

Temporal organization of phytoplankton communities linked to physical forcing

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Abstract The performance of individual phytoplankton species is strongly governed by the thermal stratification's impact on vertical mixing within the water column, which alters the position of phytoplankton relative to nutrients and light. The present study documents shifts in phytoplankton structure and vertical positioning that have accompanied intensified long-term stratification in a natural ecosystem. Ordination analysis is used to extract gradients in phytoplankton composition in Lake Tahoe, an extremely nutrient-poor lake, over a 23-year period of records. Community structure in the 1980s was associated most strongly with resource availability (low nitrogen to phosphorus ratios, deeper euphotic zone depth), while intensified stratification dominated the phytoplankton structure since the late 1990s. Within diatoms, small-sized cells increased with reduced mixing, suggesting that suppressed turbulence provides them with a competitive advantage over large-sized cells. Among the morphologically diverse chlorophytes, filamentous and coenobial forms were favored under intensified stratification. The selection for small-sized diatoms is accompanied by a shoaling trend in their vertical position in the water column. In contrast, the motile flagellates displayed a deeper vertical positioning in recent years, indicating that optimal growth conditions shifted likely due

to reduced upwelling of nutrients. As the thermal stratification of lakes and oceans is strongly linked to climate variables, the present study confirms that climate warming will alter phytoplankton structure and dynamics largely through effects on nutrient availability and sinking velocities. Intensified stratification should favor the expansion of small-sized species and species with the capability of buoyancy regulation, which may alter primary productivity, nutrient recycling, and higher trophic productivity.

Keywords Lakes · Algae · Nutrients · Water-column stability · Mixing

Introduction

Phytoplankton communities consist of a number of diverse species with different ecophysiological and morphological characteristics, resource requirements, growth rates, and sinking velocities (Hutchinson 1967; Reynolds 2006; Tilman 1977). The structure of these communities, such as species size and composition, is governed by various environmental interactions. Vertical mixing is one of the key variables that conditions the growth performance of individual phytoplankton species within the water column (Bouman et al. 2006; Diehl et al. 2002; Huisman et al. 2004; Salmaso 2005), as mixing processes are usually accompanied by changes in resource availability of light and nutrients. Many studies have highlighted the seasonal periodicity of phytoplankton assemblages in lakes and oceans linked to seasonal variations in physical forcing of mixing dynamics, temperature, and the solar cycle (Sommer et al. 1986; Lewis 1978; Noges et al. 1998; Anneville et al. 2002). Similarly, experimental (Berger et al. 2007; Diehl et al. 2002; Ptacnik et al. 2003; Reynolds et al. 1983)

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and theoretical (Diehl 2002; Huisman et al. 2004) work documented shifts in algal community structure and dynamics related to physical mixing processes by affecting the distribution of algae in the water column and the light regime experienced by individual species. Few studies document floristic shifts in natural phytoplankton communities in relation to change in physical mixing processes linked to climate interactions (Chavez et al. 2002; Findlay et al. 2001; Karl et al. 1997; Lehman 2002; Schindler et al. 1990). Besides these well-documented observations, we know little about how natural phytoplankton communities respond to long-term changes in vertical mixing processes that would likely accompany climatic changes.

Vertical mixing of natural waters is largely determined by meteorological variables. Heat exchange processes and wind action create two opposing tendencies—the tendency to stratify and suppress mixing, and the tendency for inputs of turbulent kinetic energy to promote mixing (Wetzel 2001). The seasonal cycle of summer stratification and winter mixing is a product of the time varying nature of these two tendencies. It stands to reason that changes in meteorological forcing due to long-term climatic change would result in a modification of the balance between stratification and mixing. Marine and freshwater environments have experienced increased surface-water stratification and a decrease in mixing depth linked to climate warming over last decades (Boyd and Doney 2002; King et al. 1997; Livingstone 2003). The most significant climatic effects on phytoplankton species composition will most likely be mediated through changes in thermal stratification patterns such as the extent of the growing season and vertical mixing processes (Diehl et al. 2002; Rodriguez et al. 2001; Schindler et al. 1996; Smol et al. 2005). Detecting changes in natural phytoplankton assemblages associated with mixing regimes, however, is in part complicated by confounding factors of anthropogenic nutrient alterations, which often obscure mixing effects on algal species composition (Anneville et al. 2005; Edmondson 1994; Gaedke and Schweizer 1993).

