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Lake Stechlin

Spatial and temporal pattern of development and decline of the spring diatom populations in Lake Stechlin in 1999

J. Padisák[1], W. Scheffler[2], C. Sípos[1], P. Kasprzak[2], R. Koschel[2] and L. Krienitz[2]

with 11 figures

Abstract: Integrated samples from the euphotic layer (mostly 0-25 m) were taken between January 1994 and December 2000 in the open water of Lake Stechlin. Monthly sampling was carried out in January-April 1999 and bi-weekly in May-June 1999 at depths of 0, 10, 20, 30, 40, 50 and 60 m. Phytoplankton, with special attention to diatoms, was qualitatively and quantitatively investigated. These data, together with water chemistry and zooplankton monitoring information, were used to describe spring development and decline of the phytoplankton. Results were compared to predictions of the PEG-model. i) The large variety in timing and species composition of early-season diatom growth allows one to conclude that in lakes, which can be either mono- or dimictic, it is primarily not the trophic state that determines spring growth/composition, rather it is the presence, absence or duration of ice-cover and weather conditions during the onset of the thermocline. ii) Physical stresses (low temperatures, low light, complete turbulent mixing) upon phytoplankton in such lakes has been less severe than growth limitation set by scarcity of nutrients. Diatom growth starts soon after the complete autumnal overturn. Thermocline development, instead of initiation of the spring bloom as stated in the PEG model, terminates growth since diatoms cells sink rapidly into the hypolimnion. iii) „Life time" of unicellular planktonic centric diatoms was the longest in the stage when they turn to decaying or dormant cells. Empty frustules dissolve rather quickly. Frustules of planktonic pennatae diatoms were apparently more persistent than that of centrics. iv) Because of their low abundance, metazooplankton cannot play a significant role in the elimination of spring the phytoplankton crop. v) After the onset of thermocline, rejuvenating diatoms can be found in small numbers throughout the hypolimnion. This study demonstrates that one should be careful with using the term "vegetation period" since the bulk of growth of planktonic primary producers might occur during the isothermal period prior to onset of the thermocline. Moreover, driving forces during this period are largely determined by climatic factors or actual weather, such as the duration of the ice-cover or the onset time of the thermocline.

Key words: Planktonic diatoms, sinking, grazing, limitation, PEG-model

Authors' addresses:

[1] Department of Limnology, University of Veszprém, H-8200, Egyetem u. 10, P. O. B.158, Hungary, e-mail: padisak@tres.blki.hu.
[2] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department Limnology of Stratified Lakes, Alte Fischerhütte 2, D-16775 Stechlin-Neuglobsow, Germany, e-mail: scheff@igb-berlin.de, daphnia@igb-berlin.de, rko@igb-berlin.de, krie@igb-berlin.de.

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Introduction

Diatom populations, especially centric diatoms, have been the dominant group of spring phytoplankton bloom in deep lakes in the temperate region (e.g. ALVAREZ-COBELAS & ROJO 1994). Among the reasons leading to spring diatom dominance are their i) superior ability for competing for nutrients, especially phosphorus (SOMMER 1988) and ii) the fact that photosynthesis of many species becomes light saturated at relatively low light intensities (KIRK 1983, KOHL & GEISDORF 1991, SOMMER 1988). However, due to their siliceous cell walls diatoms are heavy and sink fast. According to REYNOLDS' (1984) calculation, a diatom will sink, at minimum, twice as fast as the non-diatom with similar size and geometrical properties. However, most are sinking 3–5.5 times faster. The velocity at which cells leave the surface strata is not identical with their sinking velocity, assuming laminar flow, because turbulence will resuspend cells. In such conditions, the number of cells, which remain in the upper layers (epilimnion) of the water column will depend on the initial cell number, the sinking velocity and the mixing depth (SOMMER 1988). Therefore, diatoms need a relatively deep mixing depth to remain in suspension.

The first coherent model, the so-called PEG model (SOMMER et al. 1986) for plankton successions, was published decades after the principal (e.g. CLEMENTS 1916, GLEASON 1917, 1927) or more recent (GRIME 1979) theories were developed for terrestrial plant successions. The PEG model outlines a generalized sequence of events during one plankton year, taking both physical constraints (low temperatures, low light and deep-layer mixing in winters) and trophic relationships (zooplankton grazing) into consideration. The usefulness of the PEG-model has widely been justified in many publications (e.g. GAWLER et al. 1988, ANDERSEN et al. 1989, DEBERNARDI et al. 1990, MICHALOUDI et al. 1997) especially if studies were carried out in deep, stratified, temperate lakes. In some cases the PEG-model proved to be a good predictor of planktonic events despite obviously different morphological characters of the studied water bodies (NÕGES et al. 1998, GRIGORSZKY et al. 2000) including marine systems (ROELKE 1999). Possible reasons for unpredictability of the model, such as shallowness and high flushing rates, were considered in the original publication (SOMMER et al. 1986). Later, further reasons of deviations were described, such as lake morphologies, mixing properties, trophic states or interferences with the microbial loop (e.g. CHORUS & WESSELER 1987, LAIR & AYADI 1989, DIAZ & PEDROSO 1993, BRANDL 1994, MASSANA et al. 1994, TRYFON et al. 1994).

Concerning the development and decline of spring diatom blooms, the PEG-model (at various parts but especially in statement-1, statement-2 and statement-4) assumes the following:

i) "In deep lakes, the main factor responsible for spring increase ... is the onset of stratification which allows algae to remain longer in the euphotic region."
ii) "In lakes of moderate depth spring crop starts to develop directly after ice break" and in such lakes and in oligotrophic ones large diatoms are considered to be the main forms.
iii) "In most deep lakes, the ... increase in algal biomass is halted as soon as the herbivore populations became numerous enough to exert high grazing pressure on phytoplankton composed of small edible algae." ... "In eight of the eighteen lakes (those eight lakes are deep, temperate, oligo- or mesotrophic lakes) the beginning of phytoplankton decline coincides with maximal densities of filter-feeding zooplankton."

Despite the many cautionary remarks in the original description of the model (SOMMER et al. 1986), there is a strong message that onset of stratification is a precondition for algal growth and that the decline of the spring phytoplankton bloom is due to grazing.

Lake Stechlin is a deep, oligotrophic, dimictic or warm monomictic lake and, therefore, it belongs to group a of lakes which are likely to support planktonic seasonal successional events as described in the PEG-model. A study (SCHEFFLER & PADISÁK 1997) on spring development of *Cyclotella tripartita* in Lake Stechlin has shown that this population develops during the isothermal period in January–April and stratification of the lake give no rise to "spring bloom development", rather it terminates phytoplankton growth since cells are rapidly sinking to the hypolimnion.

The aim of this study was to investigate development and loss of centric diatom populations at the beginning of the plankton year, including studies at the quantitative and also species-specific level. We also aimed to follow seasonal phytoplankton succession in Lake Stechlin as compared to predictions and statements outlined in the PEG model, with special reference to winter and early spring development of diatoms. There are many other factors that may prevent diatom development or to the waning their populations (grazing, unusual weather conditions like early and rapid temperature increases resulting in early stratification, depletion of silica, etc.). In this paper we focused on sinking losses due to the onset of stratification.

