

Convergence and divergence in organization of phytoplankton communities under various regimes of physical and biological control

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Abstract The hypothesis that physical constraints may be as important, if not more important, than biological ones in shaping the structure of phytoplankton assemblage was tested by analyzing long-term (11–29 years) phytoplankton series in eight lakes and nine sites located along a latitudinal gradient in the Northern hemisphere. Phytoplankton

biomass was used and similarity of assemblages in same months of the annual data sets was then calculated by subtracting the Bray–Curtis dissimilarity index from 1. The extent of biological and physical forcing was partly based on “expert evaluation”: the importance of four physical (light availability, temperature, conductivity, and sediment stirring up) and five biological variables (basic nutrients [SRP-, DIN-, SRSi-availability] as estimators of competition straight, importance of grazing, and importance of parasitism) was evaluated month by month by arbitrarily scaling from 1 to 5 the intensity of each variable and then summing them in the appropriate subgroup. Since the number of physical variables is less than that of the biological ones, the latter was rescaled to reach the same

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maximum attainable value of physical variables. The results showed an extremely high variability, making evident that each lake, although showing the same metabolic processes, behaves as an individual with regard to its phytoplankton structure. More generally, it was possible to highlight a largely more important role of physical constraints in shaping both biomass and composition of phytoplankton. This is especially true in winter. In addition, the results were compared to the outcomes of the PEG model, since a plasticity in the structure of phytoplankton much greater than that reported in this widely acknowledged model has been recorded in the data set used. This high variability found in this study in relation to physical constraints might also explain the different patterns of phytoplankton growth observed from Northern temperate to Mediterranean lakes as well as those occurring in shallow and deep lakes.

Keywords Phytoplankton biomass · Phytoplankton composition · Similarity · PEG model · Biological control · Ecosystem functioning

Introduction

Phytoplankton species are small (generally 10^{-2} – 10^{-7} m) and live short lives (10^4 – 10^7 s). As a consequence, except for some lakes in the tropics, many generations follow each other in a vegetation period (within a year) making the successional patterns highly dynamic.

While succession theories for terrestrial habitats date back to as early as the beginning of the last century (Clements, 1916; Gleason, 1917, 1926), analogous theories for phytoplankton were slow to develop. The highly dynamic behavior of phytoplankton assemblages in freshwater lakes puzzled phytoplankton ecologists for a long time.

The first general concept of plankton succession, the so-called Plankton Ecology Group (PEG) Model, was developed during the 1980s (Sommer et al., 1986). It was the first coherent verbal model that attributed changes in phytoplankton succession (separately for oligotrophic and eutrophic lakes) to environmental constraints. The latter were divided basically into two groups: physical and biological (especially grazing and competition for nutrients). Physical constraints involve low insolation (attributable to short days, low

incidence and mixed layer extinction), cold temperatures, and deep mixing: conditions that commonly prevail between autumn and spring in temperate regions. According to the PEG model, grazing (biological control) becomes of prime importance in breaking the spring bloom of phytoplankton and the spring grazer populations collapse rapidly because they overgraze their food supply. This scenario results in a clear-water phase (typically in May–July, depending on latitude) when neither physical nor biological (grazing) control on phytoplankton is strong; therefore, a second growth may start. During this period, competition for limiting nutrients (typically P and/or N) selects for those species that can obtain these resources with the highest efficiency (they may have a high affinity for a limiting nutrient, an enhanced capacity for storage, or they are able to exploit non-epilimnetic resources). Parallel, antipredation features (such as large size), and mechanisms for overcoming sinking loss (mucilaginous colonies, buoyancy regulation, and flagellar movement) gain increasing importance. As a consequence, by late summer, nutrient-exploitative, relatively large-sized phytoplankton (they have large cells, like *Ceratium*, or they form large, multicellular colonies, like *Microcystis*) may, if time allows, form equilibrium associations (Naselli-Flores et al., 2003). The autumnal erosion of the thermocline overcomes this competitive arena, again giving priority to physical control.

Studies investigating in detail the control exerted by physical constraints on phytoplankton were extensively performed by Colin Reynolds and date back to the early 1970s (Reynolds, 1972). Later, detailed considerations on how physical environment influences phytoplankton distribution and abundances were published by the same author (e.g., Reynolds, 1984 and literature cited therein, 1988, 1994, and 2006 for a complete literature overview). However, chemically driven explanations (e.g. nutrient ratios) of phytoplankton patterns unduly received much more attention by scientists. A detailed review of diversity of physical constraints on phytoplankton is beyond the aims of this paper. We used the PEG model as a conceptual basis of these analyses for its simplicity and wide acceptance.

There are hundreds of studies, mostly using examples from individual lakes that used the PEG model, which, in part, support its statements or else present exceptions or propose modifications. Especially, in

Mediterranean aquatic ecosystems, this “paradigm” rarely holds and several Mediterranean limnologists have attempted (and often inappropriately) to fit their data to the model (Alvarez-Cobelas et al., 2005).

During the past 25 years of research on phytoplankton ecology, many other features of development and structure of phytoplankton assemblage have been explored, such as the sensitivity of phytoplankton communities to physical disturbance (Padisák et al., 1993 and individual papers in the volume). Moreover, the definition of the functional group/assemblage concept (Reynolds et al., 2002; Padisák et al., 2009a), studies on the opportunities for development of natural equilibria/steady states (Naselli-Flores et al., 2003; Becker et al., 2008), the importance of phenotypical variability, and the adaptive value of morphology in phytoplankton ecology (Naselli-Flores et al., 2007), have each been pursued. In the meantime, our knowledge of physiological ecology of phytoplankton has significantly increased (Raven and Maberly, 2009 and many other contributions that have not been summarized yet).