A change in the intensity or duration of thermal stratification has a direct impact on turbulent diffusion and phytoplankton cell sedimentation, which are the major mechanisms causing vertical displacement for non-motile cells (Huisman et al. 2006; Livingstone 2003). Thermal stratification and vertical mixing therefore have an immediate influence on phytoplankton sinking velocities, which increase non-linearly with size (Smayda 1969), giving smaller species an advantage in an environment where turbulence is not present to resuspend all planktonic species (Bopp et al. 2005). In contrast, buoyant species and flagellates have relatively low net sinking velocities (Findlay et al. 2001; Huisman et al. 2004; Strecker et al. 2004), and the latter ones are highly motile and are capable of selecting an appropriate light and nutrient environment

in the water column (Fee 1976). Similarly, bloom-forming phytoplankton species (e.g., cyanobacteria) may contain gas vesicles to decrease their density. These functional species have a distinct competitive advantage at reduced vertical mixing (Findlay et al. 2001; Huisman et al. 2004; Strecker et al. 2004).

In addition to sinking velocities, water-column mixing affects nutrient availability for phytoplankton growth. Enhanced water-column stratification suppresses the upward flux of nutrients from deep-water layers through vertical mixing resulting in more nutrient-depleted conditions in surface waters (Livingstone 2003; O'Reilly et al. 2003; Schmittner 2005) and is accompanied by reduced primary production (Behrenfeld et al. 2006; Goldman et al. 1989; Jassby et al. 1999). Because a high surface area to volume ratio enables rapid nutrient exchange through the cell surface, small algal taxa are expected to be favored under lower nutrient concentration (Bell and Klaff 2001; Malone 1980). As a consequence, altered mixing regimes affect the competitive advantage of specific algal cell morphologies. Generalization on the basis of cell characteristics can be useful indicators of how alterations in the physical and chemical environment impact phytoplankton structure, because algae with similar cell morphologies often have similar functional properties (Huisman et al. 2006; Litchman et al. 2007; Reynolds 2006).

In the present contribution the historical phytoplankton dataset of Lake Tahoe is used to investigate how long-term changes in physical forcing alter the temporal dynamics of phytoplankton species composition. Lake Tahoe is an extremely oligotrophic lake that has experienced an increase in water-column stability over the last four decades, due to long-term climate warming (Coats et al. 2006). The phytoplankton community in the size range above 4 μm was dominated by diatoms, chlorophytes, chrysophytes, cryptophytes, and dinoflagellates, while cyanobacteria were usually under-represented. These conditions allow the investigation of mixing effects on a diverse phytoplankton assemblage. The present study describes recent floristic shifts and changes in the vertical positioning associated with changes in the strength of stratification. These results indicate that species characteristics have a major impact on the performance of individual species and that a differential response among functional groups can be anticipated with intensified stratification.

Materials and methods

Study site

Lake Tahoe is a subalpine lake located at an elevation of 1,898 m in the Sierra Nevada mountain range of California

and Nevada, USA. The lake has a surface area of 500 km², maximum depth of 501 m, mean depth of 330 m, and is free of ice the entire year. The lake is stratified from mid April to early November; the average thermocline depth is 21 m in August and increases to 32 m in October (Coats et al. 2006). It is an oligomictic lake, with the greatest depth of mixing in the late winter to early spring. Complete mixing to the bottom, however, is only seen in years of intense spring storms (Goldman et al. 1989; Wetzel 2001). Lake Tahoe is oligotrophic with a Secchi depth that currently is in the range of 20–25 m. The lake develops a deep-water chlorophyll maximum during the summer between 40 and 60 m depth (Abbott et al. 1984). Seasonal vertical profiles of environmental variables are illustrated in Fig. S1 in the Electronic Supplementary Material (ESM). The mesozooplankton population has been relatively consistent since the 1980s, dominated by the copepod species *Diaptomus tyrr-elli* and *Epischura nevadensis*, which showed low grazing pressure on phytoplankton (Elser and Goldman 1991).

Limnological data

Physico-chemical data used in this study were collected from a near-shore station (Index station, maximum sampled depth of 125 m) and a mid-lake station (maximum sampled depth of 450 m) (for a detailed map see Jassby et al. 2003), with an average sampling interval of 12 and 26 days, respectively, between 1982 and 2006. The data included in this study were restricted to this time period because phytoplankton numeration and identification have been conducted by the same observer over this period. Measurements of temperature at depths of 0, 2, 5, 10, 15, 20, 30, 50, and 100 m were combined from the near-shore and mid-lake station. Data from the two sites have typically shown very little differences at the same depths. For each depth, daily values of temperature were interpolated using cubic spline interpolation. The daily temperature profile at 1-m intervals was then derived by linear interpolation, and used to calculate volume-weighted mean lake temperature and vertical density profiles. Density was calculated as a function of temperature, salinity (assumed constant at 0.042 p.s.u.), and pressure (depth). An average density was calculated over a bin of 3 m and used to calculate vertical profiles of Brunt–Väisälä frequency (Millard et al. 1990) as an indicator of the stratification strength of the water column. This buoyancy frequency represents the strength of the vertical density gradient (N^2):

$$N^2 = \frac{-g \partial p}{\rho \partial z}$$

where g is the acceleration due to gravity, p is in situ potential density and z is depth. N^2 is a measure of the work

that must be done against gravity in order to break down thermal stratification in the water column (for further information see Fig. S2 in ESM). The stability of the lake was characterized by calculating monthly and annual average values of N^2 in the euphotic zone depth (2–60 m) as this depth region reflects the depths where phytoplankton dominate (Carney et al. 1988; Kiefer et al. 1972). Thermocline depth was calculated during the stratified season defined as depth at which density increased 0.215 g m⁻² from its surface reference value. Annual anomalies were calculated by subtracting the annual average for the entire time series.

