A8, diat.2	small diatoms	high	high	low	medium	yes	medium	no	no
A9, diat.3	large diatoms	medium	low	low	low	yes	high	no	no
A10, diat.4	large diatoms	medium	low	low	low	yes	high	no	no
A11, dino.1	<i>Gymnodinium</i>	low	very low	high	high	no	0	yes	no
A12, dino.2	<i>Ceratium, Peridinium</i>	low	very low	high	high	no	0	yes	no
A13, crypt.1	small cryptomonads	very high	high	low	low	no	0	yes	no
A14, green.1	small green algae	high	high	high	high	no	low	some	no
A15, green.2	large green algae	low	low	high	high	no	low	no	no
A16, green.3	large green algae	low	low	high	high	no	0	yes	no

Conjugatophyceae (conjugate algae)

Conjugatophyceae were not included in the analysis because none of the species in the data set contributed more than 0.1 % to the total biomass during the study period.

Aggregation of the occurrence groups into functional groups

The cluster analysis in the preceding section suggests splitting phytoplankton into the functional groups A1 to A16 (see Table 4). As this number of groups is quite large, we looked for opportunities to aggregate using the properties discussed in the previous section (Table 5). The key properties that we believe are crucial for the behaviour of the group are printed in bold in the table. Properties are only given qualitatively (e.g., high and low), indicating typical ranges of values of the parameters for one group in comparison with ranges characterizing other groups.

We based our further aggregation on the observed occurrence patterns and the properties thought to be responsible for the patterns. In some cases, we could identify a common reason for different groups having a similar occurrence pattern, in other cases the causes were quite different. We aggregated those groups that had similar patterns and similar key properties. We also aggregate groups with some common properties but a different occurrence pattern.

As a first step, we created the most obvious groups based on commonality of all “important” properties ($k_{gro,max}$, K_I , K_P , edibility, motility, v_{sed}). This led to the 11 groups B1 to B11 (Table 6). In the following, we give a brief characterization of these groups.

B1. The first group “small flagellates” consists of the Cryptophyta group (*crypt.1*) as well as the two Chrysophyceae groups containing small species (*chrys.1* and *chrys.2*). All of these groups have the key properties of very high $k_{gro,max}$, high edibility and no sedimentation due to their motility. They also have all low values of K_P and K_I . Due to their very high $k_{gro,max}$ they occur in spring and summer in all lakes. The growth rate is so high that they also occur in summer despite their good edibility.

B2. The second group “small green algae” consists only of the group *green.1* that contains mainly small green algae (also some large). Like the first group, it is characterized by its high $k_{gro,max}$ and high edibility. However, in contrast to the first group it has high values of K_I and K_P . This group occurs in spring in Greifensee only.

B3. Group B3 “small diatoms” consists of small centric diatoms (*diat.1* and *diat.2*). Due to the properties high $k_{gro,max}$, high edibility, and low K_I it occurs in spring in all lakes.

B4. Group B4 “large diatoms” contains large colony-building diatoms (*diat.3* and *diat.4*). The properties medium $k_{gro,max}$, low edibility and low K_I and low K_P lead to occurrence in spring as well as in summer, sometimes even in winter.

B5. Group B5 “large green algae” consists of *green.2* and *green.3*. The properties low $k_{gro,max}$, low edibility and high K_I and K_P result in occurrence in summer in Lake Zürich and Greifensee.

B6. Group B6 “*Dinobryon*” consists only of *Dinobryon* sp. (*chrys.3*). It occurs in summer in all

Table 6. A hierarchy of functional groups.