The central ecological topic of the 15th IAP workshop held in Israel, 2008, was the assessment of the importance of physical constraints on phytoplankton in general, with reference not only to biomass but also to assemblage structure. In this paper, we analyze both phytoplankton biomass and assemblage structure in relation to both physical and biological control mechanisms using PEG predictions and statements as a starting point. It must be mentioned that considerable knowledge accumulated on mechanisms how physical properties influence species selection and assemblage structure of phytoplankton and a number of case studies describe the major mechanisms (Reynolds, 2006). It is not the aim of this paper to review these works.

For analyzing both phytoplankton biomass and assemblage structure in relation to both physical and biological control mechanisms, we collected long-term phytoplankton data sets from lakes of variable origin, morphometry, geographical location, and trophic state. All the data sets fulfilled the following criteria:

- (i) The long-term study must cover at least 10 years.
- (ii) Sampling frequency must be monthly, at minimum, with no systematic gaps in the winter months.

- (iii) The phytoplankton data should be of the highest possible taxonomic resolution (taking limitations of the inverted microscope method into consideration) with identifications verified by an experienced phytoplankton ecologist.
- (iv) Background information on physical, chemical (nutrients), and other biological (e.g., grazing and parasitism) factors must be available and adequate to satisfy independent expert judgement.

In this article, the hypothesis that physical constraints may be as important, if not more important, than biological ones in shaping the structure of phytoplankton assemblage is tested. Phytoplankton biomass and assemblage structure development is described in relation to physical/biological control factors using data from eight very different lakes. Our main aim is to explore how much and under which conditions quantitative characteristics (biomass) and structural properties of phytoplankton are influenced by physical versus biological constraints.

Materials and methods

Description of sites and data used

On the basis of available long-term phytoplankton surveys (covering between 11 and 29 years) that satisfy the criteria listed in the introduction, eight lakes were selected along a North–South latitudinal gradient. Among these, three (Stechlin, Mondsee, and Kinneret) are deep, four are shallow (Vörtsjärv, Alte Donau, Neusiedlersee, and Balaton), and one is a Mediterranean reservoir (Arancio), alternating with seasonal abstraction between deep and shallow phases. With reference to trophic state, these lakes cover almost the entire trophic spectrum from oligotrophy (Stechlin) to hypereutrophy (Arancio). A short description of the studied sites is reported here.

Mondsee (14.2 km²) is a deep (z_{mean} : 36.0 m; z_{max} : 68.3 m), alpine lake located at 481 m a.s.l. and 47°50'N in the “Salzkammergut” lake district of Austria. As many other lakes in the world, Mondsee underwent cultural eutrophication in the 1970s but, with strict control, its status has since improved considerably. At present, the lake can be classified as oligo-mesotrophic. The period that is covered in this analysis comprises 24 years (1982–2005). Sampling

depths varied somewhat during the investigation period. Beginning from 1987, a rigorous protocol was adopted with intervals every 3 m from the surface to 20 m and wider spacing further down. In addition, an integrated sample of the top 20 m was taken at all occasions (Dokulil & Teubner, 2003a).

Lake Stechlin is a small (4.2 km²), deep (z_{mean} : 23.3 m; z_{max} : 69.5 m) lake at 59.9 m a.s.l. and 53°N latitude in Brandenburg, Germany. This glacial lake is originally oligotrophic and served as part of the cooling water supply network of a nuclear energy power plant. This use affected the pattern of stratification in the lake, with intermittent phases of relatively diatom abundance, but without impact on the trophic state of the lake (Casper, 1985). The nuclear power plant was closed in 1991, after which the pattern of stratification reverted to a more familiar seasonal variability (Koschel & Adam, 2003). Phytoplankton samples were taken at the deepest site of the lake: subsamples of water collected at 5-m intervals, from the surface to 25 m, were combined in a single integrated sample for counting (for further details, see Padisák et al. (2003a) and Salmaso & Padisák (2007). The period covered is 13 years (1994–2006), during which the trophic status of the lake varied within the oligo/oligo-mesotrophic range.

Lake Kinneret, northern Israel, is a meso-eutrophic, warm monomictic lake, stratified from April to December (Serruya, 1978), in the Syrian-African Rift Valley, at 32°50'N latitude and 210 m below sea level. At full capacity, the lake covers 170 km², contains $4,300 \times 10^6$ m³, and has a maximum depth of 43 m and a mean depth of 25 m. It experiences a Mediterranean climatic alternation between cold, wet winters and hot, dry summers. This lake provides ca. 50% of Israel's drinking water. As such, it has been subject to intensive routine monitoring since 1969, yielding a comprehensive series of publications (Hambricht & Hershcovitch, 1998). In the past, Lake Kinneret was famous for its spring blooms of the thecate dinoflagellate *Peridinium gatunense* and its diverse, low-biomass summer assemblages of nanoplankton, in a sequence repeated approximately each year (Pollinger, 1986). However, since the mid-1990s, this stable seasonal pattern has altered: N₂-fixing cyanobacteria established in the lake and have dominated the summer biomass ever since. In eight of the years since 1996, *Peridinium gatunense* blooms failed to develop (Zohary, 2004). The 13-year period

covered in the present analysis, 1994–2006, is wholly within the recent phase of reduced ecosystem stability. Phytoplankton samples were collected weekly from 13 depths at the deepest part of the lake; depth-weighted averages for each sampling date have been used here.

Lake Arancio is a hypereutrophic Mediterranean reservoir located in Sicily, Italy, at 172 m a.s.l. and 37°N latitude. It was created in 1951 by damming a temporary stream to retain water for irrigation purposes (Barone & Naselli-Flores, 1994). Mediterranean climate variability and summer usage of stored water strongly influence its morphological features and cause wide water level fluctuations. As a result, lake volume (max: 30×10^6 m³) and surface area (max: 3.0 km²), as well as z_{mean} (max: 10 m) and z_{max} (max: 28 m) may be reduced by 90% of their maximum values by the end of the irrigation period (Naselli-Flores, 2003). Moreover, the accumulation of water during winter, not balanced by any outflow, has been promoting a progressive increase of its internal loading. Dewatering during summer, not balanced by any inflow, generally causes the breaking of the thermocline at the end of July. In the rest of summer, the lake shows an atelomictic behavior (Naselli-Flores & Barone, 2005), which contributes to nutrient release from the sediment and supports very high phytoplankton biomass in summer (Naselli-Flores & Barone, 2007). The trophic state of the reservoir progressively increased during the study period. As a consequence, phytoplankton assemblage composition shifted from green—(*Closterium aciculare*, *Pediastrum* spp.) to blue-green (*Microcystis* spp.) dominance. Phytoplankton samples were obtained by mixing three samples collected from depths corresponding to 100, 50, and 1% of the surface irradiance. Data used in this analysis cover a period of 13 years (1991–2003).