Nitrate and phosphorus was measured at the mid-lake station at depths of 0, 10, 50, 100, 150, 200, 250, 300, 350, 400, and 450 m over the sampling period. For phosphorus, total acid-hydrolyzable phosphate (THP) has been measured historically in Lake Tahoe (Jassby et al. 1995). Since 2001 measurement of total phosphorus and orthophosphate concentration have been included in the sampling program. Historical THP concentration are corrected with orthophosphate concentration measured in recent years to calculate nitrogen:phosphorus molar ratios. Vertical nitrate profiles were used to estimate depth of spring mixing (for details see Pearl et al. 1975). Volume-weighted average nutrient concentrations were calculated in the upper 100-m water column after daily and depth interpolation.

Samples for phytoplankton counting and identification were collected from 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 75, 90, and 105 m depth at the Index station between 1982 and 2006 and from 0, 10, 50, and 100 m at the mid-lake station between 1992 and 2006 and fixed with Lugol's solution (no phytoplankton data are available for 1990 and 1991). Average sampling frequency for phytoplankton ranged between 13 days at the Index station and 30 days at the mid-lake station. Taxonomic phytoplankton identification and cell counts of species were analyzed from a composite sample, which was composed of volume-weighted aliquots from each depth sample based on the hypsographic curve of the lake. In addition discrete depth samples at 5, 20, 40, 60, 75, and 90 m were analyzed once a month from 1983 to 1987 and 2002 to 2006. After sedimentation of 100 ml for 72 h (Utermöhl technique; Lund et al. 1958), cells were measured and counted at the species level with an inverted microscope at 150×, 300×, and 600× magnification in order to cover the whole photoautotrophic community encompassing the nano- and microphytoplankton size range (>4 μm). For each sample a defined area of the Utermöhl chamber was counted. The first pass over the sample was viewed under low magnification, 150×, where a specific area (1 cm²) was counted for large, rare cells. At higher magnification, strips of 1 cm in length and one field of view in width were counted. A minimum of two strips, perpendicular to one another, were counted. If sample

abundances were low, up to four strips were counted with a minimum total cell count of 400 as the lower limit of acceptability. Phytoplankton biomass is expressed as cell volume and was estimated for individual species by assigning different geometric shapes that were most similar to the real shape of each phytoplankton species (Hillebrand 1999). A mean cell volume was assigned to each phytoplankton species based on current cell-size measurements. Average genus cell volume over the sampling period was estimated by correcting for the relative contribution of each species to the genus. Species composition and abundances were similar for both stations (not shown) and data from both stations were pooled for calculating monthly averages.

Data analysis

A total of 300 phytoplankton species represented by 99 genera have been identified over the course of the sampling period. Cyanobacteria and Euglenophyta were excluded in the analysis because of low abundances in the size range above 4 μm . For trend and ordination analysis, the genus level was used as the smallest taxonomic unit. It has been shown that little additional information is gained when phytoplankton are identified to species rather than genera, and genera are a reliable indicator of perturbation (Cottingham and Carpenter 1998). Rare genera, defined as those occurring in less than two annual observations and/or low biovolume, were excluded in the multivariate analysis to reduce noise in the data, which resulted in a total of 63 genera. Trends were estimated with robust nonparametric methods that are efficient in the presence of non-normal residuals and outliers. Monotonic trends in monthly series were assessed using the seasonal Kendall test corrected for serial correlation (Hirsch and Slack 1984).

Non-metric multidimensional scaling (NMDS) ordination and hierarchical clustering analysis were used to extract gradients in phytoplankton community composition over time based on the Sørensen (Bray–Curtis) distance matrix. NMDS is a powerful tool for ecological community data that include a large portion of zero values because it is not biased by the “joint absences” effect (McCune et al. 2002) and outperformed linear models (such as principal components analysis or redundancy analysis). NMDS is an iterative search for the positions of species and time on few dimensions (axes) that minimizes the departure from monotonicity in the association between distance (dissimilarity) in the original data and ordination space. It plots dissimilar objects far apart in the ordination space and similar objects close to one another. The temporal dynamics of the phytoplankton community was characterized based on biovolume averages to reflect the true contribution of individual species to phytoplankton

community composition (Interlandi and Kilham 2001). Temporal change of phytoplankton genera is conducted on a matrix of annual averages (year) by genera biovolume to extract years with similar phytoplankton structure.