A-groups	B-groups	C-groups	D-groups	E-groups	F-groups
A13, crypt.1	B1 “small flagellates”	C1 small flagellates	D1 small flagellates	E1 small	F1 small
A4, chrys.1					
A5, chrys.2	B2 “small green algae”	C2 small diatoms	D2 small diatoms	E2 small diatoms	
A14, green.1					
A7, diat.1	B3 “small diatoms”	C3 large diatoms	D3 large diatoms	E3 large diatoms	F2 large diatoms
A8, diat.2					
A9, diat.3	B4 “large diatoms”	C4 large green algae	D4 large	E4 large	F3 large
A10, diat.4					
A15, green.2	B5 “large green algae”	C5 Gymnod.	D5 blue green algae	E5 Pl. rub	F4 Pl. rub
A16, green.3					
A6, chrys.3	B6 “ <i>Dinobryon</i> ”	C6 Cer., Perid.	D6 Pl. rub	E6 Pl. rub	F6 Pl. rub
A11, dino.1	B7 “ <i>Gymnodinium</i> ”				
A12, dino.2	B8 “ <i>Ceratium, Peridinium</i> ”	C7 blue green algae	D7 blue green algae	E7 Pl. rub	F7 Pl. rub
A1, blue.1	B9 “blue green algae”				
A3, blue.3	B10 “ <i>Aphanizomenon flos-aquae</i> ”	C8 Pl. rub.	D8 Pl. rub	E8 Pl. rub	F8 Pl. rub
A2, blue.2	B11 “ <i>Planktothrix rubescens</i> ”				

lakes and has the properties medium $k_{gro,max}$, low edibility and low K_p

B7/B8. Groups B7 and B8 are, respectively, the groups *dino.1* called “*Gymnodinium*” with occurrence in spring in all lakes and *dino.2* called “*Ceratium, Peridinium*” with occurrence in summer in all lakes. Dinoflagellates have a special role and cannot be compared to the other groups because of their mixotrophy and their life cycle.

B9. Group B9 is called “blue-green algae” (*blue.1*). The main properties are medium $k_{gro,max}$, low edibility, and high K_1 and K_p . It occurs in summer in Lake Zürich and Greifensee.

B10. Group B10 is called “*Aphanizomenon flos-aquae*” and consists only of *Aphanizomenon flos-aquae* (*blue.3*). Key properties of this species are low $k_{gro,max}$, low K_1 , very low edibility and motility with gas vacuoles.

B11. Group B11 is called “*Planktothrix rubescens*” and consists only of *Planktothrix rubescens* (*blue.2*). *Planktothrix rubescens* occurs in the epilimnion during the summer and in winter in Lake Zürich. Key properties of this species are low $k_{gro,max}$, very low K_1 , very low edibility and motility with gas vacuoles.

Suggestions for further aggregation of the functional groups

As 11 groups may still be difficult to model, in the next step we further aggregate groups with similar properties. This led to the groups C1 to C8 shown in Table 6. This aggregation step required more compromises to be made. These groups have the most important key properties in common, however, there are differences in other (important) properties. The rationale behind this aggregation step are as follows. It is suggested to merge groups B1 and B2 to combine the small flagellates and small green algae together because of their common important properties of very high $k_{gro,max}$ and high edibility. There are large differences in K_1 and K_p , but we consider these properties less important for the occurrence pattern of the groups. We further suggest to merge groups B5 and B6 (large green algae and *Dinobryon* sp.) because they share the properties of low or medium growth rate and low edibility, although there are differences in light and phosphate requirements. Also the groups B9 and B10 are merged together. They have the common properties low or medium $k_{gro,max}$ and low edibility but differ in K_1 and K_p value. *Planktothrix rubescens* is kept as a

Table 7. Sizes and distances of the 6 groups at aggregation level D. See text for definitions of size, distance, and groups.

	size	D1.small.flag	D2.small.diat	D3.large.diat	D4.large	D5.blue.green	D6.Pl.rub
D1.small.flag	1.41	0.00					
D2.small.diat	1.17	0.49	0.00				
D3.large.diat	1.12	0.67	0.68	0.00			
D4.large	1.41	0.48	0.80	0.61	0.00		
D5.blue.green	1.28	0.73	1.10	1.01	0.75	0.00	
D6.Pl.rub	0.00	0.95	0.97	0.86	0.96	1.23	0.00

separate group because of its great importance and unique behavior in Lake Zürich. Suggestions for further aggregation steps are made in the columns D-, E-, and F-groups in Table 6. First, the dinoflagellates are grouped together with large green algae and Dinobryon (D-groups). In a second step, the blue green algae are grouped together with the large green algae, *Dinobryon* and dinoflagellates (E-groups). In a last step, the small flagellates and the small diatoms are grouped together because they share the important properties of high growth rate and high edibility (F-groups). This results in 4 groups, which is the highest suggested aggregation level.