Lake Võrtsjärv is a large (surface area 270 km²), shallow (z_{mean} 2.8 m; z_{max} 6 m), polymictic lake at 32.2–35.3 m a.s.l. and 58°N latitude in Estonia. The strong, climatically driven fluctuation of the water level, with a maximum amplitude of 3.3 m is one of the major factors shaping the lake ecosystem, changing the vulnerability of the sediments to resuspension and influencing the light conditions in the water column. The lake is typically ice-covered from mid-November until mid-April and the water temperature reaches its maximum in July (Nõges

et al., 2008). Heavy agricultural nutrient loading in the 1970s and 1980s turned the lake hypertrophic (Nöges et al., 2007) with *Limnothrix redekei* and *L. planktonica* taking over from the previously dominant *Planktolyngbya limnetica*. The subsequent significant load reduction has not, however, brought expected changes in the phytoplankton community where the stable dominance of the shade tolerant *Limnothrix* species continues (Nöges & Nöges, 2006). Phytoplankton data for this analysis cover a period of 29 years (1979–2007). Samples were collected with Ruttner sampler from the deepest point of the lake either from the uppermost 0.5 m or integrated over the water column (since 1995).

Neusiedlersee is located at 115 m a.s.l. on the Austrian/Hungarian border in the Danube valley, which separates the Alps from the Carpathian mountains. Because of its location, size (300 km²), and shallowness (z_{mean} : 1.3 m; z_{max} : 1.8 m), the lake is always exposed to stirring-up effect of winds that result in an almost continuous high turbidity caused by resuspension of inorganic sediments. The lake received the highest nutrient load in the 1970s that, however, did not result in substantial change in the trophic state. Phytoplankton dynamics are largely driven by periodic resuspensions and shade tolerant, meroplanktonic species, especially diatoms (*Fragilaria construens*, *Surirella peisonis*, *Campylodiscus clypeus*) are prevalent all over the year (Padisák & Dokulil, 1994). Another stress factor is the high mineral content of the lake (2000–3500 $\mu\text{S cm}^{-1}$) which, combined with harsh light conditions, results in rather species-poor phytoplankton assemblages. Phytoplankton samples were taken from the surface 0.5 m and data cover a period of 26 years (1968–1993).

Lake Balaton is the largest (surface area 593 km²) shallow (z_{mean} 3.14 m; z_{max} 11 m), polymictic lake at 46–47°N latitude, 104.4 m a.s.l. in Hungary. The originally mesotrophic lake underwent a rapid eutrophication during the 1960–1980s, as a result of which hypertrophic conditions developed in the western part of the lake (impacted most by external P load) while the eastern part reached eutrophic conditions. Sporadic *Cylindrospermopsis raciborskii* blooms (1982, 1992, 1994) rendered the lake classification to be hypertrophic but, in other years, the west–east trophic gradient was more apparent (Padisák & Reynolds, 1998; Hajnal & Padisák, 2008). Restoration of the lake started in 1983, as a result of which, no algal

blooms occurred after 1995, the western part returning to a eutrophic state and the eastern reverting to a mesotrophic condition (Istvánovics et al., 2007). Phytoplankton samples used in this study were taken with a water column sampler so data represent the whole water column. The period that is covered in this analysis covers the 13 years (1994–2006) during which the lake was recovering from the hyper/eutrophic state to eu/mesotrophic.

Alte Donau is a small (1.58 km²), shallow (z_{mean} 2.33 m; z_{max} 6.8 m), urban seepage lake located at 157 m a.s.l. in Vienna downtown and created by straightening the River Danube course and isolating the old river bed. In the past, the lake has been densely covered by stonewort (Characeae) and other submerged macrophytes (Löffler, 1988). More recently, it has undergone cultural eutrophication and shifted from a macrophyte-dominated lake to a turbid, cyanobacteria-dominated one (Dokulil & Mayer, 1996). Following a period of oligotrophication in a response to restoration measures, macrophyte cover has been re-established and phytoplankton biomass significantly reduced (Dokulil & Teubner, 2003b). Phytoplankton samples used in this study were taken with a water column sampler and the period covered comprises 11 years (1995–2005).

Phytoplankton data sets, the number of samples involved, the number of individual species-specific records, and the interval of each study period are given in Table 1.

Phytoplankton methods and similarity calculations

Phytoplankton samples were fixed with Lugol's solution and counting was performed with inverted microscopes following the method outlined by Lund et al. (1958). The altogether 81,883 individual phytoplankton biomass data were organized into a database, ALMOL, which was developed on the same basis of the existing ALMOBAL database (Hajnal & Padisák, 2008). Sampling frequency in the studied lakes varied between 1 and 4 weeks. If sampling was more frequent than monthly, species-specific monthly averages were calculated. In an earlier study, Padisák et al. (2009b) showed that pooling data of species, each having a biomass share <10%, does not change similarity patterns. Therefore, in each case and each month, species having a biomass of <10% were

Table 1 The data sets used for the analysis

Lake	Number of samples	Number of individual records	Average species number per sample	Period covered	Number of plankton years
Mondsee	566	13477	24	1982–2005	24
Stechlin	416	15895	38	1994–2006	13
Kinneret	338	11605	34	1994–2006	13
Arancio	157	939	6	1990–2002	13
Vörtsjärv	521	13207	25	1979–2007	29
Neusiedlersee	132	1534	12	1968–1993	26
Balaton	550	16538	30	1994–2006	13
Alte Donau	238	8688	37	1995–1005	11

pooled into a category “others”, thus compacting the data set.

