

Rarity, ecological memory, rate of floral change in phytoplankton—and the mystery of the Red Cock

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Abstract In this article, we attempt to estimate the contemporary phytoplankton species pool of a particular lake, by assessing the rate of floral change over a period of 15 years. Phytoplankton time series data from Lake Stechlin, an oligo-mesotrophic lake in the Baltic Lake District (Germany) were used. Of the 254 algal species recorded during the 15-year of studies with roughly biweekly sampling, 212 species were planktonic. In the individual plankton years, the recorded total number of species changed between 97 and 122, of which the number of dominants (>1% contribution to the annual average of total biomass)

was only 10–19. The 15-year cumulative number of species exhibited an almost linear increase after an initial saturation phase. This increase was attributed to two reasons: increase of sample size and immigration of species new to the flora. Based on a probabilistic model developed in this study, we estimated the number of co-existing planktonic species of the lake as some 180, and the rate of floral change as 1–2 species per year. Of these co-existing species, only few maintain the matter–energy processing ecosystem functions in any particular plankton year. Selection of these dominants is probably driven by mesoclimatic cycles, coupled with human-induced forcing, like eutrophication. All others are hiding as an ecological memory, in the sense of the capacity or experiences of past states to influence present or future responses of the community. Data analyses suggest that selection of the ‘memory species’ that show temporary abundance increases over shorter (several years) periods are

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largely dependent upon the dominants. These results show that interspecific interactions and the particular autecological features of the dominants, together with their effects on the whole ecosystem, act as a major organizing force. Some phytoplankton species, like *Planktothrix rubescens*, are efficient ecosystem engineers with cascading effects of both a top-down and bottom-up nature. Historical scientific data on *Planktothrix* blooms in Lake Stechlin suggest cyclic patterns in long-term development of phytoplankton which, as the legend of the Red Cock suggests, dates back much further than scientific archives.

Keywords Rarity · Phytoplankton assemblages · *Planktothrix rubescens* · Floral change · Community ecology · Ecological memory · Lake Stechlin

Introduction

Rare is interesting. Rare is special and valuable. It could be a precious gem or an old railway ticket from a remote place—regardless of what the rare item is, rarity is, in itself, attractive. A substantial part of natural science was built upon observations and events that were observed only sporadically or even accidentally. From Aristotle to the modern metaphysicians, scientists were looking for observations that proved their hypotheses. They did not investigate the multitude of cases where facts were inconsistent with theory. The need to apply a vast number of statistical tests to large data sets to prove or falsify a scientific hypothesis is the requirement of the modern scientific paradigms, and we have to confess that these trials, in themselves and if applied automatically, often result in nonsense.

Biology is no exception. A whole regiment of biologists and naturalists have been searching for extreme habitats where they hoped to find rare species that are new to science. Whilst in ancient times a rare species was simply interesting or increased the reputation of the scientist who described it, the ecological term ‘rarity’ gained importance in modern science, especially in conservation biology. Nature protection needed definitions. The number of categories that concern rarity is almost infinite (e.g. Munton, 1987). Rarity in biology is often understood as being either spatially limited or low in abundance. According to

Reveal (1981) ‘... rarity is merely the current status of an organism which, by any combination of biological or physical factors, is restricted either in numbers or area to a level that is demonstrably less than the majority of other organisms of comparable taxonomic entities.’

Regarding abundance, this concept needs quantification (abundance proportions) of species in an assemblage so that we can make a distinction between frequent and rare. However, finding appropriate criteria for quantifying ‘rare’ is difficult, especially if exactly quantified species proportions are unknown. A number of criteria were used for defining rare species of different biota, such as ‘found less than five times’ (birds; Thomas, 1979), ‘not more than 10 individuals or three clumps in the field’ (plants; Usher, 1986) or ‘recorded in 15 or fewer 10 km squares of the British national grid since 1950 during an extensive field survey’ (mosses; Longton, 1992).

In the previous paragraph, we purposely used examples from terrestrial macrobiota. Birds, plants and mosses make strikingly apparent the difficulty that we face with phytoplankton. The short generation time of phytoplankton made this group excellent for testing hypotheses such as competitive exclusion (Hardin, 1960) resource partitioning (Tilman, 1982), the Intermediate Disturbance Hypothesis (Connell, 1978; Reynolds et al., 1993; Sommer et al., 1993), or the equilibrium concept (Naselli-Flores et al., 2003). However, we do not see phytoplankton with the naked eye. It means that even the simplest floral survey needs sampling and instrumentation (microscope). We cannot search for rare species in nature and the microscopic search is limited to the samples that were taken in advance. Though there is a huge number of articles on phytoplankton having a title like ‘rare and interesting algae’ (e.g. Watanabe, 1985; Schmidt et al., 2003), we have to admit that phytoplankton is not an easy group to study when rarity is addressed. The best indication is that red lists for microalgae (e.g. Mollenhauer & Gutowski, 1996; Németh, 2005) started to be published only quite recently, as opposed to dozens of years ago for wild flowers or mammals.

Interestingly, understanding rarity in aquatic biota (at least from protists to macroinvertebrates) did not lack the concept of species proportion of contribution to the total. For example, Faith & Norris (1989) defined rarity of macroinvertebrates as ‘have abundances comprising $\leq 0.5\%$ of total abundance of all taxa’.

Such considerations are common in phytoplankton ecology (although least in the context of rarity); many studies consider only those species that have a $\geq 5\%$ (sometimes $\geq 10\%$) contribution to total phytoplankton biomass. This approach is largely justified by the fact that major patterns can be described at the level of the few dominants, and this practice can be supported statistically (Padisák et al., 2009b, 2010). However, process-based understanding of aquatic ecology must take rarity into account. For example, the only certified locality of occurrence of *Cylindrospermopsis raciborskii* (Woloszynska) Seennayya & Subba Raju between 1938 and 1978 was Lake Kastoria, Greece (Skuja, 1938). Since then, the ‘rare and interesting alga’ called *C. raciborskii* rapidly became a pest species, invading most lakes of not only Europe but the entire world. Thus, rarity, commonness and biological invasions should not be separated.

In this article, we restrict the meaning of rarity to the phytoplankton flora of Lake Stechlin, a deep, oligo-mesotrophic lake in the Baltic Lake District, Germany. Rarity, as suggested by Gaston (1994), will be quantified on the basis of the relative contribution of each species to total biomass. Use of biomass data of species is essential whenever interest is directed towards patterns of competitive relationships among species or matter–energy flow. For rare species, the number of individuals would make a similarly good measure. However, we analysed quantity of rare species also on the biomass level since we also wanted to consider patterns of development. Nevertheless, for giving weight to mere occurrence, two other quantitative measures were used besides biomass: the number of occurrences of a particular species in the 15-year phytoplankton record (1994–2008) and the frequency in the *whole* sample. Overall rarity, in sense of how often any given species can be found in other lakes, will not be touched upon.

The research aims of this analysis were

- i. to find tools for quantifying species that occur in the samples only sporadically;
- ii. to compare temporal changes of two fractions (one composed of frequent and the other of rare species) of the phytoplankton assemblage;
- iii. to assess the number of species representing the contemporary flora of the lake; and
- iv. to estimate the annual rate of floral change in the context of floral constancy.

Site description, materials and methods

Lake Stechlin is a medium-sized (4.2 km²), deep (z_{mean} : 23.3 m; z_{max} : 69.5 m) lake at 53°N latitude in Brandenburg, Germany. This glacial lake was originally oligotrophic. Between 1966 and 1989, water from this lake was used for cooling a nuclear power plant. This use affected the stratification pattern of the lake with intermittently high diatom share but apparently did not change its trophic state. The nuclear power plant was closed in 1991, after which the lake’s stratification pattern was released from this destabilizing management (Koschel & Adams, 2003).

Phytoplankton samples were taken at approximately 2 week intervals from a fixed station at the deepest part of the lake, from a series of depths in 5 m increments. Subsamples from the 0–25-m layer (euphotic zone) were mixed, and a subsample of this mixture was Lugol preserved for microscopic phytoplankton counting. Further sampling details are given in Padisák et al. (2003a) and Salmaso & Padisák (2007). The period covered in this analysis comprises 15 years (1994–2008) during which the lake’s trophic status varied in the oligo/oligo-mesotrophic range, becoming more meso- than oligotrophic as time progressed without apparent change in nutrient loads. Some data for *Aphanizomenon flos-aquae* from 2009 to 2010 were also included in the analysis.

Ideally, the studies considering the appearance of rare species should be based on the same number of samples per year, distributed in similar seasonal intervals. Deviations from these rules may increase sampling-strength biases. Due to logistic and meteorological reasons (periods of unstable ice), the samplings were not evenly distributed among and within years. Nevertheless, at least one sample was taken in every month of the 15-year period, and, therefore, seasonality is covered by the sampling design. The number of species found annually was positively correlated with the annual number of samples ($r = 0.34$; $n = 15$). Since this correlation was not statistically significant, we assume that unevenness of sampling did not substantially bias our results.