Quantification of cluster sizes and distances

Table 7 summarizes the sizes and distances of the 6 clusters at aggregation level D given in Table 6. These are calculated based on the following metric: First, the distance between the occurrence patterns of two species i and j is defined as

$$d_{ij} = \sqrt{\frac{1}{n} \sum_k (w_{ik} - w_{jk})^2} \quad (1)$$

where w_{ik} is the smoothed and normalized value of the occurrence pattern at time k , and k runs through the days of the year. The distance between clusters is then calculated as the distance between their centres of mass, the size of a cluster as the maximum distance between species within the cluster. Table 7 shows that the groups D5 and D6 clearly separate from all of the other groups, whereas the distances between the groups D1 and D2 and between the groups D1 and D4 are significantly smaller. D1 and D2 both consist of small, fast growing algae and are, consequently merged at the next aggregation level (see Table 6). Despite the small distance between D1 and D4 they still have a different occurrence pattern and they have very different properties. Therefore, these groups are not merged despite their small distance.

Quantification of cluster sizes and distances allows us to compare our approach quantitatively (with respect to occurrence) to the purely taxonomic approach. The average cluster size and distance for

the 6 relevant taxonomic groups (Table 4) are 1.25 and 0.64, respectively. This improves for the aggregation level D, which consists of the same number of clusters to 1.06 and 0.89 respectively. This demonstrates that the clusters D represent the empirical occurrence pattern significantly better than the taxonomic groups. In addition, the properties are also much better represented. This is important for characterizing the groups in mechanistic models.

Succession of the functional groups

To give an overview of the occurrence of the functional groups described above (see Table 6), in this section we show the succession of the D-Groups for each lake for the years 1993 – 1996.

Walensee is dominated by diatoms (groups D2 and D3) and small flagellates (group D1) (Fig. 3). Small diatoms (group D2) occur in spring and autumn in most years. Large diatoms (group D3) usually also have a spring peak and stay the most important group throughout summer. Small flagellates (group D1) grow throughout the year. Also large species D4 regularly occur in summer. In Walensee they are dominated by chrysophytes (*Dinobryon sp.*) and dinoflagellates.

In Lake Zürich, more groups contribute significantly to total biomass than in Walensee (Fig. 3). Diatoms (groups D2 and D3) also have a large biomass contribution in most years and there is a pronounced spring peak with small diatoms (group D2). Large diatoms (group D3) also usually contribute to the spring peak and have a second peak in summer. Small flagellates (group D1) also make a large contribution to the biomass and grow throughout the year. *Planktothrix rubescens* (group D6) grows in the epilimnion each summer and forms a large biomass peak each winter.

Large species (group D4) can reach high biomass concentrations. In Lake Zürich they consist of dinoflagellates, large green algae and large chrysophytes (*Dinobryon sp.*). The biomass contributions of group D5 are comparably low.

In Greifensee there is again a completely different pattern (Fig. 3). Small flagellates (group D1) form a spring peak, disappear during the clear water stage