Similarity of phytoplankton was estimated by comparing the corresponding abundances of the species x in the month y for each year of the survey in each of the lakes. The similarity index used for this calculation was obtained by subtracting the Bray–Curtis dissimilarity index from 1. This index reflects the compositional similarity of communities, as a relative proximity of point pairs in a coordinate system. On the basis of species-specific monthly biomass estimates, the similarity semi-matrices were calculated with SynTax 2000 software (Podani, 1988). The data in these matrices were used for calculation of the arithmetic averages and standard deviations (SD). The calculation method of the monthly similarity averages and standard deviations shown in Fig. 2 is detailed in Appendix (Annex 1—Supplementary Material). Co-variance of biological/physical drivers with phytoplankton biomass and compositional similarity was estimated using the simple linear correlation function.

Physical and biological constraints evaluation

The impact exerted on phytoplankton growth by five physical- and five biological-driven constraints was evaluated month by month based partly on measured values (temperature, nutrients, and conductivity) and partly on “expert judgements”. The physical constraints considered included light availability, conductivity, mixing regime (only for stratifying lakes: i.e. Stechlin, Mondsee, and Kinneret), sediment stirring up (only for shallow lakes: Balaton, Neusiedlersee, Vörtsjärv, and Alte Donau), and temperature.

Biological constraints were nutrient (SRP, total inorganic nitrogen and silica availability) concentrations in the euphotic or mixing zone, and the importance of grazing and parasitism pressure. Nutrients were considered as biological factors for two reasons:

- (i) Competition for limiting resource is one of the major interspecific interaction that drives phytoplankton assemblage changes. It can be directly judged by uptake affinity of different species (see some data in Padisák, 2003) or from outcomes of chemostat experiments (e.g. Sommer, 1985). Field techniques to estimate resource competition have not been developed yet. Moreover, uptake affinity data are known only for a limited set of species. Expert judgement in this case would have been done only on basis of nutrient availability therefore we found it reasonable to use nutrient concentration directly, as measure of competition straight.
- (ii) Introduction of a background variable called “chemical constraints” would have reduced biological ones to grazing and parasitism (both entirely based on expert judgement). Additionally chemical background acts on very different ways: high ionic content (high conductivity) reduces species number and is rather a stress factor like most physical constraints are, while nutrients (especially N and P) are resources to compete for and therefore can be considered biological constraints.

The importance of each variable in each lake was evaluated by arbitrary numerical values spanning from one to five as described in Table 2. Only for Lake Arancio, due to its peculiar hydrological

Table 2 List of the different physical- (upper part) and biological-driven constraints (lower part) to phytoplankton growth and of their score-related attributes

Variable/score	1	2	3	4	5
Physical					
Light availability	Excellent	Good	Medium	Poor	Very scarce
Conductivity ($\mu\text{S cm}^{-1}$)	0–700	701–1,200	1,201–1,700	1,701–2,400	>2,400
Deep mixing	Stratified	–	Stratifying/destratifying or under ice	–	Fully mixed
Stirred up sediments	Rarely stirred up sediments	Seldom stirred up sediments	Frequently stirred up sediments	Often stirred up sediments	Always stirred up sediments
Temperature ($^{\circ}\text{C}$)	>20	15–20	10–15	5–10	<5
Biological					
SRP ($\mu\text{g l}^{-1}$)	>10	7–10	5–7	3–5	Below molibdenate method detection
TIN ($\mu\text{g l}^{-1}$)	>100	70–100	50–70	30–50	<30
SRSi ($\mu\text{g l}^{-1}$)	>1000	500–1000	400–500	300–400	<300
Grazing	Very important	Important	Medium	Might be of some importance	Unimportant
Parasitism	Very important	Important	Medium	Might be of some importance	Unimportant

The *dashed line* separates the two groups

regime, both mixing regime and sediment stirring up were contemporarily considered, and the score was attributed averaging the values of these two variables. The monthly importance of the two sets of forcing in each lake was then calculated by summing the single scores. Since the maximum theoretical attainable value for physical-driven forcing is in this way 20 and that of biological one is 25, the latter values were standardized to 20 by multiplying the original value by 0.8 to make them immediately comparable to physical-driven constraints. Detailed calculations are given in Appendix (Annex 2—Supplementary Material).