Material and methods

Phytoplankton composition and abundance – i) Integrated epilimnetic (mostly 0–25 m) samples were taken between January 1994 and December 2000 in the open water of the lake as described in PADISÁK et al. (this volume). ii) Between January and December 1999 samples were taken monthly (January–April) or bi-weekly (since May 1999) in depths of 0, 10, 20, 30, 40, 50 and 60 m (Fig. 1). Phytoplankton species were identified using the most up-to date phycological manuals and literature. A minimum of 400 settling units (cells, filaments or colonies) were counted in each Lugol-fixed sample giving a counting accuracy of $\pm$ 10% for total phytoplankton. Autotrophic picoplankton (APP) was counted preferably immediately after sampling in unpreserved samples. If it was not possible, unpreserved samples were deep-frozen within 1 hour after sampling and APP was counted in melted samples no later than one month after sampling (PADISÁK et al. 1997). Phytoplankton biomass was estimated by geometrical approximations using a computerized plankton counter (HAMILTON 1990, GOSSELAIN & HAMILTON 2000). Centric diatoms were identified in parallel diatom preparates (gentle burning procedure); their species-specific biomasses were calculated from total centric numbers with an inverted microscope and from percentage contributions in diatom preparates (PADISÁK et al. 1999). In samples taken at different depths in 1999, centric diatoms were counted under an inverted microscope in four size classes (< 6 µm, 6.1–15 µm, 15.1–25 µm and > 25 µm and *Aulacoseira* was counted as filaments) and four morphological groups in each size class:

1) living cells with structured cell content and intact chloroplasts;
2) cells that possess some cell content but there are no intact chloroplasts and in general it is difficult to decide whether they are alive, decaying or dormant (d/d cells);
3) empty and intact frustules and
4) broken or eroded frustules.

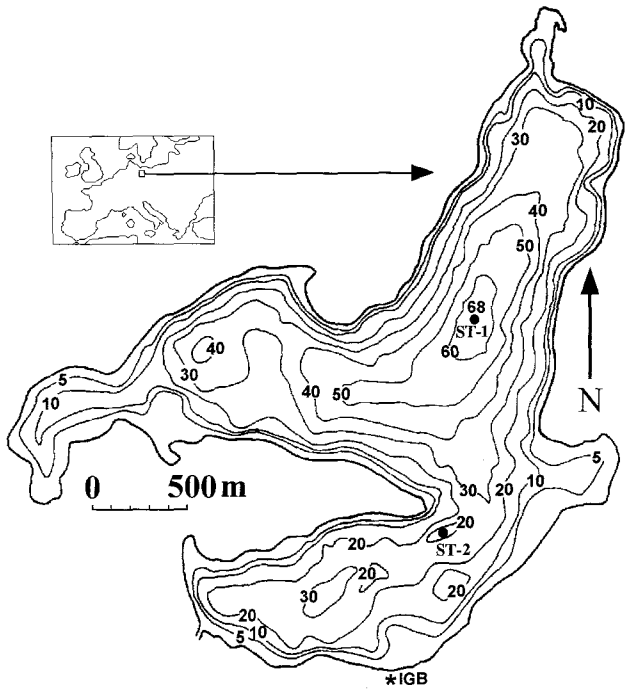

Fig. 1. Location of the sampling sites in Lake Stechlin.

A minimum of 400 cells were counted in each samples, therefore the counting error for the total diatom assemblage is < ± 10%. Apparent net doubling/halving times were estimated from net growth as follows: $k = (\ln N_2 - \ln N_1)/(t_2 - t_1)$ and $t_d = \ln 2/k = 0.693/k$, where N_1 is the density (ind l^{-1}) at t_1 time, N_2 is the density (ind l^{-1}) at t_2 time (difference is expressed in days), k is the net growth rate (ln units d^{-1}), and t_d is the doubling time (days). For d/d cells and empty frustules it is more correct to specify accumulation time (t_a) instead of growth rate and doubling time, however, from the point of view of numerical calculations $t_a = t_d$.

Zooplankton composition and abundance – Crustacean plankton was collected by vertical tows from the mean depth to the surface (0–22 m) using a cone-shaped closing net (mesh-size 90 μm, opening 237 cm^2, length 1.2 m, Hydrobios, Kiel, Germany) at the deepest point of the lake (central basin). The lake was sampled biweekly from April to October 1999. For the rest of the year monthly sampling was applied. Samples were preserved in 4% sugar-formaldehyde solution. Sub-samples containing at least 100 individuals of dominating species or group were counted using a compound microscope. Mean lengths were estimated by measuring 30–40 individuals. Biomass of the crustaceans was calculated using published length-weight relationships (Bottrell et al. 1976, Kasprzak 1984). Dry weight was converted to carbon following Winberg et al. 1971; Carbon = 0.5 DW.

Water chemistry – Water chemical data were analyzed according to the OECD standards and standards of Deutsche Einheitsverfahren. PO_4-P, TP, NO_3-N, NO_2-N, NH_4-N, TN and silica were measured with the Perstop flow injection analysis system TECATOR FIA STAR

5010/5030. The analyses followed the Tecator Application Notes (ASN) 60-05/90 for PO_4-P (detection limit 0.002 mg l^{-1}; now ASN 5601), 60-03/83 for TP (detection limit 0.005 mg l^{-1}; now ASN 5602), 62-01/83 for NO_3-N, NO_2-N (detection limit 0.01 mg l^{-1}; now ASN 5621), 50-02/84 for NH_4-N (detection limit 0.01 mg l^{-1}; now ASN 5501), ASN 110-03/92 for TN (detection limit 0.01 mg l^{-1}), and ASTN 4/92 for silica (SiO_2, detection limit 0.1 mg l^{-1}). For TP measurements the unfiltered water samples were autoclaved for 30 min (134°C) after the addition of persulfate ($K_2S_2O_8$); for TN measurements the unfiltered water samples were autoclaved for 45 min (120°C) after the addition of oxisolv. The water samples for the determination of PO_4-P, NO_3-N, NO_2-N, NH_4-N and silica were filtered through 0.6 µm membrane filters immediately after sampling. Conductivity, O_2 and pH were measured in situ (WTW LF 196, WTW OX 196, WTW, pH 196 T).

Results

Share of diatoms in annual average biomass

Diatoms are an important group in terms of annual average biomass. Their share was 30% of total annual average biomass for the years 1994–2000. The minimum value (11%, 1998) was found when *Planktothrix rubescens* bloomed in the lake, while the maximum (50%, 2000) was attributable to an *Aulacoseira islandica* spring bloom. In all the other years the annual share of diatoms varied between 26 and 36% (Fig. 2). Of the two main groups, Centrales and Pennales, the centric forms were more abundant. On average, 70% of the annual diatom biomass was given by centric forms and only 30% by Pennales. Minimum contribution (4%) of Pennales was observed in 1995 and the maximum (59%) in 1997 (Fig. 2). Moreover, when pennatae diatoms contributed notably to the spring bloom (1996–2000) they always followed the peak of Centrales (Fig. 2).

Species composition

The most important centric diatoms in the lake were *Cyclotella* cf. *cyclopuncta*, *C.* cf. *krammeri, C. pseudocomensis* (SCHEFFLER 1994) and its morphotyp *minima* (SCHEFFLER et al. this volume), *C. radiosa, C. tripartita, Stephanocostis chantaicus, Stephanodiscus alpinus, S. minutulus,* the *S. neoastraea* group and *Aulacoseira islandica.* Besides, *Cyclotella distinguenda, C. ocellata, Cyclostephanos dubius, Stephanodiscus hantzschii, Aulacoseira granulata, Melosira varians* and *Ellerbeckia arenaria* occurred sporadically. Of the pennatae diatoms *Asterionella formosa, Fragilaria crotonensis* and *Diatoma tenuis* were the most important species. A number of other planktonic species occurred rarely and species of periphytic origin were also found in plankton samples. Size distribution of the most frequent unicellular centric diatoms is given in Fig. 3.