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 sample using the settling chamber and inverted microscope technique, giving a counting accuracy of $\pm 10\%$ for total

phytoplankton (Lund et al., 1958). Cell dimensions were recorded routinely in individual samples and phytoplankton biomass was estimated by geometrical approximations using computerized plankton counters (Hamilton, 1990; Gosselain & Hamilton, 2000; OPTICOUNT, 2008). It is essential to note here that during the entire 15 years period the phytoplankton was counted by a single investigator, therefore, the data are not confounded by differences in taxonomic concepts or expertise. In the period 1994–2001, unicellular centric diatoms were identified and their relative abundances were established in parallel diatom preparations (gentle burning procedure). Later, unicellular centric diatoms were counted in the sedimentation chambers, according to size classes (5 µm increments) rather than species. However, based on size distribution of species (Padišák et al., 2003b) the size class 5–10 µm corresponded to *Cyclotella tripartita* and *C. pseudocomensis* and the size class >15 µm to *Stephanodiscus neoastraea* (additional qualitative analyses also justified this allocation).

Autotrophic picoplankton (APP) was counted, preferably immediately after sampling, in unpreserved samples. If counting was not possible, unpreserved samples were deep-frozen within 1 h after sampling and APP were counted in melted samples no later than 1 month after sampling. See the description of counting procedure and differentiation between chlorococcalean and cyanoprokaryotic picoplankton in Padišák et al. (1997).

The inspiration of Reynolds' first attempt (Reynolds, 1980) to devise a system of classification of planktonic algae to be sensitive to environmental change resulted in elaboration of the functional group concept (Reynolds et al., 2002). In this system, species are sorted into functional groups marked with letters (coda) and each functional group comprises species providing similar responses to the change of environmental constraints. Allocation of taxa into different functional groups was made according to Reynolds et al. (2002) and Padišák et al. (2009a). *Pseudanabaena endophytica* was grouped into Codon **M** because it was seen (in this lake) only in mucilage of *Microcystis*. *Chlorella* sp. (and in this case 'Chlorella' was not a synonym for a small, unidentified, green, spherical object—it was indeed a *Chlorella*) was difficult to categorize because it is an endosymbiont of the ciliate *Stentor amethystinus*

Leidy 1880 but also occurs freely in the plankton similarly to *Siderocelis irregularis* Hindák in Lake Tanganyika (Stoyneva et al., 2008). *Scenedesmus costato-granulatus*, unlike other *Scenedesmus* spp., was placed in X1 because of markedly different temporal pattern from its generic counterparts and its co-occurrence with X1 species (*Trachydiscus*, *Pseudotetraedriella*, *Neocystis* and *Pseudodictyosphaerium*). *Gymnodinium helveticum* and *Woloszynskia* sp. were allocated into codon **W3** because of their mixotrophic behaviour.

For evaluating our 15-year dataset, we used the ALMOL European Phytoplankton Database (Padišák et al., 2010). The monthly average of the relative biomass of each phytoplankton functional group and species, and, moreover, the density data of each species were queried from the database and exported into Excel spreadsheets. Hierarchical cluster analysis was performed with Syntax 2000 software (Podani, 1988) with Bray-Curtis dissimilarity indices and the UPGMA fusion algorithm. For hierarchical clustering, the monthly averages of the relative biomasses of each species were calculated and summarized for each year of the studied period. The most common species were defined as those comprising the first 75% of the abundance rank; these contained almost 90% of the total biomass. The remaining 25% of the taxon list was used in the hierarchical clustering of the rare species. For statistical analysis of the rare species, including the hierarchical cluster analysis, the numbers of occurrence were calculated, as the number of samples in which individual species occurred during the whole 15 years of studies (its maximum equals 461, the total number of samples). For example, the sum of occurrence number of *Aphanocapsa grevillei* (Hassall) Rabenhorst is 19 (see Appendix—Supplementary material). The rank of occurrence was calculated as the sorted list of the sum of occurrence of each taxon. Number of years of occurrence represents the number of years in which an individual taxon was recorded. The maximum number is 15, the length of the studied period. Maximum number of occurrence is the maximum number of samples in which the taxon appeared in 1 year (for example, the maximum number of occurrence of *Aphanocapsa grevillei* is 6; see Appendix—Supplementary material). The cumulative number of species shows the number of items in the whole taxon list recorded from the beginning of

the study period. In the first year, the number of species is equal to the cumulative species number. If in the second year 12 new taxa appeared in the flora, the cumulative species number changes from 105 to 117. The disappearing taxa do not cause any change in the cumulative species number. Here, whole sample (multitude) means all the specimens that were registered in the total of 461 samples in the inverted microscope and since ~ 400 settling units were counted in each sample; this number is $461 \times \sim 400 = 184,400$.

Results

Overall succession

Seasonal patterns of phytoplankton overall biomass between 1994 and 2008 exhibited either spring unimodal or bimodal distribution until 2008, when the spring and summer maxima were comparable (Fig. 1). The spring assemblages during the period 1994–1997 were dominated by members of codon **A**: small centric diatoms of the genus *Cyclotella* (*Cyclotella tripartita* and *C. pseudocomensis*). In 1999–2000, though small *Cyclotella* still appeared in large amounts, species of codon **B** (*Stephanodiscus alpinus*, *Stephanodiscus neoastraea*, *Aulacoseira islandica*) appeared in increasing amounts. Of these **B**

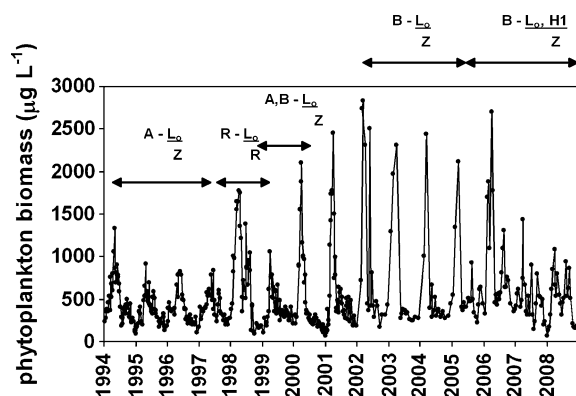


Fig. 1 Changes of phytoplankton biomass ($\mu\text{g l}^{-1}$) in Lake Stechlin between 1994 and 2008. Letters indicate the functional groups (codon) where the spring and summer dominants belong. First upper letter: spring dominant assemblage. After the hyphen (second upper letter/s): summer assemblage(s) where the upper codon (codon) indicate the epilimnetic assemblage and the lower indicates the dominant codon in the upper hypolimnion (deep chlorophyll maximum)

species, *Aulacoseira islandica* was highly predominant in the period 2001–2004. From 2005 onwards, the spring dominant was *Stephanodiscus neoastraea*, also belonging to codon **B**. The year 1998 was exceptional since the large *Planktothrix rubescens* population that started to develop in the deep layers in 1997 became overwhelmingly dominant and the spring diatom maximum did not develop.

The summer dominant assemblage in Lake Stechlin has to be divided into an epilimnetic and an upper hypolimnetic assemblage, since the annual development of the latter is a prominent feature of the lake and then it is spatially segregated. In most years, the upper hypolimnetic assemblage was dominated by the picoplanktonic *Cyanobium* species (codon **Z**). The only exception was the year 1998 when the *Planktothrix rubescens* population (codon **R**) that accumulated the nutrients of the lake in its biomass sank to the upper hypolimnion allowing little chance for *Cyanobium* to increase. Until 2005, the epilimnetic summer assemblage was dominated by a diverse **L**₀ assemblage (large species of the genera *Ceratium* and *Peridinium*; chroococcalean blue-greens such as large-celled *Chroococcus*, *Radiocystis*, *Coelosphaerium*; additionally some chlorococcalean species [codon **F**] with extended mucilage or characteristic for oligotrophic lakes like *Coenochloris* [*Sphaerocystis*], *Quadrigula*, *Willea*). From 2006 the dominance of *Aphanizomenon* and *Anabaena* species (**H1**) increased and by the end of the study (2008) they became dominant over the members of the original **L**₀.

Species numbers

During the 15 years of the studies, altogether 254 species of algae were found in the 461 depth-integrated (euphotic zone) samples. Of these 254 species, 212 were planktonic, the others were benthic or periphytic elements that occurred in the plankton samples (see Appendix—Supplementary material). In the following sections, we concentrate on the planktonic species. The annual total number of species (regardless of whether they were planktonic or benthic/periphytic) ranged between 110 and 126.

Planktonic species can be sorted into different groups. The classification takes into consideration dominance (i, ii), dominance and frequency of occurrence (iii, iv) and the tendency of frequency of occurrence (v, vi).

- i. Strong dominants: their aavb% (annual average contribution to annual average total phytoplankton biomass) exceeded 10% at least in one of the years.
- ii. Occasional dominants: their aavb% exceeded 1% at least in one of the years.
- iii. Rare but constantly present species: their aavb% remained under 1% but they occurred in most years; they were absent in the samples for no longer than 1-year intervals.
- iv. Very rare species: their aavb% remained under 1%. They occurred in the samples with 2–5 years intervals of absence.
- v. Disappearing species: they occurred at the beginning of the studied period but then they were not seen at least for 5 years and did not re-appear.
- vi. Species new for the flora: they appeared for the first time at least 5 years after the beginning of the studies and, additionally, they are not listed in the algal flora of Lake Stechlin (Casper, 1985).