Results

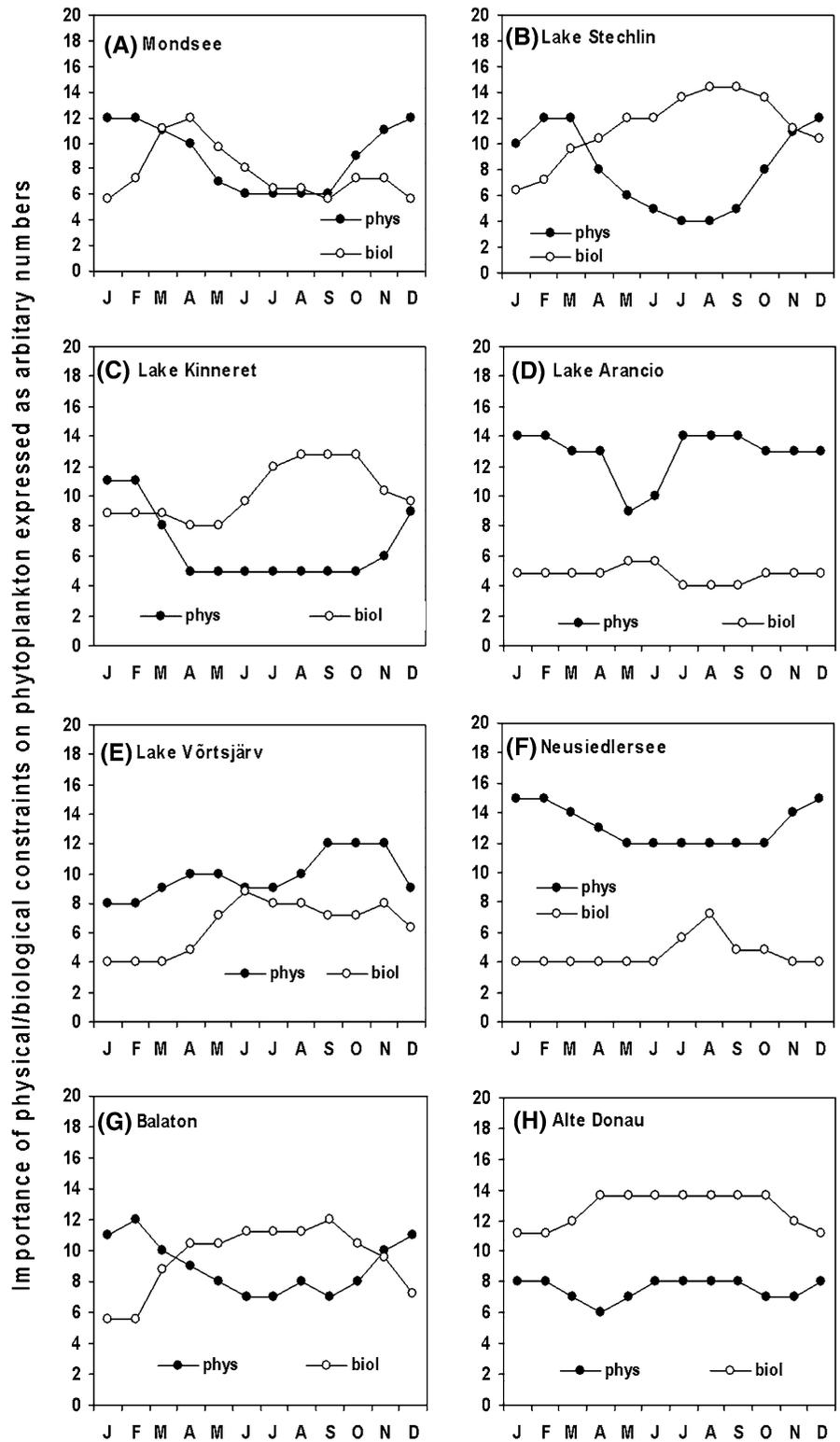
Figure 1 shows the extent to which physical- and biological-driven constraints affect phytoplankton growth month by month in the eight studied lakes. Similar patterns are shown in Lake Stechlin, Lake Balaton, and Lake Kinneret. In these environments, phytoplankton mainly depends on nutrients availability, grazing and parasitism pressure throughout the

year, but in winter physical forcing (deep mixing and/or low temperature) appears to be more important. A similar, but less pronounced pattern occurs in Mondsee. The lower impact of biological control on phytoplankton growth is in this case due to the weak grazing pressure occurring in summer.

Conversely, in both Lake Arancio and Neusiedlersee, physically driven constraints (light availability and sediment stirring up) are permanently dominant over biological-driven ones in determining phytoplankton growth. Even in Lake Vörtsjärv, physically driven constraints are generally more important. However, biologically driven influences equal those exerted by physical constraints in early summer in Lake Vörtsjärv, when nitrogen limitation occurs. Physically driven constraints very quickly dominate again in this lake, where the strong reduction in water level during summer enhances sediment stirring up.

Alte Donau represents the only case where biologically driven constraints to phytoplankton growth are permanently more important than those caused by physical forcing. This is mainly due to the severe nutrient limitation experienced by phytoplankton throughout the year.

Fig. 1 Estimated annual trends of physical and biological constraints in the studied lakes



Two main patterns in the annual trend of phytoplankton biomass (Fig. 2) can be recognized in the studied lakes: the more frequent, the unimodal distribution, characterizes Mondsee, Balaton, Vörtsjärv, Stechlin, and Kinneret. The annual peak occurs in August/September in the first three of these lakes, but in Kinneret and in Stechlin, the maximum occurs in spring. The absolute values of the various biomass peaks well reflect the different trophic states of the individual lakes, whereas the lower values are more or less comparable and are below $1,000 \mu\text{g l}^{-1}$ except in Kinneret, where higher winter temperature can still sustain biomass accumulation.

A bimodal pattern, even though characterized by high standard deviation, describes the biomass trends in Lake Arancio, Neusiedlersee and Alte Donau, even though the first of these draws on absolute values that are two orders of magnitude higher than the others.

With regard to similarity, Lake Arancio, constantly shows the lowest values (<0.2) recorded among the studied lakes, whereas Alte Donau the highest (>0.7). These two lakes represent extremes of the probability of phytoplankton species recurrence in successive years.

The mesotrophic part of Lake Balaton and the lakes Kinneret, Vörtsjärv and Neusiedlersee show comparable values of similarity, with a minimum generally occurring in early spring. All these lakes exhibit a rather high variability in the species composition of their phytoplankton with values ranging from 0.2 to 0.4.

In contrast, the higher values for the eutrophic part of Balaton, for Lake Stechlin and Mondsee (0.5–0.6) testify a relatively greater persistence of species through consecutive samplings.

Discussion

Physical versus biological control on phytoplankton biomass accumulation

The original PEG model (Sommer et al., 1986) handled physical and biological (nutrient competition and grazing) constraints in an entirely qualitative way. In this article, we tried to quantify their relevance. As a starting point, their importance was set as equal (for this reason, the sum of biological-variable scores was diminished from their original level to $4/5$ of the sum).

In this way, physical and biological constraints were given equal numerical importance, without necessarily supposing that they are, in reality, equally weighted.