Development and species composition of the spring diatom bloom (1994–2000)

Development of the spring diatom bloom started between January and March (Fig. 4), however, its timing has been quite variable. In 1994 and 1995 the spring diatom bloom started to

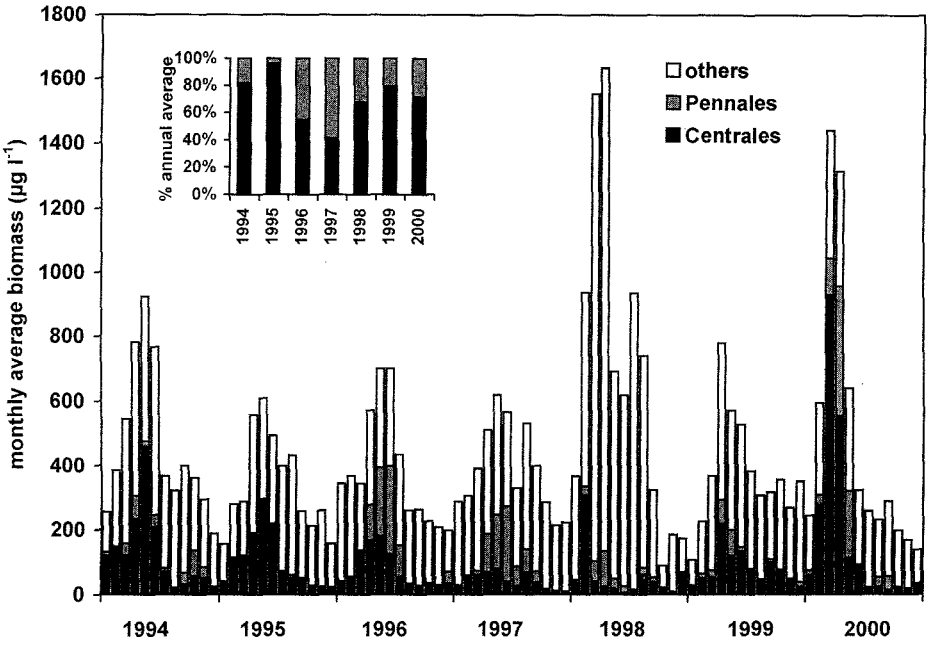

Fig. 2. Monthly average biomass (µg l^{-1}) of Centrales, Pennales and other phytoplankton in Lake Stechlin between January 1994 and December 2000. Subgraph: annual average percentage contribution (%) of Centrales and Pennales to annual average biomass of diatoms in Lake Stechlin during the same time period.

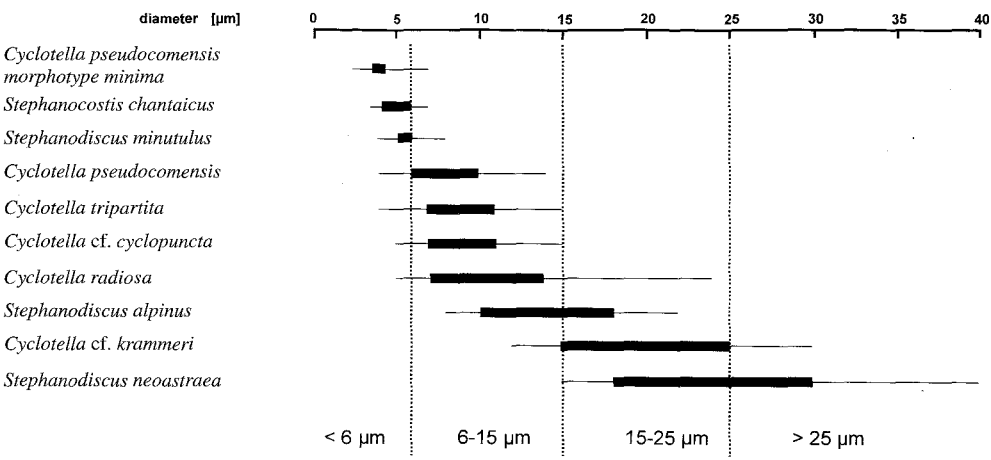

Fig. 3. Characteristic sizes of the most frequent centric diatoms in Lake Stechlin. Thick parts indicate the range which is characteristic for the bulk of the population, and thin lines indicate extreme sizes.

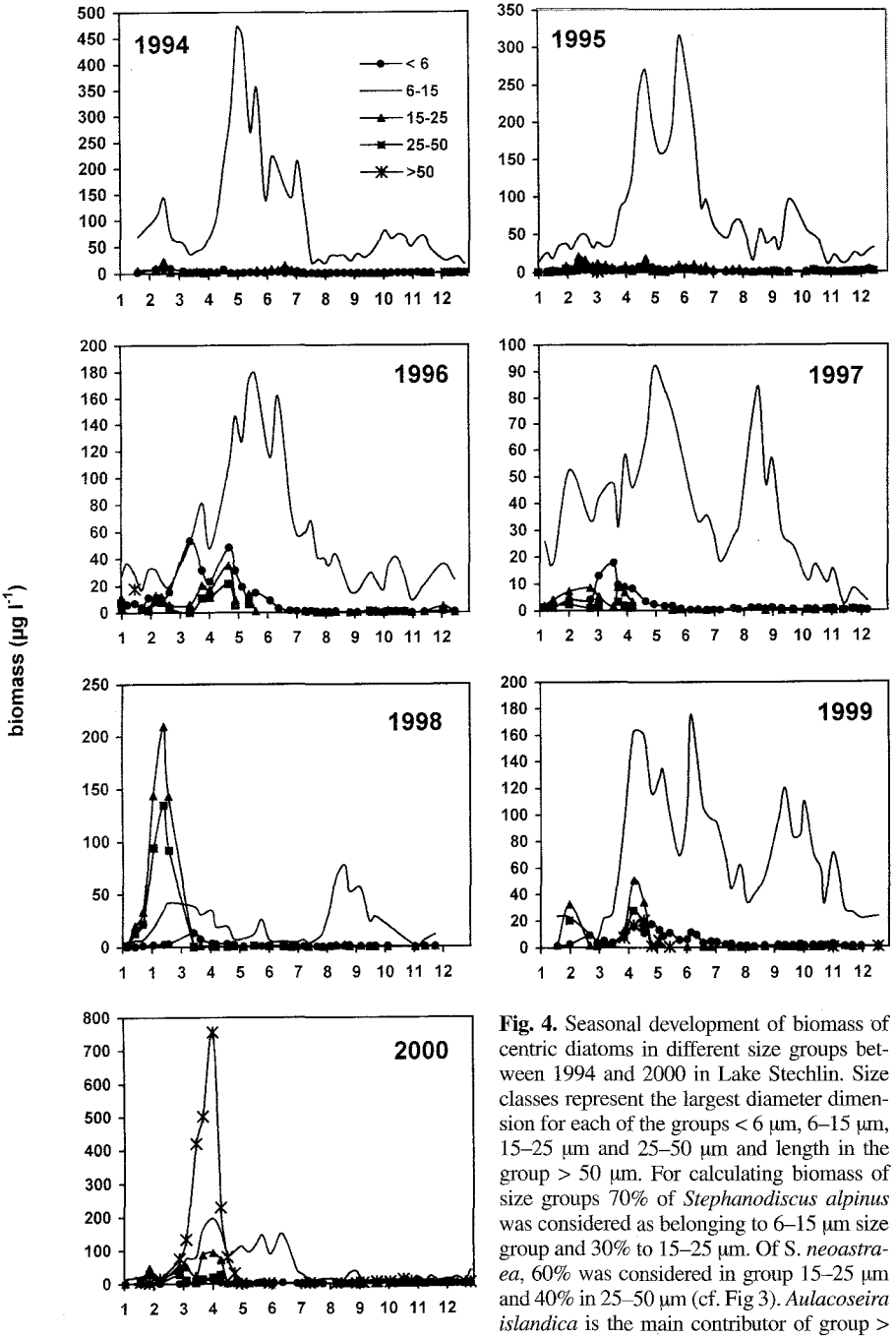

Fig. 4. Seasonal development of biomass of centric diatoms in different size groups between 1994 and 2000 in Lake Stechlin. Size classes represent the largest diameter dimension for each of the groups < 6 µm, 6–15 µm, 15–25 µm and 25–50 µm and length in the group > 50 µm. For calculating biomass of size groups 70% of *Stephanodiscus alpinus* was considered as belonging to 6–15 µm size group and 30% to 15–25 µm. Of S. *neoastraea*, 60% was considered in group 15–25 µm and 40% in 25–50 µm (cf. Fig 3). *Aulacoseira islandica* is the main contributor of group > 50 µm, however, sporadically *A. granulata* and *Melosira varians* also occurred. Note the differently scaled y axes.