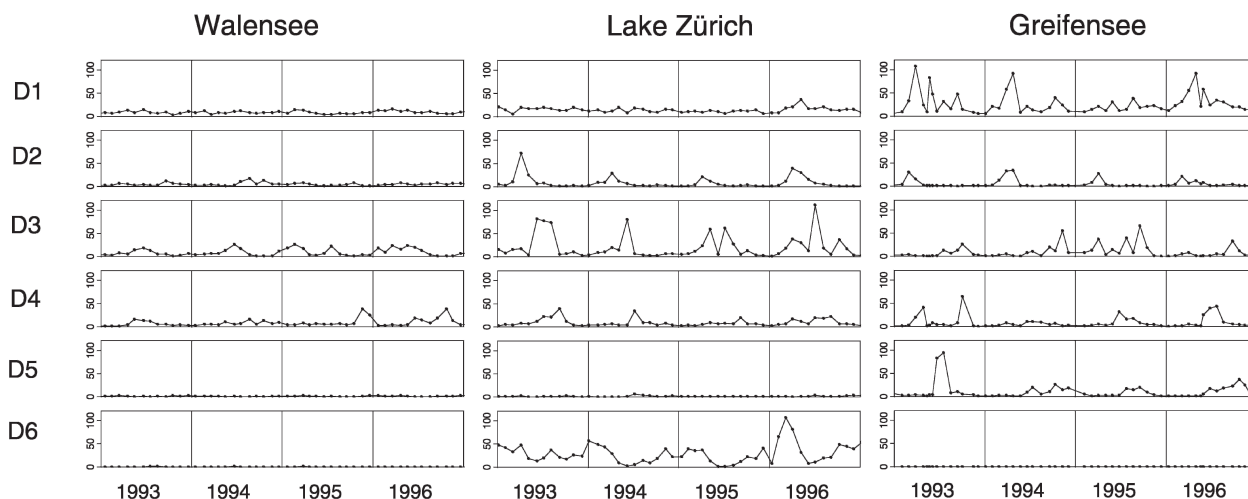


Figure 3. Time series of the biomass of the functional groups (D-Groups) in Walensee, Lake Zürich and Greifensee for the years 1993–1996. On the y-axis, the biomass is given in gWM/m^2

and form two or three peaks in summer. Small diatoms (group D2) contribute significantly to the spring peak only in some years. Large diatoms (group D3) have a summer peak in most years. In some years, if there is silica limitation during summer, large diatoms do not occur in Greifensee. Blue-green algae (group D5) form one or two high biomass peaks every summer; they are the most abundant species in some summers. Large algae (group D4) also grow each summer. In Greifensee this group is dominated by large green algae.

Discussion

We attempted to find a division of phytoplankton into functional groups that can be used to improve the representation of plankton assemblages in ecological lake models. A classification system for such a purpose should lead to groups which:

1. are different with respect to the most important properties leading to the occurrence pattern
2. are mutually exclusive (no overlap in species membership)
3. account for the major portion of the total biomass

Several approaches to dividing phytoplankton into functional groups have been suggested in the literature and used in ecological lake models (see sections “Introduction” and “Conceptual approaches of dividing phytoplankton into functional groups”). However, it is not easy to decide which approach is best for a particular water body under study. Additionally, not all approaches fulfil the above criteria. In all approaches, there is a certain variability of important

properties within the groups. It is our goal to find groups that minimize this variability of properties within the groups. Groups based on characteristic properties of the species seem promising. However, if only relatively simple (easily accessible) properties such as size, shape, or motility are used, the groups are well-defined but important properties that do not correlate with these easily accessible properties may be missed (criterion 1). This is the same problem faced by strictly taxonomic approaches. If, on the other hand, only physiological properties such as growth rate, nutrient and light requirements, are used, the behavioural patterns may be better defined, but it can be very difficult to assign less well-known species to the groups (criterion 2).

We propose a general method for identifying functional groups that combines empirical information of the occurrence of phytoplankton species in particular lakes with biological knowledge of the properties of these species. Species that respond similarly to environmental conditions might be expected to occur jointly at certain times of the year. In our approach, we identify such groups by grouping together species with similar occurrence patterns. This method is first applied within taxonomic groups. One problem of this approach is that species might have similar occurrence patterns for different reasons. This is why combining the data analysis with biological knowledge is important. In a later stage of the analysis, identified occurrence groups are aggregated across taxonomic boundaries based on the similarity of the key properties of species.

Application of the proposed procedure to data from three lakes of different trophic state in Switzerland started with the 6 taxonomic groups listed in the left column of Table 4 as step 1. Step 2 led to the

further division of these 6 taxonomic groups into 16 occurrence-related groups described in columns 2–4 of Table 4. Table 5 gives the property-based interpretation of these groups required in step 3 of the procedure. Finally, Table 6 suggests possible levels of aggregation to 11, 8, 6, 5 and 4 functional groups. The successional patterns of these groups, shown in figure 3 for the different lakes, demonstrate that our approach led to relatively clear (in view of the diversity of properties among species) response patterns of these functional groups. A comparison of the suggested approach with a purely taxonomic approach shows that the cluster distances increase by about 40 % and the cluster sizes decrease by about 15 %.

The functional groups found by our analysis are rather similar to those already suggested in the literature and used in previous modelling studies (König, 2006, Benndorf and Recknagel 1982, and references in Table 1). However, our approach adds an important component of empirical data analysis to the taxonomic, life strategy, and property-based foundations of previous classification systems. This will assist in deciding which functional group approach should be applied to a particular water body.

Our approach provides a rational method for combining the prior knowledge of earlier functional group approaches with the information contained in extensive available data collections. These features make the approach promising as a basis for both empirical limnology and mechanistic modelling of phytoplankton populations. As a next step, we implemented the functional groups identified in this study in the lake model BELAMO (**B**iogeochemical **e**cological **l**ake **m**odel) (Omlin et al., 2001; Mieleitner and Reichert, 2006) to test its suitability. The results are described by Mieleitner and Reichert (2007).