Analyses on importance of physical versus biological background resulted in quite different patterns and only few of them correspond to the PEG model. Actually, the assumption that biologically driven constraints start influencing phytoplankton growth when a physical constraint (e.g., temperature) weakens is upheld only in Lake Stechlin, Lake Kinneret, and Lake Balaton. Mondsee and Lake Vörtsjärv less clearly and only marginally follow what is forecasted in the PEG model. In the Estonian lake, this is clearly attributable to its shallowness, to its phosphorus richness, and to the constant impact exerted by sediment-derived turbidity. With regard to Mondsee, the effect is more subtle and depends on the specific composition of its phytoplankton as discussed later.

In Alte Donau, where water income is regulated according to technical guidelines, no alteration between physical and biological control over biomass accumulation could be detected. In this lake, phytoplankton growth is permanently governed by biological constraints as represented either by nutrients or light limitation imposed by the submerged macrophytes. Moreover, these plants are responsible for the very low phosphorus availability in this lake.

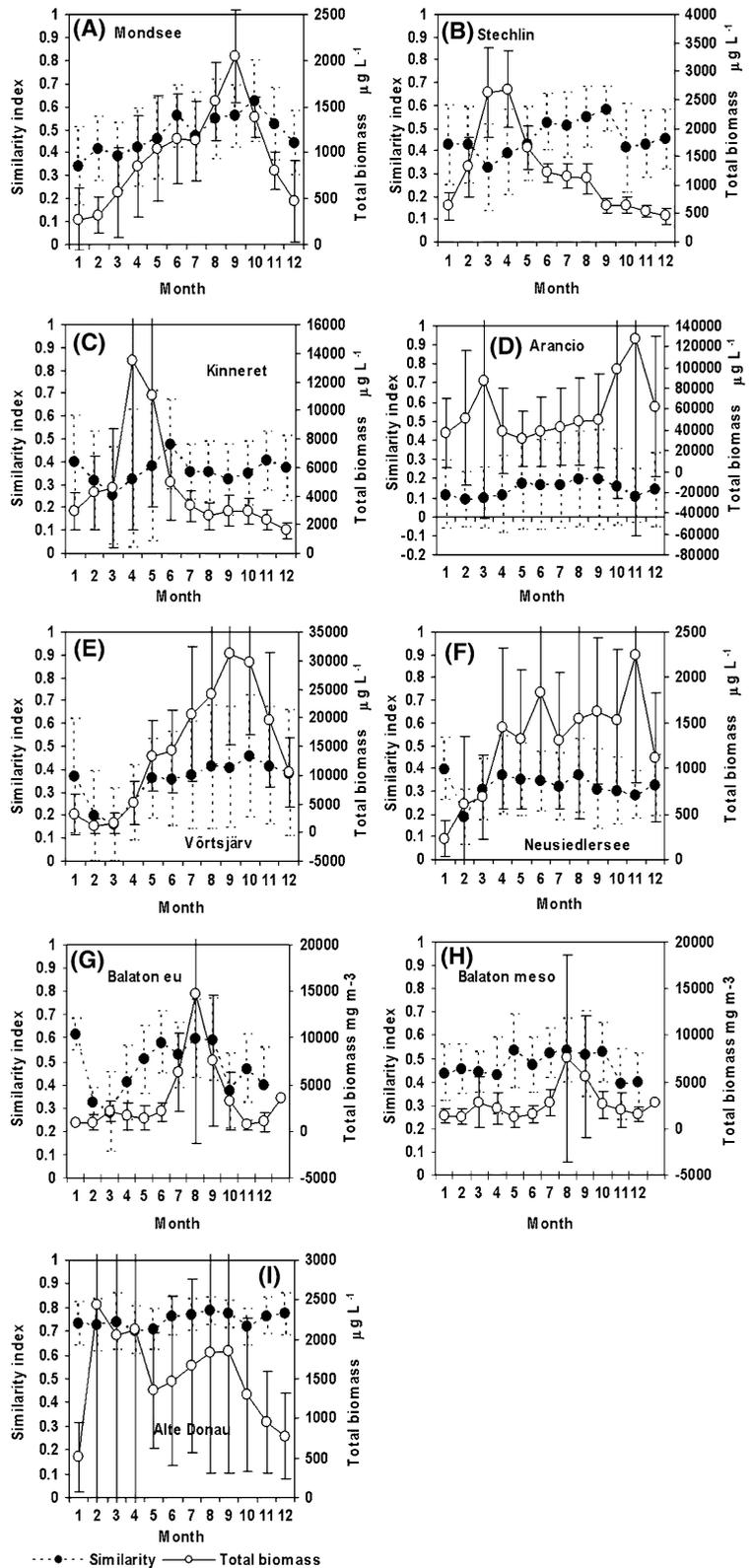
The two remaining lakes (Arancio and Neusiedlersee) represent “special cases” where no nutrient limitation occurs and light availability is the only limit to phytoplankton biomass accumulation. In both these lakes, the impact exerted by the physical constraints is strong enough to completely override any biological control upon phytoplankton growth.

Biomass responses

The primary aim of this paper was to analyze how, and to what extent, phytoplankton long-term data from eight lakes and from nine sites conform to the provisions of the PEG model.

According to the PEG model, the development of annual biomass is unimodal with spring maximum in the oligotrophic lakes and bimodal in eutrophic ones. As shown in the results, only Lake Stechlin and Lake Kinneret show a spring-unimodal pattern, one of them is oligotrophic the other one eutrophic. Three lakes showed a summer-unimodal pattern: the deep mesotrophic Mondsee and the large shallow lakes

Fig. 2 Annual trends of total phytoplankton wet weight biomass and compositional similarity in the studied lakes and sites. Vertical lines indicate SD



Balaton (both meso and eutrophic sites) and Vörtsjärv (eutrophic). The bimodal pattern was found in three very different lakes (Arancio, Neusiedlersee and Alte Donau), characterized by totally different standing crops but all experiencing a strong light limitation due to different causes: in Lake Arancio self-shading of phytoplankton occurs, whereas in Neusiedlersee the high amounts of suspended inorganic material severely limits light availability. In the Alte Donau light penetration is diminished by the plant (macrophyte) cover.