develop in middle May and was composed almost exclusively by centric diatoms belonging to the size-class 6–15 μm (dominants: *Cyclotella tripartita* in 1994 and *C. pseudocomensis* in 1995). In the winter of 1995/1996 a long-lasting and thick ice-cover of the lake broke not before middle April. The small (< 6 μm) centric diatom *Stephanocostis chantaicus* exhibited remarkable growth under the ice, and other centrics of the size group 6–15 μm also developed. These under-ice populations declined along with the ice-break up, and as spring circulation occurred algae belonging to each size groups (except those > 50 μm) started to develop. All forms except the group in the 6–15 μm sizes were depleted soon and the spring maximum was based on algae having diameter of 6–15 μm, especially *C. tripartita, C. pseudocomensis* and at a lesser extent *C. radiosa*. The peak biomass of Centrales was lower than in the previous two years, but Pennatae diatoms contributed significantly to the spring bloom especially in its second part. In 1997 a moderate standing crop of diatoms was also observed under the ice (chiefly *C. pseudocomensis*), but remarkable diatom growth occurred only in April (main species: *C. tripartita*). The peak biomass of Centrales in this year was far below that of the previous years since Pennatae diatoms reached a higher biomass than centrics. As a consequence of a cold summer, thermocline erosion started early, which gave rise to a second Centrales peak in August. Dominant species were *C. pseudocomensis* with *C. radiosa* and *C.* cf. *cyclopuncta* as subdominants. In 1998 the spring diatom maximum occurred very early (middle January–March) and was formed by relatively big centric diatoms in the 15–25 and 25–50 μm size class (especially *Stephanodiscus neoastraea;* subdominants: *S. alpinus, Cyclotella krammeri*). Main species in the second Centrales maximum in August were *Cyclotella radiosa, C. krammeri, C. ocellata* and *C. cyclopuncta*. In 1999, the spring bloom was formed by centric diatoms of the 6–15 μm size group (especially *C. tripartita*). The size-groups > 15 μm peaked at the very beginning of the spring bloom, and their peaks were given by *Stephanodiscus neoastraea, S alpinus* and *Aulacoseira islandica. Cyclotella pseudocomensis* and *C. radiosa* contributed mainly to the second Centrales peak in September. In 2000, peak biomass of algae belonging to size groups 6–15 μm (especially *Cyclotella tripartita*), and 15–25 μm (especially *Stephanodiscus alpinus* and *S. neoastraea*) was not lower than in the previous years (100–200 μg l^{-1} peak biomass). However, the overall dominant species was *Aulacoseira islandica* which reached almost 800 μg l^{-1} during its peak biomass.

Spatial and temporal pattern of different morphological/size groups of spring diatom bloom throughout the entire water column in 1999

During the spring of 1999, Centrales dominated in each morphological group (living cells, d/d cells, empty frustules) at each sampling date and depth (Fig. 5). On average, Pennatae diatoms represented 3.1% of living cells, 6.2% of d/d cells and 12.5% of empty frustules.

In principle, pennatae diatoms can be divided into two groups: planktonic species and those that drifted to the plankton from shallow sediments or were of periphytic origin. Planktonic forms were: *Asterionella formosa, Diatoma tenuis, Fragilaria crotonensis,* (these are the dominants), *Nitzschia* sp., *Fragilaria ulna* (*acus*-forms, *angustissima-forms* and *ulna* forms), *Fragilaria construens, Fragilaria dilatata* and *Cymatopleura solea*. Periphytic/benthonic taxa were: *Achnanthes minutissima* "Sippen-komplex", *Cymbella* spp., *Diatoma vulgaris, Diploneis* spp., *Epithemia* spp., *Gomphonema* spp., *Navicula* spp. and *Rhopalodia gibba*.

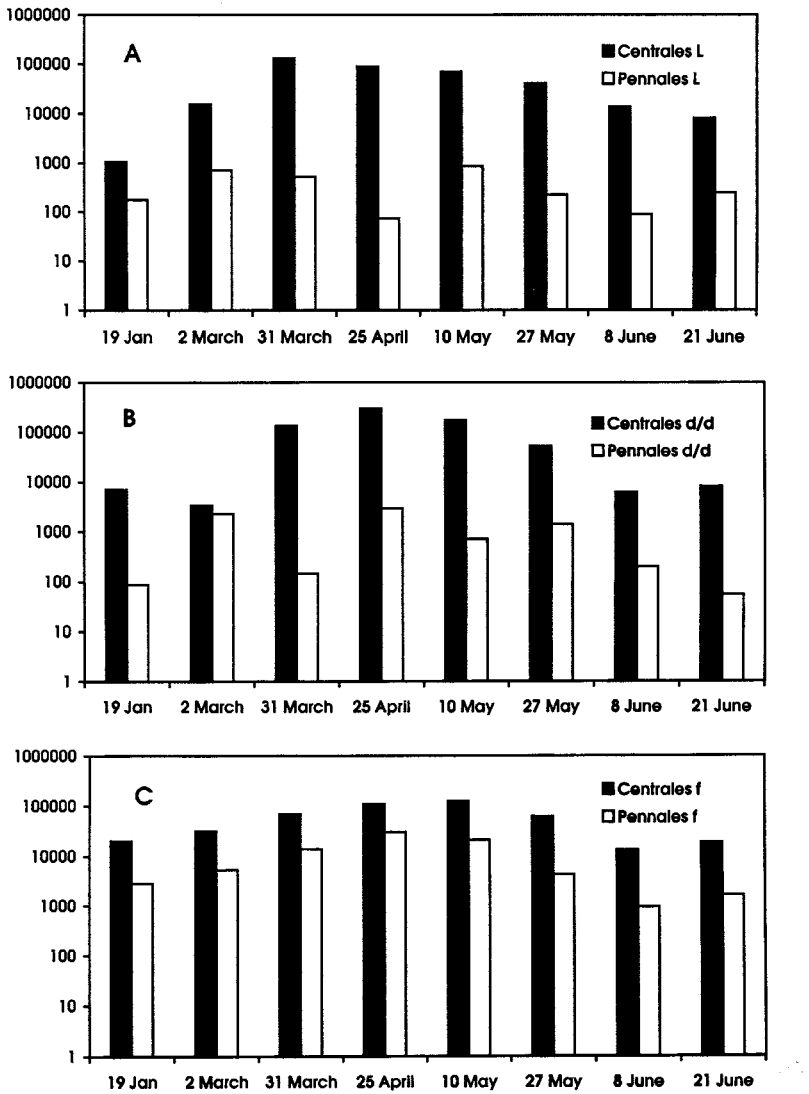

Fig. 5. Density (numbers l^{-1}) of Centrales and Pennales cells subdivided by living cells (A), d/d cells (B) and empty frustules (C) in Lake Stechlin between 19 January and 21 June 1999. Data represent average of the 60 m water column (logarithmic scale).

At a species level, data for each species were rather scattered and therefore carry a considerable counting error. Therefore analyses were done at a group-level.