Strong dominants (6 species)

The number of species that exceeded 10% biomass contribution to annual total biomass was very small. One of them was the picoalgal species, *Cyanobium* (Fig 2a). This species started to increase in density in January, peaks developed in April–May, then the cells accumulated in the upper hypolimnion where they formed a persistent deep chlorophyll maximum (DCM). This pattern was recurrent every year though its extent varied 7-fold in the 15-year study period. The other species forming a DCM in Lake Stechlin was *Planktothrix rubescens*. It was very rare in most of the years (Fig, 2b; note log-scale) when it occurred largely in the form of greyish hormogonia. It started to increase after the erosion of thermocline in 1997, continued growth during the following winter isothermal period, and parallel with the thermocline development in 1998 it formed a DCM. Dense populations of *Planktothrix rubescens* in Lake Stechlin had typical bright pink colour. In 1998, the DCM was shared between *Cyanobium* and *Planktothrix* with some spatial segregation (see data in Padisák et al., 2003c). *Cyclotella tripartita* and *C. pseudocomensis* dominated the spring diatom maxima between 1994

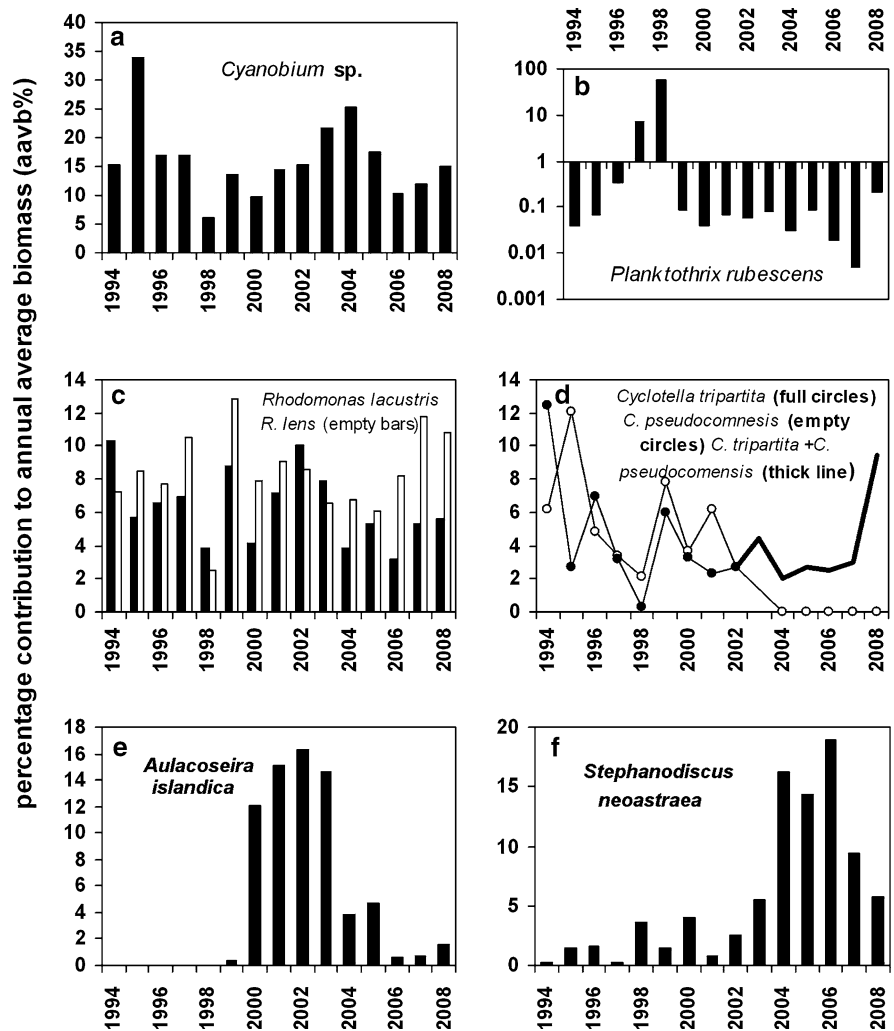
and 1996 (Fig 2d). In the following years, they contributed to the spring bloom, but did not dominate. *Aulacoseira islandica* was not observed in the samples until 1999, when some specimens appeared (Fig 2e). Then, in January–March 2002 a very early diatom peak developed which was dominated exclusively by *A. islandica*. This event was repeated in the next 2 years (and, to a lesser extent in 2004 and 2005) and the species became sporadic from 2006 onwards. Only a few specimens of *Stephanodiscus neoastraea* were present in the samples until 2002 (Fig 2f). In the subsequent years the species became dominant in the spring diatom bloom. The other two quantitatively important species were *Rhodomonas lacustris* and *R. lens* (Fig 2c). The basic difference between these two was that *R. lens* typically formed population maxima after the autumnal erosion of thermocline while *R. lacustris* provided ephemeral peaks in almost any season with a high level of unpredictability. Nevertheless, both species were prominent throughout the study period.

Occasional dominants (33 species)

The number of occasional dominants was relatively high. Most of the species in this group (typical representatives: *Anabaena lemmermannii*, *Pseudo-sphaerocystis lacustris*, *Botryococcus terribilis*, green picoalgae, *Scenedesmus costatogranulatus*, *Staurastrum planktonicum*, *Chrysochromulina parva*, *Ceratium hirundinella*, *Gymnodinium helveticum*, *Peridinium umbonatum*, *Cyclotella radiosa*, *Asterionella formosa*, *Fragilaria crotonensis* and *Synedra ulna*) appeared fairly constantly during the 15-year record (Fig. 3). Characteristic increases in relative contribution were traced for almost every species from this group (Fig 3a, b, c, f, g). In some years, they exhibited much higher biomass than in others. *Botryococcus terribilis* peaked only in 2003. In 2008 (and also in 2009), not a single specimen was found in the regular samples. However, in the shoreline bloom of *Aphanizomenon flos-aquae* (see later) which occurred in December 2009, a number of *Botryococcus* colonies were seen (Fig. 3c).

Some species in this group of occasional dominants decreased during the study period. A typical example is *Chroococcus dispersus* (Fig 4a) that was frequent in late summer samples in 1994–1995. In the following years, it decreased, and in the last years it was only, if

Fig. 2 Percentage contribution to annual average biomass of species belonging to the ‘strong dominants’ group. **a** *Cyanobium* sp.; **b** *Planktothrix rubescens*; **c** *Rhodomonas lacustris* and *R. lens*; **d** *Cyclotella tripartita* and *C. pseudocomnesis* (from 2002 on they were counted together as 5–10 µm size class of unicellular centric diatoms); **e** *Aulacoseira islandica* and **f** *Stephanodiscus neoastraea* in Lake Stechlin between 1994 and 2008



at all, sporadically seen. *Stephanocostis chantaicus* is an overall rare centric diatom. It occurred in small amounts until 2000, then it was not recorded (Fig. 4b). Although the species is very small (diameter 3.5–9.5 µm) it can be identified even in the inverted microscope since the ornamentation of the valves is very strong. The only year when the species reached high abundance was 1996 when it was dominant in the phytoplankton under thick ice and snow. *Diatoma tenuis* exhibited high density only in 2000, but otherwise remained at a low level (Fig. 3f).

Some other species substantially increased in abundance during the 15 years. Both *Anabaena circinalis* and *A. flos-aquae* became common after 2005 (Fig. 4c). *Woloszynskia* sp. appeared in considerable abundance after the decline of the *Planktothrix*