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References

- Anneville, O., S. Souissi, S. Gammeter and D. Straile, 2004. Seasonal and inter-annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri-alpine lakes over a period of 28 years. *Freshw. Biol.* **49**: 98 – 115.
- Benndorf, J. and F. Recknagel, 1982. Problems of application of the ecological model SALMO to lakes and reservoirs having various trophic state. *Ecol. Model.* **17**: 129 – 145.
- Bowen, J. D. and J. W. Hieronymus, 2003. A CE-QUAL-W2 model of Neuse Estuary for total maximum daily load development. *Journal of Water Resources Planning and Management-ASCE* **129**: 283 – 294.
- Bossard, P., S. Gammeter, C. Lehmann, F. Schanz, R. Bachofen, H. R. Bürgi, D. Steiner and U. Zimmermann, 2001. Limnological description of the Lakes Zürich, Lucerne and Cadagno. *Aquat. Sci.* **63**: 225 – 249.
- Butterwick, C., S. I. Heaney and J. F. Talling, 2005. Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. *Freshw. Biol.* **50**: 291 – 300.
- Cleveland, W. S., E. Grosse and M. S. Shyu, 1992. Local Regression Models. In: Chambers, J. M. and T. J. Hastie (ed.), *Statistical Models in S*. pp. 309 – 376.
- Cleveland, W. S. and S. J. Devlin, 1988. Locally-weighted regression: An approach to regression analysis by local fitting. *J. Am. Statist. Assoc.* **83**: 596 – 610.
- Cleveland, W. S. and E. Grosse, 1991. Computational Methods for Local Regression. *Statistics and Computing* **1**: 47 – 62.
- Elliott, J. A., A.E. Irish, C. S. Reynolds and P. Tett, 1999a. Sensitivity analysis of PROTECH, a new approach in phytoplankton modelling. *Hydrobiologia* **414**: 45 – 51.
- Elliott, J. A., C. S. Reynolds, A. E. Irish and P. Tett, 1999b. Exploring the potential of the PROTECH model to investigate phytoplankton community theory. *Hydrobiologia* **414**: 37 – 43.
- Elliott, J. A., A. E. Irish, C. S. Reynolds, and P. Tett, 2000. Modelling freshwater phytoplankton communities: an exercise in validation. *Ecol. Model.* **128**: 19 – 26.
- Frey, L. C. and E. F. Stoermer, 1980. Dinoflagellate phagotrophy in the upper great lakes. *Trans. Amer. Micros. Soc.* **99**: 439 – 444.
- Frisk, T., Ä. Bilaletdin, H. Kaipainen, O. Malve and M. Möls, 1999. Modelling phytoplankton dynamics of the eutrophic Lake Võrtsjõrv, Estonia. *Hydrobiologia* **414**: 59 – 69.
- Gammeter, S., R. Forster and U. Zimmermann, 1997. Limnologische Untersuchung des Zürichsees 1972 – 1996, Wasserversorgung Zürich, 62 pp.
- Gagnani, A., M. Scheffer and S. Rinaldi, 1999. Top-down control of cyanobacteria: A theoretical analysis. *Am. Nat.* **153**: 59 – 72.
- Grime, J. P., 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**: 1169 – 1194.
- Håkanson, L., 2004. Break-through in predictive modeling opens new possibilities for aquatic ecology and management – a review. *Hydrobiologia* **518**: 135 – 157.
- Håkanson, L. and V. V. Bouillon, 2003. A general dynamic model to predict biomass and production of phytoplankton in lakes. *Ecol. Model.* **165**: 285 – 301.
- Hamilton, D. P. and S. G. Schladow, 1997. Prediction of water quality in lakes and reservoirs. Part I – Model description. *Ecol. Model.* **96**: 91 – 110.
- Happay-Wood, C. M., 1988. Ecology of freshwater planktonic green algae. In: C. D. Sandgren (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*, Cambridge Press, Ambridge, pp 175 – 226.
- Hastie, T., R. Tibshirani and J. H. Friedman, 2001. *The Elements of Statistical Learning*, Springer, New York, 533pp.
- Heaney, S. I., J. W. G. Lund, H. M. Canter and K. Gray, 1988. Population dynamics of *Ceratium* spp. in three English lakes, 1945 – 1985. *Hydrobiologia* **161**: 133 – 148.
- Holm, P. N. and D. E. Armstrong, 1981. Role of nutrient limitation and controlling the populations of *Asterionella formosa* and