At the beginning of the investigations (19 January) planktonic pennatae were represented chiefly as empty frustules (Fig. 6). Their spring development started at the beginning of March and extended throughout the entire water column. At the end of April a second growth phase was observed, and each of the forms were rather evenly distributed in the water col-

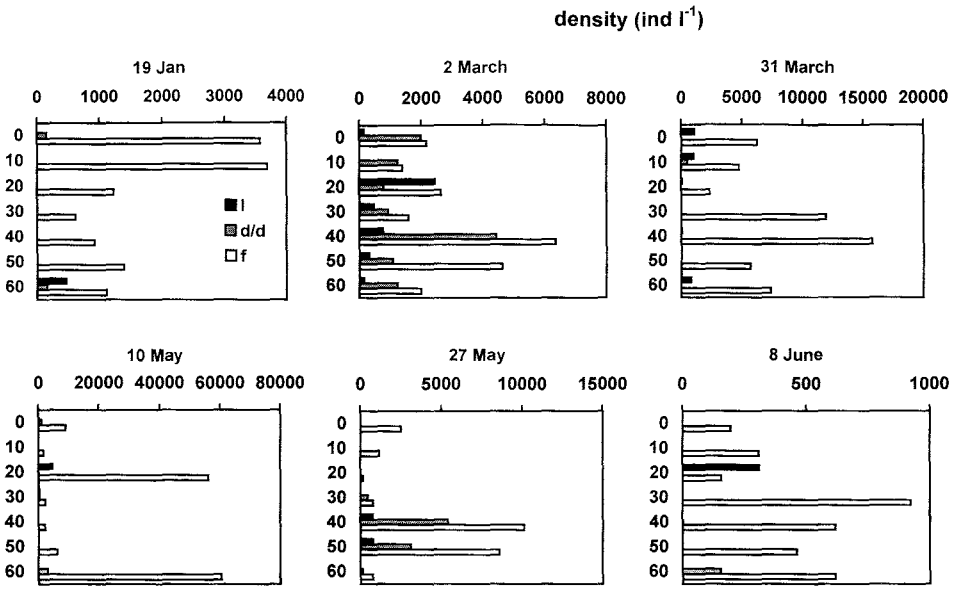

Fig. 6. Vertical distribution of planktonic Pennatae diatoms in Lake Stechlin between 19 January and 21 June 1999. Abbreviations – l: living cells; d/d: decaying or dormant cells; f: empty frustules.

umn. By the end of May these cells sank to deeper layers where numbers of d/d cells and empty frustules exceeded significantly that of the living cells. In June, numbers of planktonic pennatae had reached a very low level (< 1000 unit l^{-1}), and they were rather homogeneously distributed in the water column, especially in the end of the month (21 June).

Similar data for centric diatoms were analyzed not only as morphological groups (living, d/d, frustules) but also as size groups. Cell numbers in size-group 3-6 μm was very low, therefore detailed analysis was not possible. This partly holds for size group > 25 μm. However, some important ecological trends remained detectable.

Living cells in the size group 6–15 μm started to grow intensively in March (Fig 7A) and their doubling time for this period was 9.5 days. The d/d cells also started to accumulate in March (t_a = 5.4 d) but this trend was extended to April (t_a = 23.8 d). As numbers of d/d cells well exceeded that of the living cells it is reasonable to suppose that living cells were quickly transformed to d/d cells and their „life-time" was rather extended. Number of empty frustules also increased in March–April but their t_a values were much lower (24 d for March and 34.6 d for April). During May, numbers of each form in the size class 6–15 μm decreased significantly and remained at a low level in June. Regarding the vertical distribution of cells in this size-group (Fig. 8, series A) it can be concluded that development of living cells started already in January and accelerated by March. During the January–March period, each of the forms (living cells, d/d cells, frustules) were rather homogeneously distributed throughout the 60 m water column. At the end of April, living- and d/d cells were very abundant in the upper layers, however, d/d cells formed from the March-April population were found in large numbers in the deeper layers. In May (time of thermocline development), the upper layers lost the bulk of diatoms, and sinking cells formed dense layers first in the upper then in the

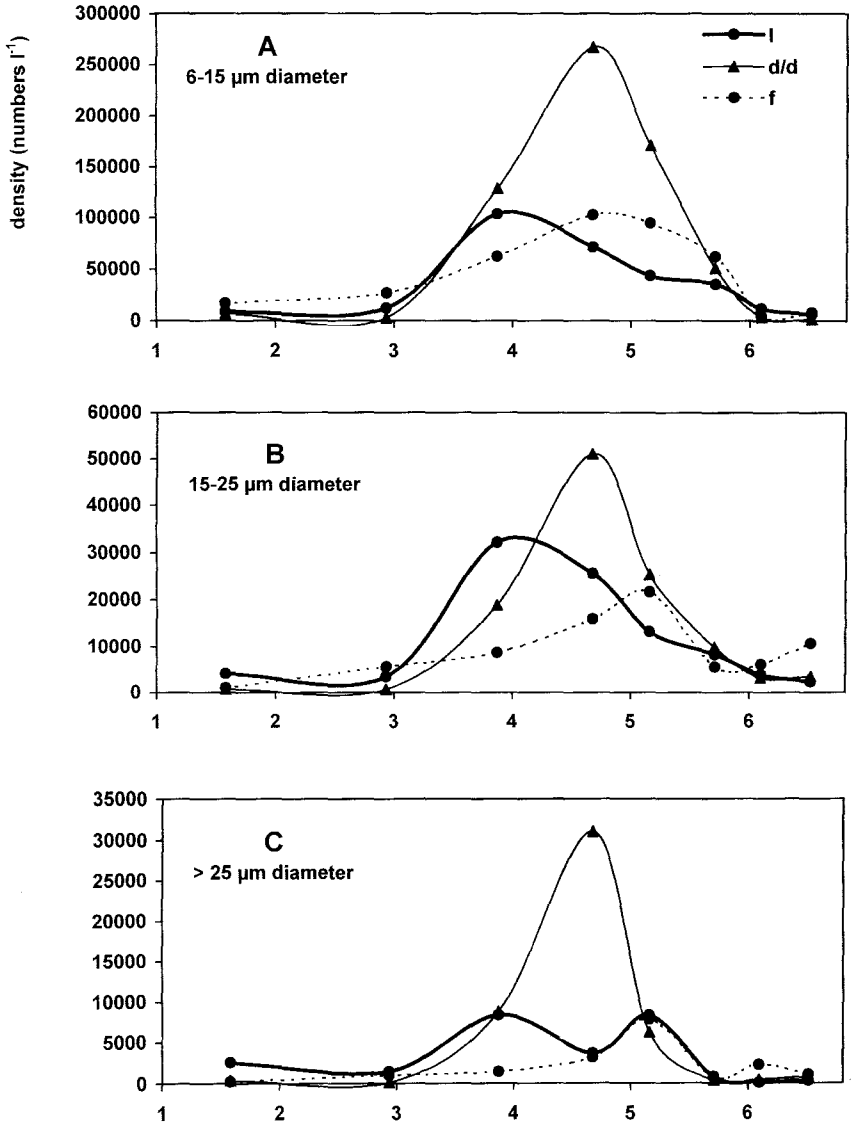

Fig. 7. Temporal development of different morphological groups of centric diatoms in size class 6–15 µm (A), 15–25 µm (B) and > 25 µm (C) in Lake Stechlin between 19 January and 21 June 1999. Data represent average of the whole water column. Abbreviations as on Fig. 6. Numbers on the x axis represent months of 1999.

lower portion of the hypolimnion. By June, numbers in each morphological groups (l, d/d, f) decreased, and they stabilized at a low-density level. Proportion of l-, d/d- and f-cells in the end of June indicated that production/sinking/decay/resuspension reached a kind of equilibrium, i.e. evenly distributed in the water column which was stratified by that time.