The different patterns observed can be explained only considering the entire scenario, comprising latitudinal/altitudinal effects, stratification patterns, external/internal nutrient load, biomass accumulation periods, and species composition, but the trophic status is uncoupled from the uni- or bimodal pattern.

The similarity observed in the biomass trends in Lake Stechlin and in Lake Kinneret is a good example of different causes for mutually similar output patterns. Apart from the spring dominance of *Peridinium gatunense* instead of some diatom species, Lake Kinneret follows nicely the PEG provision for the spring patterns: after the escape from deep mixing (physical control) and with sufficient nutrients coming from the catchment, an intense spring bloom occurs. The second peak expected by the PEG model in late summer does not occur in Lake Kinneret because of the strong stratification and lack of significant external water and nutrient supply from its Mediterranean catchment, where there is no substantial rainfall in summer, leading to nutrient depletion of the epilimnion. As a result, summer-fall standing stocks are relatively low (Zohary, 2004). Lake Stechlin is strikingly different: nutrients are always below limiting levels except for a short period after the complete autumnal over-turn (November). Therefore, in winter (December–February) growth of shade adapted species (mainly diatoms) occurs. In the absence of grazers, the biomass accumulates and exhibits a maximum before the onset of the stratification. As diatoms are heavy and need deep mixing for remaining in suspension, they suddenly sink to the hypolimnion (Padisák et al., 2003a, b). Thereafter, biomass remains at very low levels due to biological constraints, as predicted by the PEG model.

The eutrophic, shallow Lake Vörtsjärv, the mesotrophic, deep Mondsee, and both the eutrophic and

mesotrophic sites of the shallow Lake Balaton show similar patterns of phytoplankton biomass. Even though we discuss biomass patterns here, it is impossible to disregard species composition in the case of Mondsee. A unique feature in this data set is the perennial occurrence of *Planktothrix rubescens* in this lake (Dokulil & Skolaut, 1986; Dokulil & Teubner, 2003a). The species forms metalimnetic maxima in the stratified period and is evenly suspended during the isothermal period when it is capable of luxury uptake of nutrients, while other species remain nutrient limited in spring either before or after the onset of thermal stratification. Thus, in terms of biomass, the spring peak of phytoplankton diatoms is less pronounced in Mondsee in years with significant winter growth of *P. rubescens* (Dokulil, 1987, 1991). A similar process took place in Lake Stechlin in the winter of 1997/1998 (Padisák et al., 2003c) when winter development of a *P. rubescens* population prevented occurrence of the spring diatom peak. In spring, Mondsee is fed by cold waters coming from snow melt. Later in the year, calcite precipitation removes considerable amounts of inorganic phosphorus from the epilimnion (Dittrich & Koschel, 2002). As a result, biomass is only slowly increasing during summer with a peak at the end of stratification period (Dokulil & Teubner, 2005).

In shallow lakes, a spring maximum of phytoplankton growth is often missing. The biomass pattern observed in Lake Balaton is clearly due to internal phosphorus loading from the sediments (Honti et al., 2007) in summer. As phosphorus is never a limiting resource in Lake Vörtsjärv but nitrogen periodically is (Nöges et al., 2008), the continuous increase of phytoplankton biomass between April and September is due to several causes: one is the fast turnover of nutrients and their additional supply from the catchment throughout the entire vegetation period, the other is the gradual development of slow-growing, non-grazeable cyanobacteria that accumulate in the water column (Agasild et al., 2007). Biomass accumulation in this lake is further enhanced by water level decrease during summer, which contributes, through various mechanisms, to the increase of algal biomass (Nöges & Nöges, 1999).

The bimodal patterns experienced by the three studied lakes are due to different reasons: Lake Arancio spring peak is coincident with the onset of

stratification. Due to its location at low-latitude, temperature inhibits growth just for a short period (December–January). Later, biomass starts accumulating again and external load promotes the spring bloom. Then, light availability rapidly decreases and biomass accumulation slows down. The use of water for irrigation decreases the water level till the breaking of the thermocline in mid-summer when atelomictic behavior makes nutrients available and sustains a slow growth throughout summer. The second peak occurs when the lake volume reaches its annual minimum as a consequence of biomass concentration and full circulation events (Naselli-Flores, 2003; Naselli-Flores & Barone, 2003, 2005, 2007). In Neusiedlersee, external load and higher solar radiation also promote the first peak. Due to the high inorganic turbidity, however, light is always poorly available, growth is slow, and biomass reaches its peak only in early summer. The reduced summer water income, coupled with the higher evaporation, contributes to a significant increase in conductivity. Only a few entirely planktonic species (e.g. *Chaetoceros muelleri*) can cope with this increase in conductivity; other species prevail but at lower doubling rates and total biomass is thus reduced. Income of freshwater in autumn decreases conductivity and again promotes biomass accumulation. In Alte Donau, total phytoplankton biomass is highly dependent on macrophyte growth and its shading and nutrient competition effects. The spring bloom occurs in February, before the establishment of a macrophyte canopy. After the period of maximum plant growth (May), phytoplankton slowly start increasing again and reach a second peak when macrophytes are declining or removed by management practices. Thus, three different mechanisms can be invoked to explain the three biomodal patterns: self-shading and mixing pattern in Lake Arancio, conductivity and light availability in Neusiedlersee, and the annual growth/decline of submerged macrophyte vegetation in Alte Donau.

Compositional responses

In all the lakes studied, the highest similarity values were recorded in late summer, whereas the lowest ones in winter. According to the PEG model, phytoplankton communities undergo significant changes during particular years. During the seasonal

succession of phytoplankton, the competitive arena is changing and dozens of species and generations of individual species are involved.

Late summer assemblages integrate the preceding successional events (including onset of stratification and disturbances) and are likely to be determined by the competitive arena that any given lake type offers (Padisák et al., 2006). Individual lake morphologies together with recurrent seasonal cycles and combinations of the main environmental variables, both physical and biological, provide recurrent competitive arenas that allow the “best adapted” species to dominate repetitively in this period of the seasonal succession.