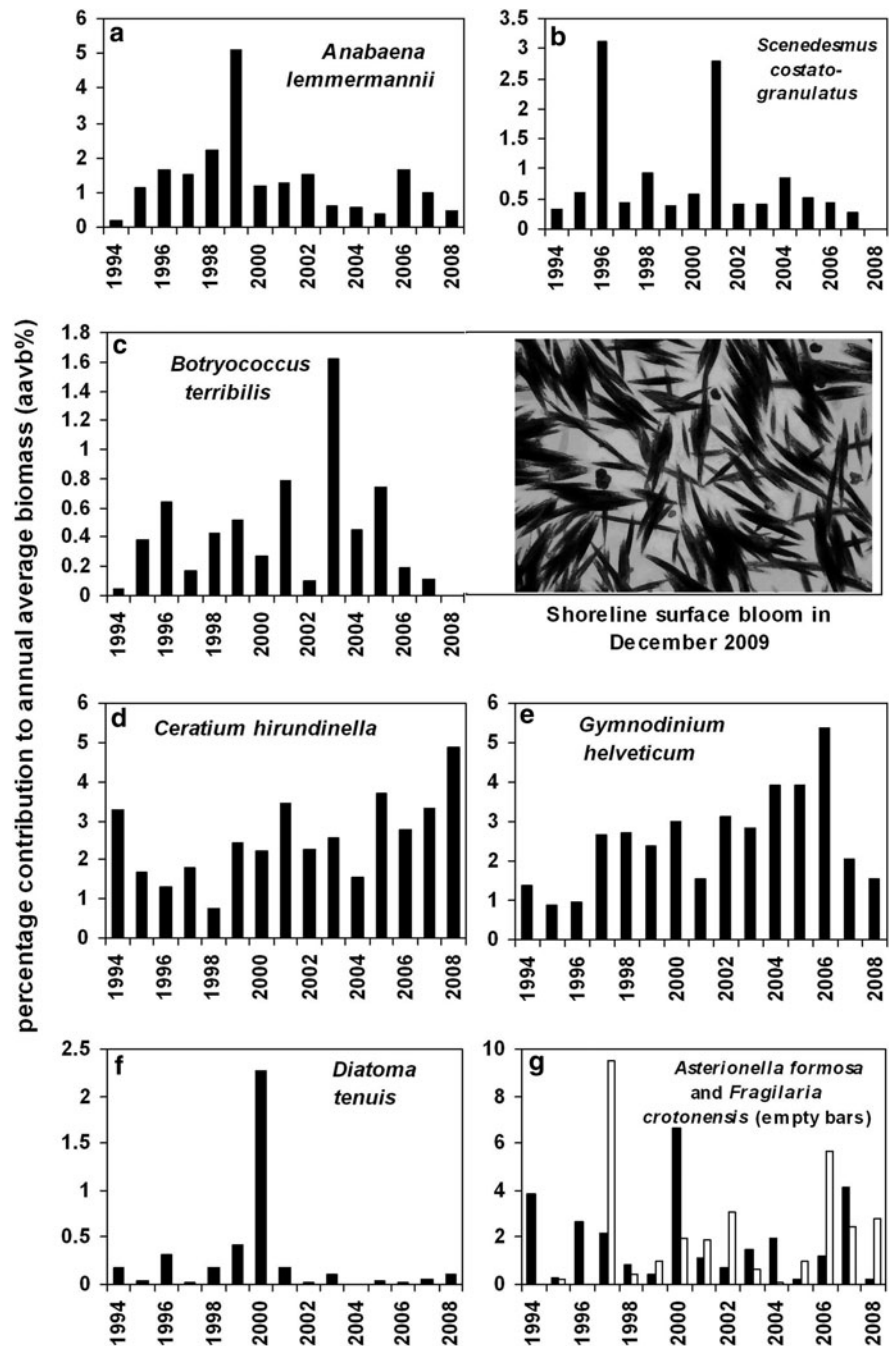
rubescens dominance and remained a permanent element of the phytoplankton (Fig. 4d).

Rare but constantly present species (35 species)

Species that did not exceed a contribution of >1% to annual total biomass typically exhibited either an increase in density with time (*Closterium acutum* var. *variabile*—Fig. 5d) or, more frequently, a decrease in density over time (*Radiocystis geminata*—Fig. 5a; *Quadrigula pfitzeri*—Fig. 5b; *Willea wilhelmii*—Fig. 5c; *Pseudotetraedriella kamillae*—Fig. 5e; *Trachydiscus sexangulatus*—Fig. 5f; *Cosmarium depressum* var. *planktonicum*—Fig. 5h). *Cymatopleura elliptica* (Fig. 5g) peaked in the middle of the study period.

Fig. 3 Percentage contribution to annual average biomass of species belonging to the ‘occasional dominants’ group.

a *Anabaena lemmermannii*; **b** *Scenedesmus costato-granulatus*; **c** *Botryococcus terribilis*—on the inserted photo the species is seen among *Aphanizomenon flos-aquae* clusters; **d** *Ceratium hirundinella* and **e** *Gymnodinium helveticum*; **f** *Diatoma tenue*; **g** *Asterionella formosa* and *Fragilaria crotonensis* in Lake Stechlin between 1994 and 2008



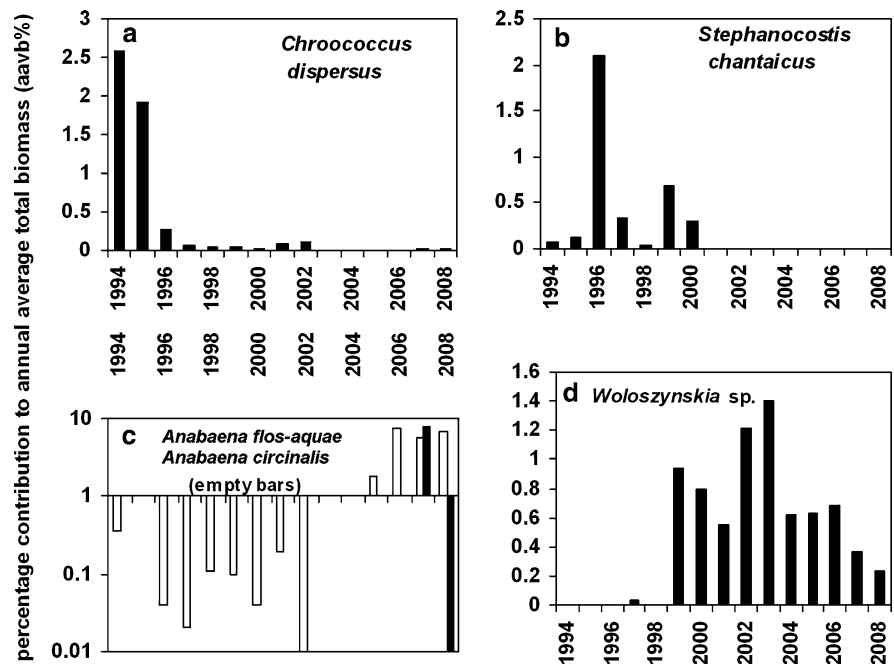
Very rare species (altogether 78 species)

The majority of species belong to the group that can be classified as very rare: specimens occurred occasionally, with years of absence between occurrences. For this reason, no trends in their 15-year changes can be traced.

Species that disappeared (12 species)

The number of species that disappeared during the study was not high. These species are so distinct and easy to identify that it was almost impossible to miss or misidentify them (*Planktolynghya circumcreta*, *Carteria* sp. 2; *Ankistrodesmus fusiformis*, *Coelastrum*

Fig. 4 Percentage contribution to annual average biomass of additional species belonging to the ‘occasional dominants’ group. **a** *Chroococcus dispersus*; **b** *Stephanocostis chantaicus*; **c** *Anabaena flos-aquae* and *A. circinalis* and **d** *Woloszynskia* sp. in Lake Stechlin between 1994 and 2008



astroideum, *Crucigenia rectangularis*, *Dictyosphaerium* sp., *Pediastrum duplex*, *Scenedesmus communis*, *Cosmarium bioculatum*, *Staurodesmus incus*, *Dinobryon acuminatum* and *D. suecicum*).

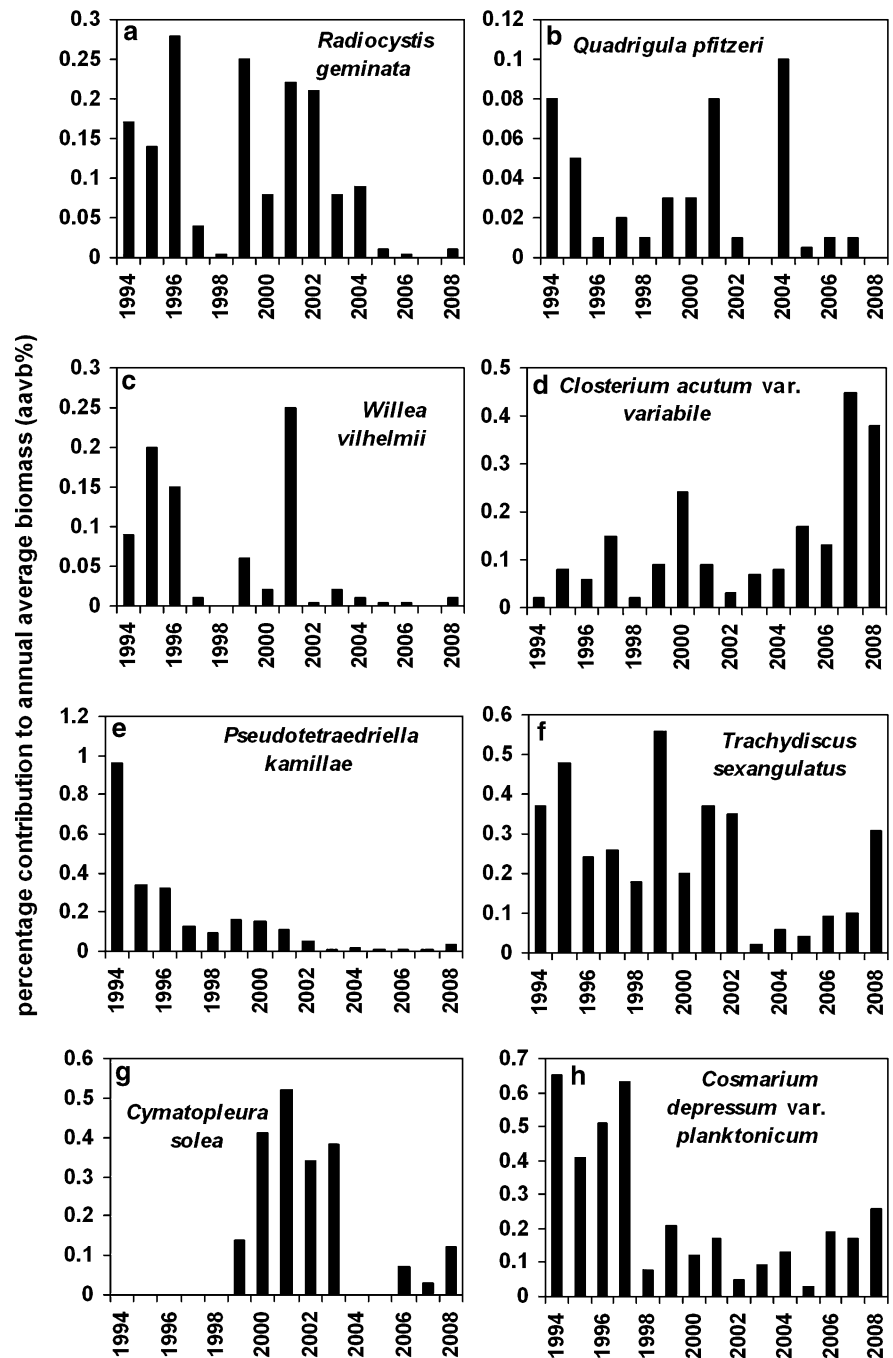
Immigrants (25 species)