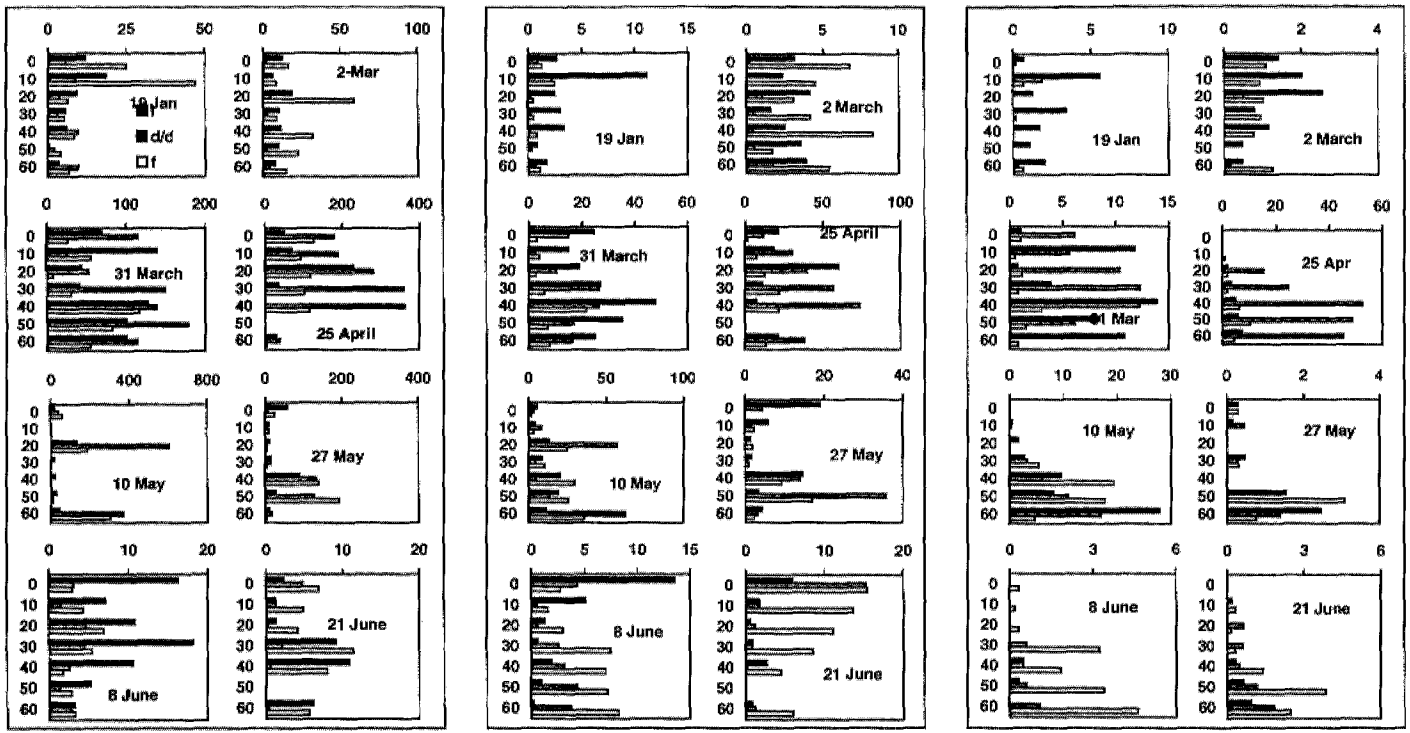

Fig. 8. Vertical distribution of different size groups (Series A: 6–15 μm; Series B: 15–25 μm; Series C: > 25 μm) of centric diatoms in Lake Stechlin between 19 January and 21 June 1999. Abbreviations as on Fig 6.

Living cells in the size-class 15–25 μm also started to grow in March and their doubling time (9.1 d) was very close to that of the smaller size group (Fig. 7B). However, their transformation to d/d cells was more prolonged: slower in March (t_a = 6.1 d) and faster in April (t_a = 17.4 d) than that of the corresponding valves in the 6–15 μm size group. Accumulation of empty frustules in this size class was even more delayed; rates were 17.6 d in February, 46.3 d in March and 23.5 d in April. As follows from the above described pattern, different morphological groups in this size class formally exhibited a Lotka-Volterra type of temporal dynamics: density of living cells had a peak (33,000 ind l^{-1}) at the end of March – early April, d/d cells were maximum in late April (51,000 cells l^{-1}) and empty frustules were the most abundant (22,000 frustules l^{-1}) in early May. Concerning vertical distribution (Fig. 8, series B), living cells of this size group were most abundant in the uppermost layers in January, however this winter crop (and the successive d/d cells and frustules) became evenly distributed during February. The main growing season was March when numbers of living cells exceeded that of d/d cells and empty frustules. Here, just as in the 6–15 μm size group, sinking was predominant in May and it also occurred in the form of distinct layers over the water column (Fig. 8). In June, living and d/d cells characteristically occurred in large numbers in the epilimnion. However, distribution was rather evenly distributed throughout the sampling depths.

Cells in the > 25 μm size class exhibited two growth periods: the first occurred in March, the second in late April, early May (Fig. 7C) with doubling times of 11.5 days and 12.9 days, respectively. Maximum (30,000 cells l^{-1}) of d/d cells was observed in April with accumulation rates of 4.6 d (March) and 13.7 d (April). Transformation to empty frustules was strongly delayed. Cells from the March-population appeared as frustules only in early May. The second population did not appear as d/d cells, however, they were observed as frustules in June. The bulk of living cells of the size group > 25 μm was found in the upper layer of the water column in January and February (Fig. 8, series C). Nevertheless, the number of living cells was also considerable in the deep layers. In April, sedimentation of each of the forms (l, d/d, f) were characteristic. In May a second growth phase occurred in the epilimnion, even though at a lesser extent than in the early months of the year. In June, hardly any centric diatom cells > 25 μm occurred in the epilimnion and their density increased along with the water depth.

Zooplankton density

Crustacean zooplankton (Copepoda and Cladocera) biomass in 1999 started to increase in early April, but it remained at a low level (< 40 μg C l^{-1}) until late June (Fig. 9). The maximum was observed by the end of July at 64 μg C l^{-1}. Then a gradual decrease took place. Therefore, zooplankton biomass exhibited a considerable delay as compared to phytoplankton (Fig. 9; for phytoplankton 10% of freshweight was considered as C; PADISÁK & DOKULIL 1994). Copepods (main species: *Eudiaptomus gracilis, Eurytemora lacustris, Thermocyclops iothonoides, Cyclops* spp.) started to increase in April, and this increase was temporarily interrupted in early May (subgraph of Fig. 9). Nauplius stages appeared in highest density only on 8 June, and the maximum biomass was observed on 20 July (39 μg C l^{-1}). Cladocerans (chiefly *Diaphanosoma brachyurum, Daphnia hyalina x galeata,, D. cucullata, Bosmina coregoni* and B. *longirostris*) increased significantly only between 5 and 20 July (subgraph of Fig. 9).

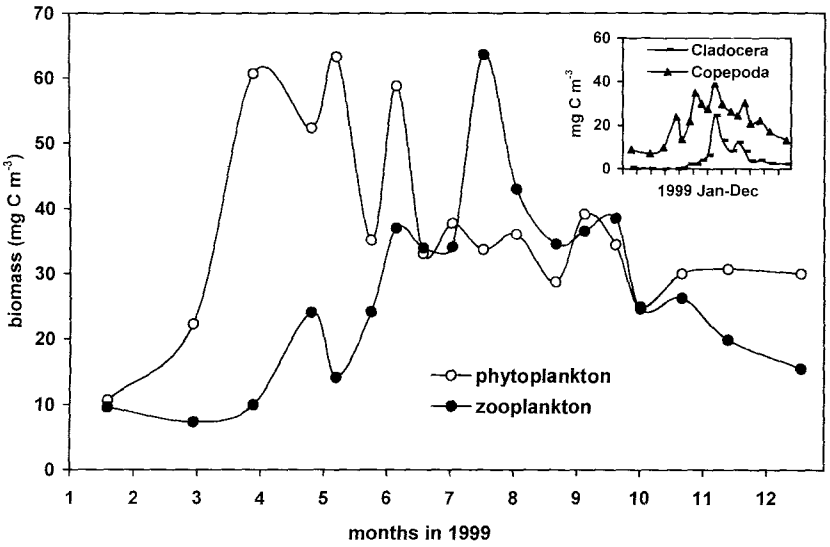

Fig. 9. Development of phytoplankton and zooplankton (both are given as mg C m^{-3}) in Lake Stechlin during 1999. Numbers on the x axis represent months of 1999. Subgraph: Biomass changes (mg C m^{-3}) of Cladocera and Copepoda in 1999.