Conversely, in winter, there are several explanations for the high species variability. Individual stress-tolerance of the different species adapted to winter conditions might be the major reason. If so, this can be strongly affected by the actual winter weather, especially at latitudes where development and duration of ice-cover varies significantly. We must not exclude that the observed low similarity is merely a result of “chance” events: the species arriving first will prevail (Watt, 1947). Last but not least, interannual ontogenetic cycles can be relevant for many species, especially diatoms (Padisák et al., 2004).

In other words, species of winter assemblages are largely selected by physical constraints based on individual adaptations of the species in the available species pool. This follows the community organization patterns described in Gleason’s (1926) individual concept of succession. If so, dominance patterns must be rather closely related to the actual meteorological conditions as the annual manifestation of climate. A good example is *Stephanocostis chantaicus* in Lake Stechlin that develops relatively abundant populations only if the lake has a long-lasting, thick ice-cover (Scheffler & Padisák, 2000). During summer, phytoplankton development is more intensively driven by interspecific interactions that result in characteristic series, as hypothesized in Clements’ (1916) “superorganismic” concept of succession. A good example is the *Anabaena/Aphanizomenon* → *Cylindrospermopsis* → *Planktothrix* series in many lakes where the first shift occurs because ammonium uptake of *Cylindrospermopsis* is more effective than that of *Anabaena/Aphanizomenon*. Therefore, it can delay the switch to the energetically expensive nitrogen fixation. The second shift is due to the

greater shade- and low temperature tolerance of *Planktothrix*.

It is known that physical properties (like the incidence and duration of ice-cover, and hypolimnetic temperature) of lake environments are rather closely related to climate variables; chemical properties are more difficult to relate and biological parameters remain very loosely, if at all, correlated (Dokulil & Teubner, 2002; Dokulil et al., 2009; Nöges et al., 2009). In this sense, winter phytoplankton might be a better tool for climate change research than summer equilibrium, or close-to-equilibrium assemblages when species selection are driven by interspecific interactions in many cases. Therefore, the effects of climatic forces, may remain hidden, at least until a certain threshold.

Beyond the PEG model

As has been shown, the importance, timing and severity of biological or physical constraints on phytoplankton development are rather individualistic in different lakes. Only a few common patterns are shared by at least some lakes and the biomass/compositional responses are also different. In order to disentangle which of the constraints have more influence on the phytoplankton pattern, a co-variance analysis was performed (Table 3). Compositional similarity was in most cases (Balaton both sites, Lake Stechlin, Lake Vörtsjärv, and to some extent Neusiedlersee and Lake Arancio) positively related to biological drivers which means that the stronger the biological control is, the higher is the interannual

compositional similarity (Table 3A). Conversely, with the exception of Lake Vörtsjärv and Alte Donau, similarity negatively co-varies with physical stressors indicating the higher the importance of physical control is, the higher is the level of divergence from the average pattern. This result is in accordance with what is discussed in the previous section. The sum of the absolute values of co-variance coefficients is 2.93 for biological and 4.42 for physical drivers, indicating a higher impact of physical stressors on phytoplankton composition than is due to biological ones. The biomass response to physical/biological driving forces is more diverse (Table 3B). While phytoplankton, for example, exhibits a high positive co-variance with biological variables in Lake Vörtsjärv and Lake Kinneret, the relationship is weaker or even negative in the other lakes. Increase in physical constraints largely results in decreased standing crop (Mondsee is the best example). However, biomass can respond in an opposite way, like in Lake Vörtsjärv. Here, too, the sum of the absolute values indicate that physical forcing is more determinant than biological.

The sum of the absolute values of physical and biological constraints lake by lake in the bottom rows of Table 3A, B provides an image on the responsiveness of lakes to biological and physical forcing. Lake Kinneret biomass, for example, appears to be much more responsive to environmental forcing than the composition of its biomass. The case of Lake Stechlin is just the opposite: biomass is quite irresponsive while composition is sensitive to changes. It is worth to note that man-made or

Table 3 Covariance (estimated as linear correlation coefficients) between biological and physical constraints and (A) similarity and (B) biomass response in the eight studied lakes

	Mondsee	Stechlin	Kinneret	Arancio	Vörtsjärv	Neusiedlersee	Balaton Eu	Balaton Meso	Alte Donau	lsuml physical– biological
(A) Similarity										
Biological	−0.26	0.62	−0.03	−0.15	0.73	0.20	0.36	0.58	0.00	2.93
Physical	−0.62	−0.75	−0.15	−0.44	0.56	−0.29	−0.51	−0.72	0.39	4.42
lsumlake	0.88	1.37	0.17	0.59	1.30	0.49	0.87	1.30	0.39	
(B) Biomass										
Biological	−0.18	−0.17	−0.60	−0.05	0.78	0.21	0.36	0.53	0.30	3.18
Physical	−0.84	0.04	0.30	0.31	0.78	−0.60	−0.52	−0.53	0.28	4.22
lsumlake	1.02	0.21	0.90	0.37	1.56	0.81	0.88	1.06	0.58	

Sums are calculated by adding the absolute values of the coefficients

intensively managed lakes, like Lake Arancio and the Alte Donau, in general, show a weak relation of both biomass and composition to environmental forcing.

Ecological processes sustain the functioning of each ecosystem. Thus, competition for resources, grazing, predation, parasitism, and all the activities aimed at the flow of matter and energy always act in all environments, although their intensities span over quite wide gradients and different spatial and temporal scales. As for a theatrical performances where the final quality of the dramatic presentation not only depends on the text itself but is also largely attributable to the ability of the actors as well as to the accuracy of the display of the scenario (backgrounds, lightning, costumes, etc.), phytoplankton morpho-functional variability may ensure dozens of different interpretations to the environmental play, depending both on the morphological and climatic features of the stage and on the compositional features (often determined by chance) of the lake's assemblage.

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