Among the species that can be considered as recent immigrants, cyanobacteria were represented in very high numbers (*Dactylococcopsis* sp., *Romeria* sp., *Anabaena mendotae*, *A. macrospora*, *A. solitaria*, *A. spiroides*, *A. spiroides* var. *longicellularis*, *Anabaenopsis arnoldii*, *Aphanizomenon flos-aquae*, *A. gracile*, *Planktothrix agardhii*, *Pseudanabaena endophytica*, and *P. limnetica*; Fig. 6a–g). Though some remained at the level of detection (*Dactylococcopsis* sp., *Romeria* sp., *Pediastrum tetras*) or occurred once, or in 1 year only (*Chlorogibba pentagonia*, *Ceratium furcoides*), many others became rapidly dominants or subdominants. Among them, *Chrysopora fenestrata* (Fig. 6f) and *Planktothrix agardhii* (Fig. 6c) seem to increase with time and *Stichococcus contortus* (Fig. 6e) apparently provided a single peak in 2005 and seemed to fade. *Chlorella* sp. (Fig. 6d) appeared after the breakdown of the *Planktothrix* bloom in 1998 together with its symbiont *Stentor amethystinus* and their densities probably change in parallel.

Aphanizomenon flos-aquae represents a special case. The species appeared first in the samples in 2001, and then increased in its average contribution to total biomass (subpanel Fig. 6g). As changes in its absolute biomass (main panel on Fig. 6g) show, the species was seasonal (appeared in early summer and disappeared after the autumnal overturn) until 2006 and then it became perennial with peaks in late summer. In summer 2009, the species provided a late summer peak at a level of 400–500 $\mu\text{g wet weight l}^{-1}$. After a small drop, however, a second growth started providing a winter peak at about 915–920 $\mu\text{g l}^{-1}$. In the period December 2009–January 2010, *Aphanizomenon* in itself provided 87–90% contribution to total biomass and therefore developed a sufficiently long-lasting winter equilibrium phase. In December, part of the population accumulated in a macroscopically highly visible surface bloom along the shorelines (Fig. 3c). Though its biomass dropped to around 400 $\mu\text{g l}^{-1}$ by 18 February 2010 (under 17 cm thick ice covered by 20 cm snow), it still provided 85% of total biomass.

The hierarchical cluster analysis based on the annual abundances of the most common species (Fig. 7a) indicated two clusters of years at 0.3 dissimilarity level, and the third cluster was the year 1998. On the basis of relative biomasses of the phytoplankton

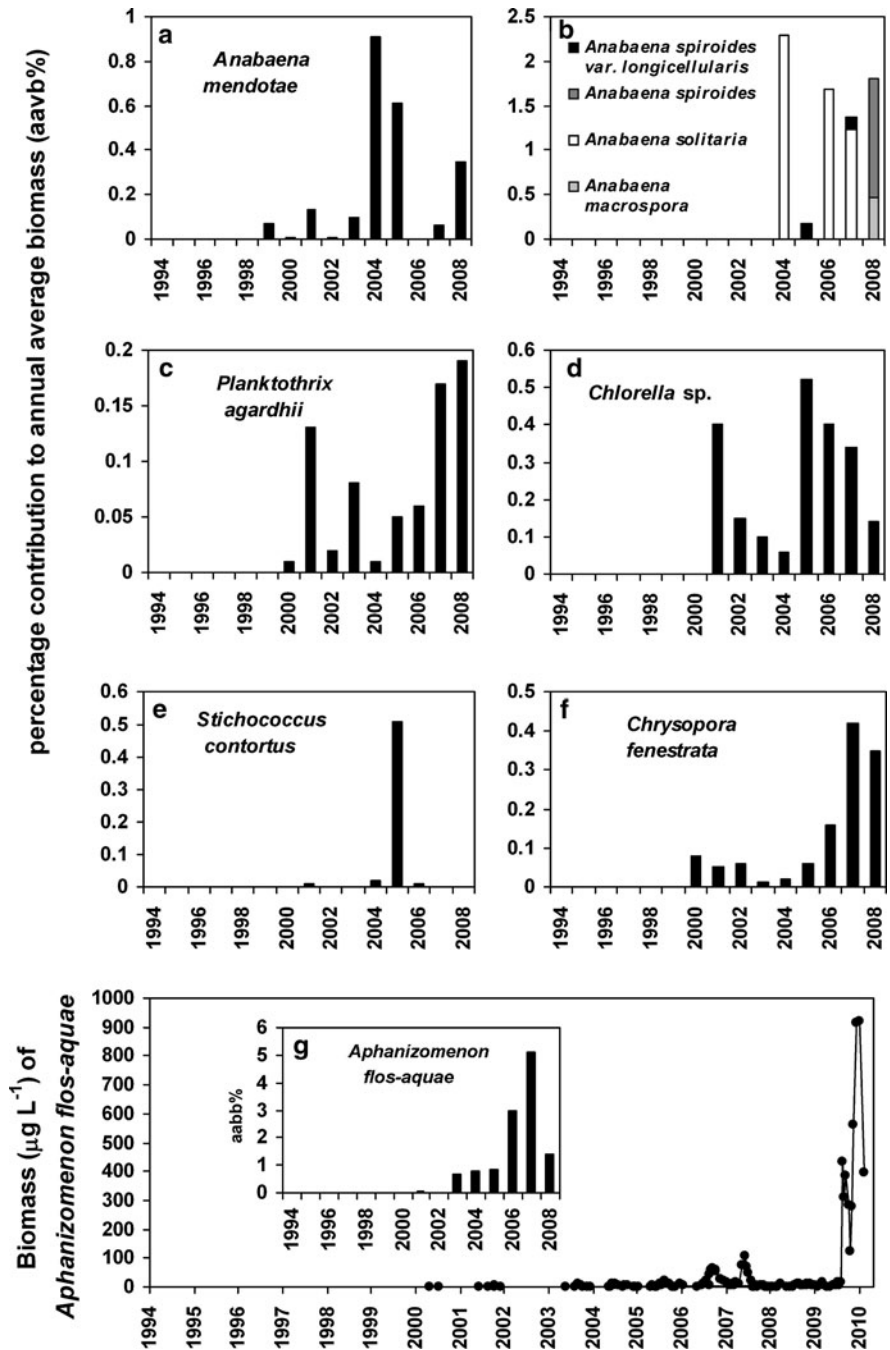
Fig. 5 Percentage contribution to annual average biomass of species belonging to the rare but constantly present group. **a** *Radiocystis geminata*; **b** *Quadrigula pfitzeri*; **c** *Willea vilhelmii*; **d** *Closterium acutum* var. *variabile*; **e** *Pseudotetraedriella kamillae*; **f** *Trachydiscus minutulus*; **g** *Cymatopleura solea*; **h** *Cosmarium planktonicum* var. *depressum* in Lake Stechlin between 1994 and 2008



functional groups, a similar diagram resulted (Fig. 7b). Only the year 2001 was placed into another cluster. A similar diagram, but at higher dissimilarity levels, resulted from the cluster analysis of the rare species (Fig. 7c). The diagram contains two clusters:

the years between the 1994 and 2000 period and the years 2001–2008. Thus, hierarchical clustering provided very similar data whether it was based on functional groups, the biomass of dominant species or on the occurrence number of the rare species.