- Microcystis aeruginosa* in semicontinuous culture. *Limnol. Oceanogr.* **26**: 622 – 634.
- Irish, A. E., 1979. *Gymnodinium helveticum* Penard f. achroom Skuja a case of phagotrophy. *British Phycological Journal* **14**: 11 – 15.
- Jones, R. I. and V. Ilmavirta, 1988. Flagellates in freshwater ecosystems – concluding remarks. *Hydrobiologia* **161**: 271 – 274.
- Jorgensen, S. E., 1976. A eutrophication model for a lake. *Ecol. Model.* **2**: 147 – 165.
- Jorgensen, S. E., 1979. *Handbook of Environmental Data and Ecological Parameters*, International Society for Ecological Modelling, Copenhagen, 1162 pp.
- Kaufman, L. and P. J. Rousseeuw, 1990. *Finding Groups in Data: An Introduction to Cluster Analysis*. Wiley, New York, 342 pp.
- König, M., 2006. *Analyse funktioneller Typgruppen des Phytoplanktons: Integration von Modell- und Freilandarbeiten*, Dissertation, Technische Universität, Dresden.
- Klavness, D., 1988. Ecology of the cryptomonadina: a first review. In: C. D. Sandgren (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*, Cambridge Press, Cambridge, pp. 105 – 133.
- Krivtsov, V., D. Sigee, J. Corliss and E. Bellinger, 1999. Examination of the phytoplankton of Rostherne Mere using a simulation mathematical model. *Hydrobiologia* **414**: 71 – 76.
- Lewis, D. M., J. A. Elliott, M. F. Lambert and C. S. Reynolds, 2002. The simulation of an Australian reservoir using a phytoplankton community model: PROTECH. *Ecol. Model.* **150**: 107 – 116.
- MacArthur, R. and E. O. Wilson, 1967. *The Theory of Island Biogeography*, Princeton University Press, Princeton, 203 pp.
- Micheletti, S., F. Schanz and A. E. Walsby, 1998. The daily integral of photosynthesis by *Planktothrix rubescens* during summer stratification and autumnal mixing in Lake Zürich. *New Phytol.* **139**: 233 – 246.
- Mieleitner, J. and P. Reichert, 2006. Analysis of the transferability of a biogeochemical lake model to lakes of different trophic state. *Ecol. Model.* **194**: 49 – 61.
- Mieleitner, J. and P. Reichert, 2007. Modelling functional groups of phytoplankton in three lakes of different trophic state. *Ecol. Model.*, in press, doi:10.1016/j.ecolmodel.2007.09.010.
- Omlin, M., P. Reichert and R. Forster, 2001. Biogeochemical model of Lake Zürich: Model equations and results. *Ecol. Model.* **141**: 77 – 103.
- Paerl, H. W., 1988. Growth and reproductive strategies of freshwater blue-green algae (cyanobacteria). In: C. D. Sandgren (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*, Cambridge Press, Cambridge, pp. 261 – 315.
- Pollingher, U., H. R. Bürgi and H. Ambühl, 1993. The cysts of *Ceratium hirundinella*: Their dynamics and role within a eutrophic (Lake Sempach, Switzerland). *Aquat. Sci.* **55**: 10 – 18.
- Pollingher, U., 1988. Freshwater armored dinoflagellates: Growth, reproduction strategies and population dynamics. In: Sandgren, C.D. (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*. Cambridge Press, Cambridge, pp. 134 – 174.
- Reynolds, C. S., 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. *Holarctic Ecology* **3**: 141 – 159.
- Reynolds, C. S., 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton. In: C. D. Sandgren (ed.), *Growth and Reproductive Strategies of Freshwater Phytoplankton*, Cambridge University Press, Cambridge, pp. 388 – 433.
- Reynolds, C. S., 1997. *Vegetation Processes in the Pelagic: A Model for Ecosystem Theory*, Ecology Institute, Oldendorf/Luhe, 371 pp.
- Reynolds, C. S. and A. E. Irish, 1997. Modelling phytoplankton dynamics in lakes and reservoirs: the problem of in-situ growth rates. *Hydrobiologia* **349**: 5 – 17.