Inorganic nutrients

PO_4-P concentrations remained below 10 μg l^{-1} during most of the year both in the euphotic (considered as the uppermost 0–25 m layer) and the aphotic zone (Fig. 10A). Higher values were found only in the aphotic zone in October–November. Moreover, most of the data were lower than 5 μg l^{-1}, which is considered as the analytical detection level of the molybdenate method, which was applied to measure PO_4-P concentrations.

Concentration of inorganic N forms was chiefly above the 100 μg l^{-1} in the euphotic zone between January and July and at the end of November and December (Fig. 10B). Low values were found in this layer between July and November. Concentrations in the aphotic layers have never fallen below 100 μg l^{-1}.

Dissolved reactive silica was quite evenly distributed in the aphotic and euphotic zones until July and in December (Fig. 10C). Aphotic and euphotic data exhibited marked differences in the period August–November. However, none of the measured data were below 500 μg l^{-1}.

Ice cover, thermocline development

Length of ice cover on Lake Stechlin has been rather variable ranging from no-ice cover to thick ice cover lasting for months (Fig. 11). In the period 1993–2001 the longest ice-cover, lasting for almost 4 months, was observed in the winter of 1995/1996. During three winters the lake did not freeze at all. In the winter of 1998/1999 a short-lasting ice cover developed in February 1999.

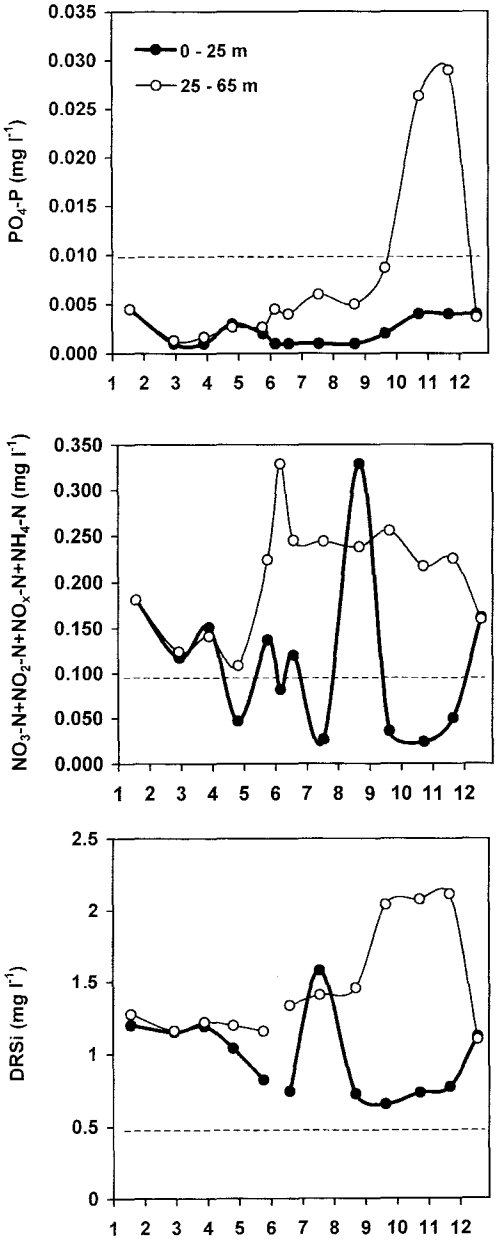

Fig 10. Concentrations of PO_4-P (A), inorganic N forms (B) and silica (DRSi; C) in Lake Stechlin in 1999. Dotted lines indicate threshold levels below which the given nutrient can be considered as limiting for phytoplankton growth according to SAS (1989).

Thermocline development in the lakes usually took place in May (Fig 11). In some years (for example, 1995 and 1996) strong winds at the end of May or early July considerably

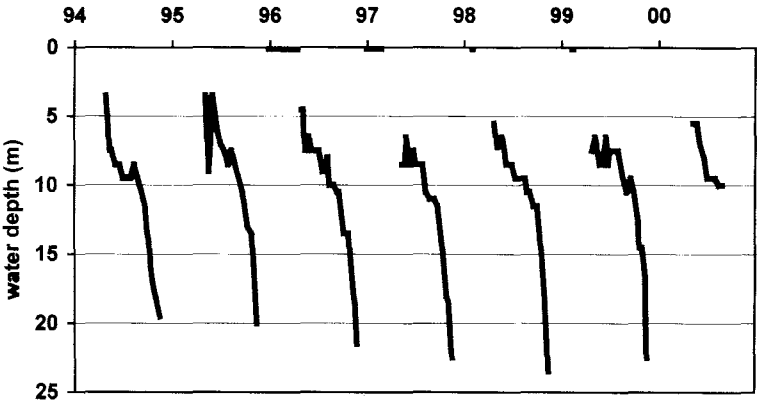

Fig 11. The depth of the thermocline (established as the depth of the greatest temperature difference) in Lake Stechlin in winters between 1994 and 2000. Thick sections along the x-axis indicate duration of ice-cover.

deepened the thermocline and it started to re-develop in late June or even in July. Erosion (accelerated deepening) of the thermocline usually started in late August or early September depending on weather conditions. It also happened (for example in 1999) that cold weather in August started to erode the thermocline, but in the upper layers it re-developed if weather in September was calm.

Discussion

By its origin, morphometry, stratification pattern (either mono- or dimictic depending on the weather during the winter) and depth profile, Lake Stechlin has been a stratifying „deep lake" with a low trophic status (annual average TP: 13–18 $\mu g\ l^{-1}$; PADISÁK et al. 1998) corresponding to oligo-mesotrophic levels (OECD 1982). Considering TP concentrations there has been no trend-like change in the trophic status of the lake, yet other variables indicated eutrophication (KOSCHEL et al. 2002).

The highest nutrient levels in the lake can usually be measured after the complete autumnal overturn, in November or December. Phosphorus can be considered as an ultimate limiting nutrient because inorganic nitrogen levels are at limiting amounts only during summer stagnation (when phytoplankton is limited both by N and P). Silica concentrations are at no time of the year decreased to a level which would prevent the development of diatoms.

Because soluble P concentration fall below limiting levels by December–January, it can be deduced that the P-pool of the hypolimnetic water has been taken up rapidly by phytoplankton although the standing crop does not increase significantly during the December–February period. The earliest species that represent the start of the next plankton year are *Stephanodiscus astraea* and *S. alpinus*. The presence, absence and duration of ice significantly influence species composition. Long-lasting ice cover, like in the winter of 1995/1996 favors small-sized diatoms, especially *Stephanocostis chantaicus* (average volume: 47 μm^3) that may occur in dense under-ice populations (SCHEFFLER & PADISÁK 2000). If there is no ice

or winter stagnation lasts for only a short period, large centric diatoms appear first and are then replaced by smaller forms (6-15 µm), especially *Cyclotella tripartita* and *C. pseudocomensis*. Diatom growth takes place during the isothermal period in December–April. This is also the time when the other main contributors to the spring bloom take place, and algae of picoplanktonic size (especially cyanoprokaryotes but also some species of green algae) have their growing season (PADISÁK et al. 1997).

Development of a spring diatom maximum in Lake Stechlin has been quite predictable. Nonetheless, apart from the above mentioned general characteristics, developmental patterns and species composition have been quite variable. In two of the investigated years (1994, 1995), species with moderate cell sizes (6–15 µm) contributed exclusively to the spring bloom. The year 1999 was similar but with two growth periods of larger unicellular centric diatoms. In 1996, under-ice population of *Stephanocostis chantaicus* was followed by growth of bigger centrics. However, larger ones (> 15 µm) declined fast, medium sized forms continued growth and peaked together with pennatae diatoms (*Asterionella formosa* and *Fragilaria crotonensis*). In 1997 pennatae diatoms reached higher biomass than centrics. The year 1998 was very exceptional since instead of algae of picoplanktonic size, *Planktothrix rubescens* grew in January-April and formed a deep-layer chlorophyll maximum (PADISÁK et al., this volume). Besides this species only a short growth period of larger centric diatoms was observable in February. In 2000, spring development pattern and abundance of size classes of unicellular centrics was similar to that in 1999. However, the overall dominant was the large, chain-forming centric diatom, *Aulacoseira islandica* (this phenomenon was repeated in 2001–2003).