Fig. 6 Percentage contribution to annual average biomass of species belonging to group of immigrant species. **a** *Anabaena mendotae*; **b** *A. spiroides* var. *longicellularis*, *A. spiroides*, *A. solitaria* and *A. macrospora*; **c** *Planktothrix agardhii*; **d** *Chlorella* sp.; **e** *Stichococcus contortus*; **f** *Chrysoptera fenestrata*; **g** internal panel: *Aphanizomenon flos-aquae*. The external panel of subgraph **g** shows the absolute biomass ($\mu\text{g L}^{-1}$) of *A. flos-aquae* in the period 16 January 1994 and 26 February 2010

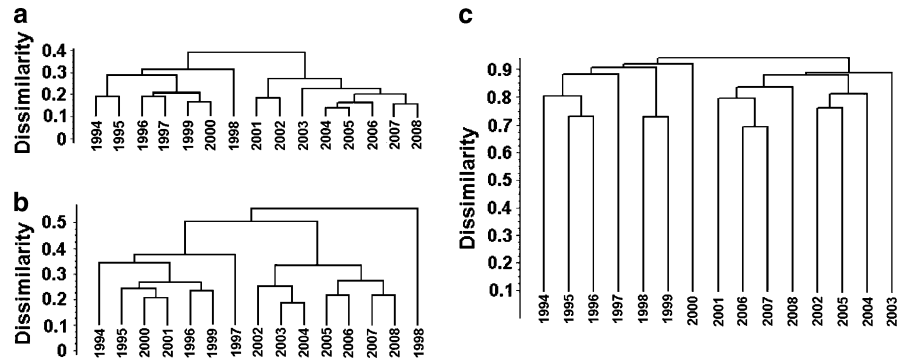


Occurrence of species

During the whole 15-year period, the occurrence of each species were summarized, the rank was calculated (Fig 8a) and an exponential distribution was found ($R^2 > 0.99$). According to this distribution, the whole range of occurrences was partitioned into 9

classes of increasing number of occurrences. Each class starts with doubling the start number of the previous class. The number of species occurring in each class was counted and an overall trendline was drawn (Fig 8b). The occurrence number in the 64–127 class extended beyond the overall trendline while the the 32–63 class fell below it. Other detailed analysis

Fig. 7 Hierarchical cluster analysis based on **a** the annual relative biomass of most common species; **b** the annual relative biomass of functional groups; **c** the occurrence number of the rarest species



showed that the number of occurrences suddenly increased in the 64–80-rank region. The interpretation of the diagram necessitated more detailed analyses. The maximum yearly occurrence number was calculated for each species and plotted against the total number of occurrences (Fig. 8c). Data of species which were found in only one year during the 15-year period are on the continuous support line. Data of the species which were present in all the water samples of the year are on the broken line. The almost-persistent species are close to this line. The rarest species with few total occurrence numbers evidently could not be persistent. The 16–60 range is poor, and in the 60–80 range there is a change from short period occurrence of species to persistence. In the 128–461 range, generalist species appear: these were present in almost the whole period studied during almost all the years. An important question is whether there is any relationship between the temporal distributional pattern and the number of years of occurrence (Fig. 8d). The number of years in which each particular species was found, and the total number of occurrences, was also calculated. Data on or close to the support line of Fig. 8d represent the persistent species, which are present in all (or almost all) samples of particular years. Moreover, the data on or close to the lower line represent species which were present in only one water sample in a year. Almost-persistent species were present only from 6 years up to the whole period. This phenomenon may be connected with the two periods calculated from hierarchical cluster analysis. The rarest species are near the continuous support line or near the y-axis of the diagram. These species may either occur only in a few years, or they could occur in almost all years of the studied period with generally low density.

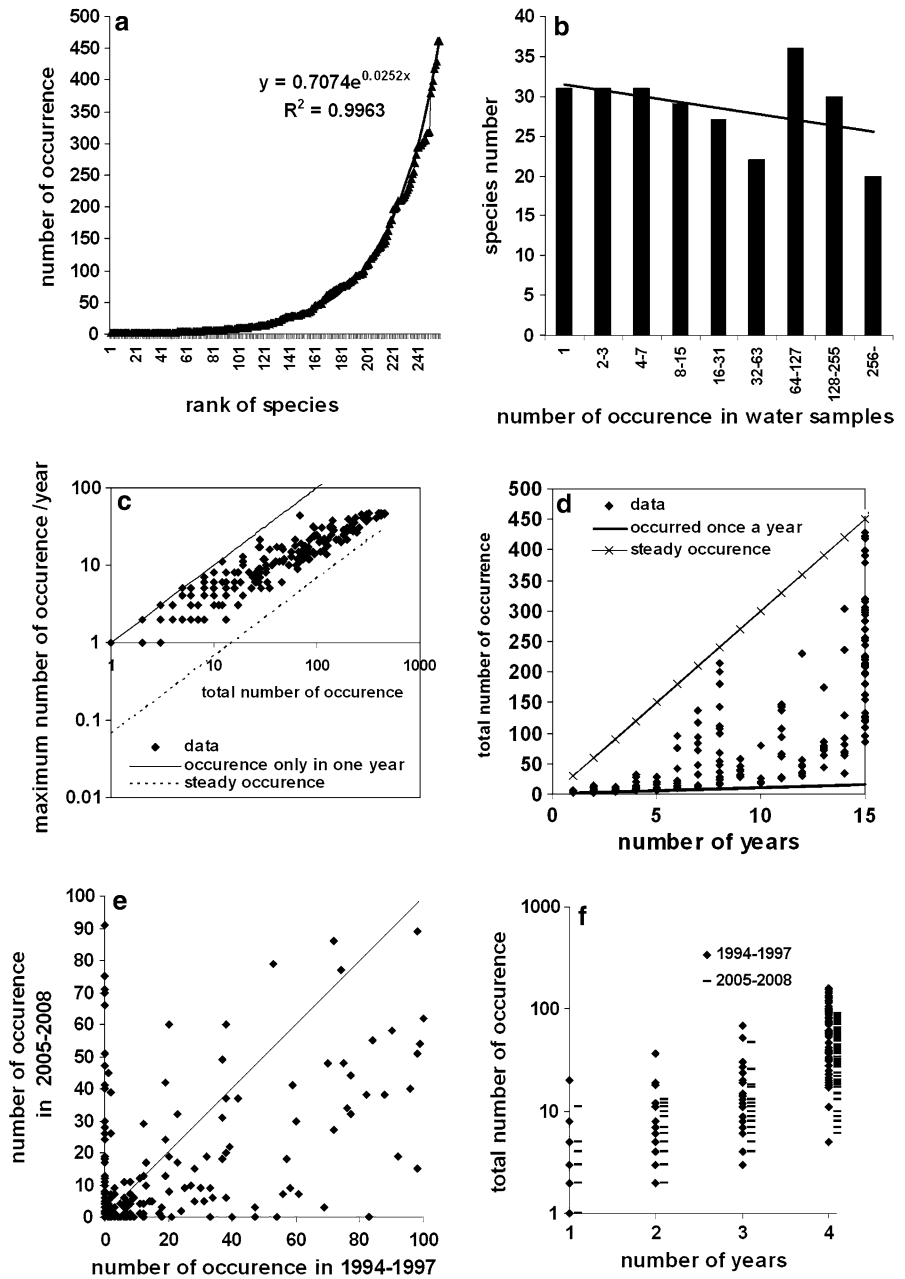
Is there any change in floral contribution and occurrences during the studied period, and is there any

relationship with the hierarchical cluster results? To examine this, two equal continuous periods were selected. These are the years between 1994 and 1997, and between 2005 and 2008. These years were clustered together by all the three methods (Fig. 7). The total number of occurrences, the number of years of occurrence, and the maximum of yearly occurrence were calculated for all species. There were more than 2-fold differences of total occurrence at 139 species from the whole taxon list (~250) between the two periods (Fig. 8e). Moreover, 33 species—which were found only once in the whole period—were excluded from this analysis. Most species which were present in the first period had fewer occurrences in the second period. The taxon list did not become quantitatively poor, but the occurrence number of the most species narrowed (Fig. 8f). It means that the occurrence number of the rarest species became larger, and the most common species became fewer. In return, there were 50 species that occurred in the second period, but were absent in the first period, and only 43 species were present in the first period and disappeared later. These are seen in the two axes of the diagram (Fig. 8f). The appearing and disappearing species were usually, but not always, the rarest. The most common disappearing species (*Cosmarium bioculatum*) was present in 29% of water samples of the first period, and, symmetrically, the most common appearing species (*Uroglena* sp.) occurred in 28% of water samples of the second period.

Rate of floral change

The cumulative number of species and, to a lesser extent, the number of species found in each year increased with time (Fig. 9). For interpretation of these quantities, two groups of species have to be

Fig. 8 Statistical records of phytoplankton species in Lake Stechlin between 1994 and 2008. **a** The rank of the total occurrence number, and its trend; **b** the species number in the different occurrence ranges, and its trend; **c** the maximum occurrence and the total occurrence relationship (logarithmic scale); **d** relationship between the total occurrence and the number of years between 1994 and 2008; **e** total occurrence between 1994 and 1997, and between 2005 and 2008; **f** relationship between the total occurrence and the number of years in two periods (logarithmic scale)



defined. A part of the species was qualified as statistically frequent species. They occurred at least once at a defined probability level (usually 95%) in every year during the investigation period (see Appendix—Supplementary material). From the database, 47 species match this definition. The others occurred with lower probability; those were the rare species in a statistical sense. The consequence of this partitioning is that all frequent species will appear in

the taxon list in any year (at 95% probability level), but only a small part of the rare species will be found. If the number of rare species in multitude is much larger than the number of species counted annually in water samples, different rare species will be found in consecutive years. Therefore, the cumulative species number may increase linearly over the years without any ecological change (Fig. 9). The linear trend of the cumulative number of species means that the

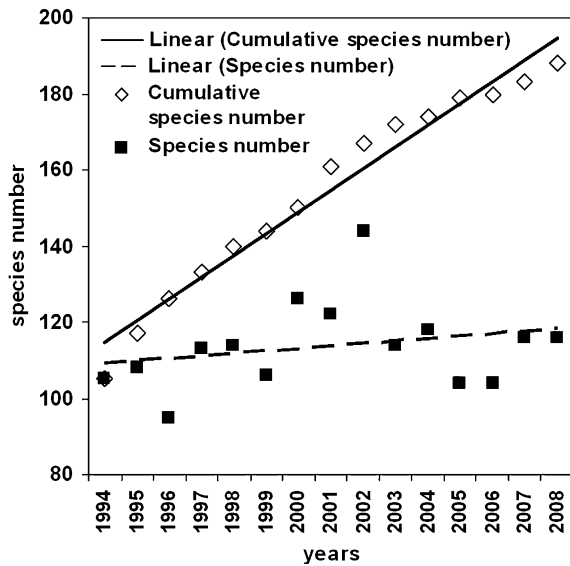


Fig. 9 Changes of the cumulative species number and the annually registered species number between 1994 and 2008 in Lake Stechlin

number of species in the phytoplankton community might be substantially larger than the maximum of the cumulative species number.