- Reynolds, C. S., A. E. Irish and J. A. Elliott, 2001. The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecol. Model.* **140**: 271 – 291.
- Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores and S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.* **24**: 417 – 428.
- Riley, M. J. and H. G. Stefan, 1988. MINLAKE: A dynamic lake water quality simulation model. *Ecol. Model.* **43**: 155 – 182.
- Roelke D. L., 2000. Copepod food-quality threshold as a mechanism influencing phytoplankton succession and accumulation of biomass, and secondary productivity: a modeling study with management implications. *Ecol. Model.* **134**: 245 – 274.
- Romero, J. R., M. R. Hipsey, J. P. Antenucci and D. Hamilton, 2004. *Computational Aquatic Ecosystem Dynamics Model: CAE-DYM v2, v2.1 Science Manual*, Centre for Water Research, University of Western Australia.
- Salomonsen, J. and J. J. Jensen, 1996. Use of a lake model to examine exergy response to changes in phytoplankton growth parameters and species composition. *Ecol. Model.* **87**: 41 – 49.
- Sandgren, C. D., 1988. The ecology of chrysophyte flagellates: their growth and perennation strategies as freshwater phytoplankton. In: C. D. Sandgren (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*. Cambridge Press, Cambridge, pp. 9 – 104.
- Schanz, F., 1985. Vertical light attenuation and phytoplankton development in Lake Zurich. *Limnol. Oceanogr.* **30**: 299 – 310.
- Struyf, A., M. Hubert and P. J. Rousseeuw, 1997. Integrating robust clustering techniques in S-PLUS. *Computational Statistics and Data Analysis* **26**: 17 – 37.
- Sommer, U., 1983. Nutrient competition between phytoplankton species in multispecies chemostat experiments. *Arch. Hydrobiol.* **96**: 399 – 416.
- Sommer, U., 1986. The periodicity of phytoplankton in Lake Constance (Bodensee) in comparison to other deep lakes of central Europe. *Hydrobiologia* **138**: 1 – 7.
- Sommer, U., Z. M. Gliwicz, W. Lampert and A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie* **106**: 433 – 471.
- Sommer, U., 1988. Growth and survival strategies of planktonic diatoms. In: C. D. Sandgren (ed.), *Growth and Reproduction Strategies of Freshwater Phytoplankton*. Cambridge Press, Cambridge, pp. 227 – 260.
- Sommer, U., 1989. The role of competition for resources in phytoplankton succession. In: U. Sommer (ed.), *Plankton Ecology: Succession in Plankton Communities*, Springer, Berlin, pp. 57 – 106.
- Tilman, D., S. S. Kilham and P. Kilham 1982. Phytoplankton ecology: the role of limiting nutrients. *Ann. Rev. Ecol. Syst.* **13**: 349 – 372.
- Tilman, D. and R.L. Kiesling, 1984. Freshwater algal ecology. Taxonomic trade-offs in the temperature dependence of nutrient competitive abilities. In: M. J. Klug and C.A. Reddy (eds.), *Current Perspectives in Microbial Ecology*, Amer. Soc. Microbiol., Washington, pp. 314 – 319.
- Uehlinger, U., 1980. *Untersuchungen zu Autoökologie der planktischen Blaualge Aphanizomenon flos-aquae*, Diss. ETH Zürich Nr. 6723, Zürich, 124 pp.
- Walsby, A. E., Z. Dubinsky, J. C. Kromkamp, C. Lehmann and F. Schanz, 2001. The effects of diel changes in photosynthetic coefficients and depth of *Planktothrix rubescens* on the daily integral of photosynthesis in Lake Zürich. *Aquat. Sci.* **63**: 326 – 349.
- Weithoff, G., 2003. The concepts of 'plant functional types' and 'functional diversity' in lake phytoplankton – a new understanding of phytoplankton ecology. *Freshw. Biol.* **48**: 1669 – 1675.
- Zimmermann, U., R. Forster, and H. Sontheimer, 1991. *Langzeitveränderung der Wasserqualität im Zürich-, Zürichober- und Walensee, Wasserversorgung Zürich, Zürich*, 89 pp.