The large variability in the timing of diatom growth, and especially species composition, allows one to conclude that in lakes which can be either mono- or dimictic it is not so much the trophic state that determines spring growth/composition (as considered in the PEG-model, SOMMER et al. 1986) but rather the presence, absence or duration of ice-cover and weather conditions during the onset of the thermocline.

Growth of species during the development of the spring bloom has not been very fast as compared to in situ growth rates of summer species (1–3 days for species with moderate cell volume; PADISÁK, in press). Doubling times of 9.1–11.5 days were calculated in this study. These numbers are in agreement with estimates based on weekly sampling for *Cyclotella tripartita* (5.5 d; SCHEFFLER & PADISÁK 1997) and picoplankton (5-8 d, PADISÁK et al. 1997).

Secchi-disk transparency of lake Stechlin during the spring isothermal period has been typically 8-10 m, from which a euphotic depth (1% of subsurface light) of 22–27 m can be estimated (REYNOLDS 1984). This roughly corresponds to the average depth (22 m) of the lake. However, surface irradiation during this time of the year is low. Values of 400–600 µmol m^{-2} s^{-1} can be considered characteristic. Photosynthesis of shade adapted species (like many planktonic diatoms, picoplanktonic cyanoprokaryota, *Planktothrix rubescens*) can be light saturated at irradiances as low as 10–20 µmol m^{-2} s^{-1} (PADISÁK, in press), and from these values it can be supposed that photosynthesis has been light saturated in the upper 17–20 m of the water column. This corresponds to 40-45% of total lake volume (KREY, 1985). In other words and assuming complete and effective mixing of the whole water column, each cell has to spend 55–60% of its life-time in the aphotic region which provides a reason for longer doubling times. The effect of low water temperature can be another reason for slow growth. Since autecological studies for the species mentioned are lacking, it is difficult to estimate. Nevertheless, increasing evidence substantiates (VINCENT 1981, LAYBOURN-PARRY et al.

1997, SPAULDING et al. 1994, MÜLLER-HAECKEL 1985) that cold temperatures do not prevent fast growth of cold-adapted species. Based on the above calculations and other evidence, physical stress factors (cf. PEG model; SOMMER et al. 1986) were probably weaker than the growth-limitation effect of nutrient availability.

Seasonal growth patterns, but more markedly the vertical distribution of living cells throughout the water column indicate precisely that the growth of centric diatoms (the most typical contributors of the spring phytoplankton maximum) takes place in the period January–April when the water column indicate has been completely mixed and isothermal (years with extensive ice cover may be exceptions). As data from January 1999 show, the diatom growth, independent of size, started in the euphotic layer. However, cells were soon effectively mixed throughout the water column, with transformation to d/d cells and empty frustules; this became more and more abundant in the deeper layers. Transformation of living cells to d/d cells took place rather quickly, with a significant delay only observed for algae > 15 μm. A maximum density of d/d cells significantly exceeding that of the living cells indicate that the „life-time" of the d/d (dormant, decaying, senescent) phase was longer than that of the living phase for some time in the growing season. Although layers of sinking diatoms are perfectly observable in the lower strata (especially during May), sinking rates are difficult to calculate for two reasons: i) life-time of different forms (living, d/d) is unknown apart that the latter is longer than the former; ii) sinking rates of d/d cells can be even 4 times faster than that of living cells (REYNOLDS 1984). The much lower number of empty frustules than d/d cells indicate that transformations from d/d to empty cells are rather quick. Part of the silica frustules also dissolve. Halving time of silica frustules for centrics > 15 μm was calculated as 8 d which is, if due to dissolution, a much faster dissolution rate than 50 d as given by LAMPERT & SOMMER (1993). However, it cannot be excluded that the bulk of the frustules accumulated in the layer of 60–65 m layer (which was not sampled), since daily sinking amplitude of diatoms of this size can be calculated as about 2 m d^{-1} (REYNOLDS 1984). Such a mass accumulation would suppose completely still water in these depths, which is not very likely. The fact that broken or eroded frustules (although they were counted separately) were very rarely found in the samples also supports the quick dissolution of silica. Frustules of pennatae diatoms have been probably more persistent since, in this study, only 3.1% of living cells belonged to this group while their share in d/d cells was 6.2% and among frustules 12.5%.

Despite the above detailed uncertainties about transition times between different forms and their sinking rates, the data clearly demonstrate that early-season growth of diatoms takes place in the isothermal period. Instead of giving rise to a spring bloom, as stated in the PEG model, thermocline development terminates growth since diatom cells sink fast into the hypolimnion. The thermocline develops usually at 4–5 m depths in May, and by July it deepens to 7–9 m. Based on sinking velocities for living and senescent cells, given in REYNOLDS (1984), and correcting the data with the Stokes equation for senescent centric diatoms of 6–15 μm, a daily sinking amplitude of 0.5 m can be estimated. This means that these cells sink below the thermocline within 8–10 days, exactly corresponding to the length of warm and calm periods that enable thermocline development. However, most of the cells become senescent and sink earlier then the development of the thermocline.

Fast-growing Cladocera appear in considerable amounts only in July. A moderate standing crop of copepods develops in late-April or early-May. At that time the bulk of diatoms can be traced into the deeper layers, where crustacean biomass is generally low (< 20 μg C l^{-1})

throughout the year. Moreover, KASPRZAK & RONNEBERGER (1985) have shown that the use of phytoplankton by herbivores in Lake Stechlin is only significant during the period from July to October when *Daphnia* spp. contribute substantially to the total crustacean plankton.

Therefore, elimination of the spring bloom of phytoplankton is due to sinking and not to grazing in Lake Stechlin. There are no data about protists and heterotrophic or mixotrophic flagellates. Nevertheless, from the point of clearance rate the microbial loop may play a very important role in retaining nutrients in the euphotic zone. Chrysoflagellates, and other actual or potential mixotrophic flagellates, appeared in large numbers during breakdown of the spring diatom bloom (PADISÁK et al. 1998). According to microscopic observations, *Ochromonas* specimens may contain 1–3 diatoms cells, and picoalgae are readily grazeable for *Dinobryon* that may also form population maxima in this period. This way, even though later frustules sink to the hypolimnion, the effectiveness of the microbial loop may play a key role in epilimnetic retention of nutrients (especially P and N) and this can have a major effect on planktonic events and the food-web during the summer stagnation period.

Diatoms do not contribute significantly to the phytoplankton after the development and stabilization of the thermocline. Vertical distribution patterns at the end of June indicate that a kind of equilibrium develops between sinking, decaying, resuspension (within hypolimnion) and re-juvenation. While hypolimnetic living cells of centrics of 6–25 µm size class are probably remnants of the preceding growth, those in size group > 25 µm and Pennales are likely to originate from re-juvenation since their numbers are higher than numbers of living cells at the previous sampling in the upper layers. This re-juvenation is in accordance with the high capacity of diatoms to rise as soon as mixing depth increases, and in this way it has been a fundamental survival strategy (SOMMER 1988).

Ecologists, among them plankton ecologists, often use the term "vegetation period", which, in the case of plankton, is often understood as the period between onset and erosion of the thermocline. This study demonstrates that one should be careful when using this term since the bulk of growth of planktonic primary producers might occur during the isothermal period prior to the onset of the thermocline. Moreover, driving forces during this period are largely determined by climatic factors or actual weather, like duration of ice-cover or onset time of thermocline. Furthermore, composition and size distribution of spring phytoplankton has been a determinative factor for summer plankton development.

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