Assuming that the probability of occurrence of rare species in multitude is nearly equal to each other, and their abundance (units ml^{-1}) and proportion contribution to total biomass is almost constant over time, each species will be found with equal probability in the consecutive years, and therefore the number of rare species will be constant. As the number of frequent species is constant by definition, the number of species in each year must be steady.

In such circumstances, the observed increase of the species number in water samples must be a result of appearance of species new to the flora. If a frequent species appears, it will be found with 95% probability, but the probability of the new rare species appearing in the sample is much lower. It is

$$P = \frac{n_R}{N_R},$$

where n_R is the number of species in a year, N_R is the number of species in the phytoplankton community and P is the probability of getting in.

Since the total number of individuals of rare species is much lower than that of the frequent ones and supposing that this ratio in the community from

where the new species is coming is similar, the appearance ratio is

$$R = \frac{IND_R}{IND},$$

where IND_R is the number of individuals of the rare species, IND is the total individual number in the lake phytoplankton in a particular year, and R is the appearance ratio. The probability of finding a rare species in a sample is the probability of appearing (P) multiplied by the appearance ratio (R). After the estimation, the probability of finding a new rare species in the counted water samples is near zero. It means that the number increase of observed species is either a result of the appearance of a frequent species, or a previously rare species became more frequent. Since the frequent species were immediately detected, the number increase of measured species indicates an equal change in the multitude. This number is 1–2 species yearly by the linear trend of the diagram of the yearly counted number of species (Fig. 9). In other words, the number of species that are new in the flora can be estimated as 1–2 species per year.

Discussion

According to the classical assumptions of Island Biogeography (MacArthur & Wilson, 1967), species number in an unexplored ecosystem increases as long as ‘sufficient’ sampling effort discovers all the biota. Therefore, it is expected that the number of species in any ecosystem will increase with increasing sampling effort. However, any observed increase in the number of species involves at least two components. Part of the increase is due to the sampling effort in itself (we explore more and more species that are present in the given ecosystem but are so rare that the probability of finding them is low). Another part of the increase is due to immigrations: new species appear in the flora and fauna. Extinctions may counterbalance this increase over time, resulting again in a saturating type of function concerning the overall number of species in the given ecosystem and approximating the total number of species. Nevertheless, whether the immigrants establish or not, they will increase the cumulative total number of species in which extinctions are not included. Lake Stechlin’s planktonic algal flora seems to follow the theoretical assumptions. Most of

the increase in the cumulative total number of species can be attributed to increase in the sample size. A modelling approach has shown that immigration/extinction is responsible for only a small fraction of the observed change and can be estimated as 1–2 species per plankton year. Thus, the species pool (species that are present in the flora in any given time) of phytoplankton can be estimated as some 180 species, of which, due to sample size reasons, we find some 110 species annually. The rest of the species are so rare in the assemblage that for probability reasons they are not found every year. Since the number of dominant species (defined here as those that reach a minimum of 1% contribution to annual total biomass in any given plankton year) was 10–19 species annually (see Appendix—Supplementary material), we may conclude that the bulk of the species pool (160–170 species) is silent in individual plankton years and constitute the ecological memory of the ecosystem. Ecological memory is defined here according to (Padisák, 1992) as the capacity of the ecosystem or its experiences from past states to influence present or future responses of the community.

Survival strategies of different species are inevitably highly species-specific. Many may have specialized resting propagules in their life cycles (cysts of chrysophytes, dinoflagellates; akinetes of nostocalean blue-greens); however, most do not. They exist in perennial populations, like one of the crucial species of Lake Stechlin, *Planktothrix rubescens*, which is found in low numbers as greyish hormogonia in most years. *Aulacoseira islandica* represents a special case. Although it has been known for a long time that planktonic diatoms may have dormant hypolimnetic populations (Sicko-Goad et al., 1989) ready to rejuvenate when environment allows, Lake Stechlin represent a unique case where it was supported by observation. Viable cells of *Aulacoseira* appeared above the sediment at the deepest part of the lake (60 m) in January 1999. By the time the lake stratified, *Aulacoseira* was rather evenly distributed in the 40–60 m depth, but only inhabited the entire water column parallel with the autumnal overturn (see Fig. 5 in Padisák et al., 2003b). Whether or not its rejuvenation was triggered by the preceding *Planktothrix* bloom and consequent changes in chemical features in the lower hypolimnion remains at the level of speculation but certainly cannot be ruled out.

Though the probabilistic model of rarity that was developed in this study with its necessary simplifications and assumptions disregarded possible pluriannual patterns, their existence is apparent. Hierarchical clustering resulted in very similar patterns, whether it was based on functional groups, dominant species or rare species. The similarity of the functional and dominant species clustering is not surprising but the very similar pattern of the cluster of rare species is. It means that temporal proliferation of a certain set of the memory species is strongly connected to the behaviour of the actual dominants. In other words, however, scarce and seemingly unimportant most species are most of the time, interspecific interactions through ‘ecosystem engineering’ of the dominant species are important in species selection. The alternative explanation that the same interannual variations in the environment can favour parallel sets of different dominant and rare species is less likely since the subsequent behaviour has been rather apparent (see further discussion on consequences of *Planktothrix rubescens* dominance).

Indeed, we rarely mention ecosystem engineers (beavers are the best known in aquatic ecosystems) in the context of phytoplankton, though some species inevitably act this way. The best example in this data set is *Planktothrix rubescens*.

Planktothrix has been a permanent element of Lake Stechlin’s flora although it usually maintains a low, perennial population (Fig. 2b). Krieger (1927) first mentioned the presence of the species in the lake. Historical data (Casper, 1985) report on dense populations in 1969–1972 and 1976–1978. In January–March 1963, in holes broken into the ice cover, red flocks of *Planktothrix rubescens* were observed to float on the water surface. The only ‘deviant’ environmental variable prior to early and present blooms has been the long-lasting, thick ice cover in the preceding year. In fact, *Planktothrix rubescens* started to grow vigorously in winter 2008/2009 and was represented by several bright pink, long filaments in the winter samples. It appeared again in the summer samples with a maximum density of 400 filaments l^{-1} ; however, it disappeared after *Aphanizomenon flos-aquae*, a species that had never been observed in the lake prior to 2000, became dominant. The *Planktothrix* dominance in 1997/1998 was accompanied by basic changes in the competitive arena:

- a. In the winter–spring isothermal period when a diatom bloom commonly develops in Lake Stechlin, most of the plant nutrients were incorporated in *Planktothrix* filaments and therefore other species remained at very low levels experiencing strong competition for nutrients.
- b. Transparency of the water increased since the bulk of phytoplankton occurred in large, therefore optically ‘clear’ filaments of *Planktothrix* which, additionally, accumulated as a hypolimnetic maximum (Padisák et al., 2003c).
- c. Since *Planktothrix* filaments exceed the sizes that are suitable for zooplankton grazing, the density of zooplankton and with it the efficiency of the grazing food chain decreased (Padisák et al., 2003a).
- d. As large filaments of *Planktothrix* sank very slowly through the hypolimnion and accumulated somewhat on the sediments of the lake, hypolimnetic oxygen levels dropped to lower levels than usual. This was particularly true for the sediment surfaces where a higher level of hypoxia might have changed the sediment–water transfer processes (Gonsiorczyk et al., 2001, 2003). This might have triggered the rejuvenation of the *Aulacoseira islandica* population. An indication of changes in sediments might be the appearance of new species (*Gloeocapsa*, Rhodophyta sp.) of profundal origin in the plankton samples (Appendix—Supplementary material).
- e. Since during the *Planktothrix* bloom concentration of dissolved inorganic nitrogen compounds fell below the threshold that is considered limiting ($100 \mu\text{g l}^{-1}$; Sas, 1989) even in the hypolimnion (see Fig. 8 in Padisák et al., 2003a), it is difficult not to interpret the subsequent population increase (Fig. 3a) of *Anabaena lemmermannii* (the only N_2 -fixing blue-green species at that time) as the ecosystem’s need for more N.

The size of the dominant diatom species during the spring diatom maximum is another feature that has consequences for the species selection of the subsequent time. Though it was not analysed in detail, it is apparent that the larger the dominant species is, the sooner the diatom peak develops and declines. While *Cyclotella tripartita* and/or *C. pseudocomensis* peaked in April and declined only parallel with the stratification of the lake, during the *Aulacoseira* and

Stephanodiscus neoastraea years the peak occurred some time in February and the large and heavy diatom cells sank to the deep hypolimnion by the end of March, extracting the nutrients from the euphotic zone. As a consequence, the length of the clear water stage (Sommer et al., 1986) increased, sometimes lasting from March to July. During these times, the importance of mixotrophic flagellates increased and the ciliate *Stentor amethystinus* (together with *Chlorella*, its endosymbiont) appeared in large amounts.

The seasonal succession of phytoplankton was often claimed to follow similar pathways in individual years (Sommer, 1986). Indeed, in studies lasting the ‘usual’ (2–4 years) periods it may seem apparent and was attested later using morpho-functional groups from two lakes (Salmaso & Padisák, 2007). This study, covering 15 plankton years, has shown that it is not necessarily the case. There are some different patterns which may alternate. Moreover, species that become equilibrational dominants (sensu Sommer et al., 1993; Naselli-Flores et al., 2003) are often very rare in other periods and their temporal dominance may have substantial changes at ecosystem level.

If we consider only the 15-year data set that is analysed in this article, two main periods (with the *Planktothrix* year between them) can be clearly discriminated and their dominant assemblages outline an apparent eutrophication between 1994 and 2008. Spring dominants of codon **A** were successively replaced by species of codon **B** characteristic rather for meso- than for oligotrophic lakes and the summer **L_o** by **H1**, also indicating an increase in trophic conditions (Reynolds et al., 2002; Padisák et al., 2009a). The carrying capacity of Lake Stechlin for total plankton can be estimated at around $1 \text{ mg fresh weight l}^{-1}$, part of which is embedded in the biomass of other groups (fungi, zooplankton, bacteria, protists) in the warm months. This carrying capacity did not change significantly during the 15 years of this study. Still, replacements in functional groups, both in the spring isothermal period and the summer stagnation, report an increase in trophic status. Since frequent and rare species (and also functional grouping) provided very similar patterns in hierarchical clustering, the results of this study support some earlier observations that floral change occurs prior to quantitative changes (Padisák & Reynolds, 1998). The reasons for these trophic changes have been unclear, since no apparent external nutrient loading

could be traced. There are speculations on effects of forestry management and the subsequent changes in groundwater flow regimes; however, their effects on water quality and ecological status of the lake have not yet been studied and quantified. Nevertheless, it is possible to conclude that Lake Stechlin changed its oligotrophic status to mesotrophic during the studied period, which is in accordance with other observations (Koschel et al., 2002; Gonsiorczyk et al., 2003). Concerning the mass appearance of nostocalean blue-greens after 2000, one may wonder if it was the consequence of ongoing climate change. According to some estimates, a 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude (in the temperate zone). Therefore, species are expected to move towards the poles in response to shifting climate zones (Hughes, 2000; Parmesan, 2006). A recent study (Cellamare et al., 2010) reported on the appearance of a number of tropical species in France, and other signs of the effect of climate change on phytoplankton started to accumulate (Zohary et al., 2010).

Considering the available historical records, especially those of *Planktothrix rubescens*, it can also be hypothesized that, similar to terrestrial vegetation, there might be successional cycles (e.g. van der Maar, 1988) in plankton with recurrent characteristic assemblage types. Such cycles were already found in a very different lake (the saline and shallow Neusiedlersee; Padišák & Dokulil, 1994; Padišák, 1998) and were attributed to mesoclimatic cycles and consequent water level and salinity changes. Such changes in the water balance of Lake Stechlin cannot be traced, but the climate sensitivity of its plankton in comparison with other European lakes was demonstrated (Padišák et al., 2009b, 2010) and it is connected to the recurrent association of *Planktothrix* dominance with unusually cold winters with long-lasting ice cover. But the story of *Planktothrix* in Lake Stechlin is older than scientific records report.

The mystery of the Red Cock—a freshwater Phoenix

If you visit the Stechlin region, you will see a Red Cock, on T-shirts, in advertisements of tourist agencies, and on the logo of the local Natural Protection Agency. Why a red cock?

Lake Stechlin, though surrounded by many other lakes, is exceptional. An apparent feature is its clarity, and silence. That it is the deepest among all the others, one cannot see, but in some curious way one can feel it. The atmosphere of the lake may be repellent for those who like the bustle of cities but for others it is attractive, fascinating, almost addictive.

Theodore Fontane (1819–1898), the great realist of German literature, described it as ‘Here and there appear some rushes and reeds, but no boat ploughs the water, no bird sings, and only seldom a hawk flies over, casting its shadow on the mirror-like surface. All is still. And yet, from time to time things become lively on just this very spot.... when rumblings and grumbings begin far away out in the world, whether in Iceland, in Java, or even when the ashes from Hawaiian volcanoes rain far out over the southern seas. Then stir begins here too....’ (Fontane, 1898, p. 1, in Casper et al., 1985).

The second part of the above citation refers to the legend of the Red Cock, that is, by now, placed among the Brandenburgian legends. According to this legend, the Red Cock lives on the deep bottom of the lake. Whenever it appears, it is red and angry, beats the lake with its wings until it foams and surges, causing deaths, as the death of the fisherman Minack (Burkhardt, 1960).

Again and again people were impressed by the Lake Stechlin legend and many tried to unravel the background of the tale. Between 1733 and 1826 a family called Minack lived in the nearby village (Menz), as the parochial archives prove. However, there is no report of death by drowning. The odd water movements of Lake Stechlin causing the death of the fisherman Minack were coupled with the huge earthquake in Lisboa, Portugal, in 1755. Some other explanations were also based on tectonic activities, going to such extremes as in the 1930s, when the mining engineer C. Häner related the mysterious eruptive activity of Lake Stechlin to subterranean connections with waters far away in distant parts of the Earth and suggested the establishment of an earthquake early warning station on the shores of the lake.

As stated in the section above, explanations of the deviant behaviour of the lake were largely based on tectonic activities (Krausch, 1968) in an otherwise tectonically inactive region (at least since the lake was formed). Interestingly, there is no indication in

the literature that anybody ever noticed, or wondered about, the colour of the Cock. It was red. Any specimen of any kind of local waterfowl the size of a cock can be red if emerges from the water, from a hole dug into the ice, or, more likely, during a storm that causes ice break-up. Anyway, such an event may occur in the periods when populations of *Planktothrix rubescens* (the famous ‘Burgunderblutalge’ in the Swiss legend) developed in the upper hypolimnion and the subsequent winter stagnation in the lake and accumulated below the ice, as Casper’s (1985) description reports. In 1997/1998 when we observed a *Planktothrix* bloom in the lake, no such surface accumulation was seen, which suggests that such accumulations are even rarer than the blooms themselves. In fact, surface accumulation of *Planktothrix* in the lake combined with sudden and stormy ice break-ups seem to be sufficiently rare to serve as the basis of a legend, but these events are certainly not rare enough to become extinct from the memory of human populations that, without written records, may extend to several generations. In this way, the Red Cock legend parallels the Phoenix legends in people of coastal regions, who repeatedly experienced the resurrection of the ‘firebird’: any kind of waterfowl glowing from the luminescence of marine dinoflagellates. The Red Cock did not appear very often, but often enough to instigate legends and to reinforce them from time to time. The Red Cock is the Phoenix of a freshwater lake.

For the purpose of this article, the Red Cock legend provides ethnographical evidence for recurrent *Planktothrix rubescens* blooms in the lake further back than scientific recording allows.

G. E. Hutchinson was one of the few scientists who imposed paradigmatic influence on the science of ecology and limnology in the twentieth century. He was fascinated by the diversity of plankton that confronted the low number of limiting resources (Plankton Paradox; Hutchinson, 1961). How many species are there in Lake X, and how many species there should be? He certainly had this question on his mind when visited the sanctuary of Santa Rosalia on Monte Pellegrino close to Palermo, Sicily. When the first author of this article visited that same place, the sanctuary was quite abandoned but not as much as the ‘lake’ where neither *Corixa punctata* or *C. affinis* (Hutchinson, 1959) were present, since it was no more and no less than a dry basin (it was in summer),

convenient for walking on. However, the steps of the first author on the lake’s sediment were careful: she was sure that the sediments carry the necessary amount of propagules of all species that are hiding there, as an ecological memory of the lake, waiting for winter rains and ready to rejuvenate year by year. Hutchinson’s influence on contemporary ecology and limnology is immeasurable. It is interesting to view the recent literature. Sometimes his articles are often referenced, at other times almost abandoned. Then, again, one or another of his hypotheses is re-examined and referenced frequently. If somebody decides to explore Hutchinson’s influence, he/she will find a periodic rediscovery of his bits and pieces of science. What else can better show his influential life-work? Hutchinson, in the end, will not be indignant at mixing science with legend. And is there a more reliable witness than Santa Rosalia?

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