Data were transformed by square root transformation and double standardized (species by maximum species biovolume and dates to unit totals). NMDS is started from random starting configurations and the solution with the lowest “stress” was selected from 500 runs. Stress measures departure of fit between the ordination and the data and is calculated as a departure from monotonicity between the two series of distances. A stable three-dimensional solution was identified for all ordinations. Orthogonal rotation of the NMDS solution was used to maximize correlations of axes so that the variance of points is maximized on first dimension. Environmental variables were related to the strongest gradients (axes) in species composition and, using overlays, in the ordination space towards which the environmental vectors change most rapidly and to which they have maximal correlations with the ordination configuration. Linear regression was used to relate the environmental data of nutrient concentration, optical and physical (mixing) properties, as well as zooplankton (crustacean) density to the NMDS axis scores (Jovan and McCune 2005). Multivariate analysis was conducted using the vegan package in R.

Species indicator values (Dufrêne and Legendre 1997) are calculated to characterize phytoplankton genera within the time periods of similar phytoplankton community identified by cluster analysis. The indicator value of each genus is calculated as the product of the relative frequency and relative average abundance in clusters. The maximum indicator value for each species among all clusters was retained (Dufrêne and Legendre 1997).

Results

Long-term trends and seasonal phytoplankton succession

Available phosphorus (orthophosphate) concentrations were slightly elevated in the 1980s in Lake Tahoe and decreased thereafter according to the seasonal Kendall test ($\tau = -0.31$, $P = 0.001$; Fig. 1a) and were at a consistently low level of 1–1.5 $\mu\text{g l}^{-1}$ between 1990 and 2006 ($\tau = -0.01$, $P = 0.93$). In comparison, average annual total phosphorus concentration in the top 100 m water was 7.4 $\mu\text{g l}^{-1}$ (± 1.7 SD) between 2001 and 2006 (data not shown). Average annual nitrate concentrations showed high interannual variability ranging between 4 and 11 $\mu\text{g l}^{-1}$ and no consistent trend ($\tau = 0.13$, $P = 0.24$; Fig. 1b). The depth of spring mixing explained about 68% of the

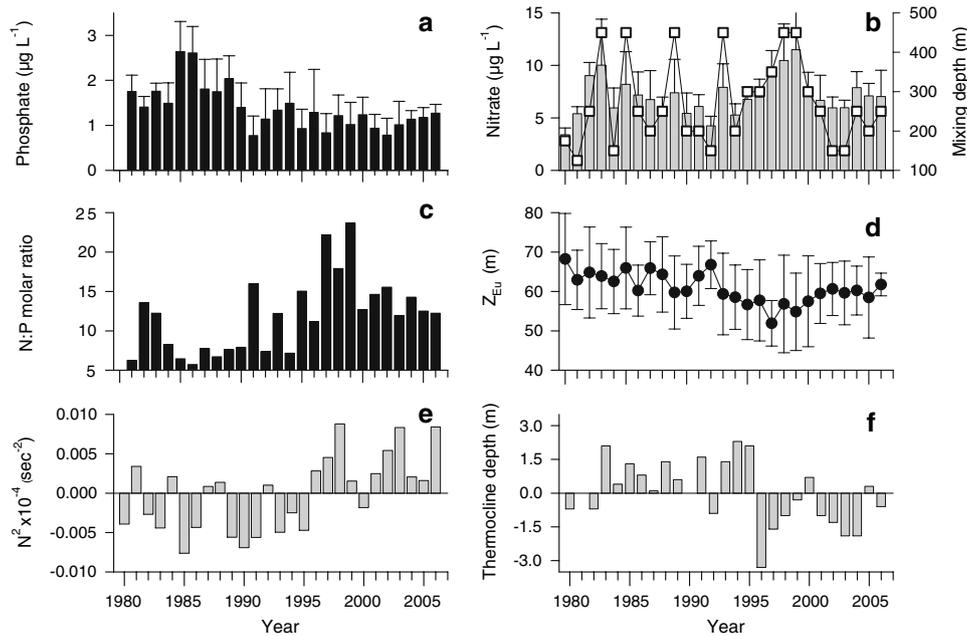


Fig. 1a–f Annual averages of nutrient concentrations and physical properties in Lake Tahoe, California, USA between 1980 and 2006. **a** Orthophosphate concentration (no data are available for 1980), **b** Nitrate concentration ($\mu\text{g L}^{-1}$, gray bars) and depth of spring mixing (open symbols) and **c** nitrogen:phosphorus molar ratio ($N:P$) are average estimates of the upper 100-m water column. **d** Euphotic zone

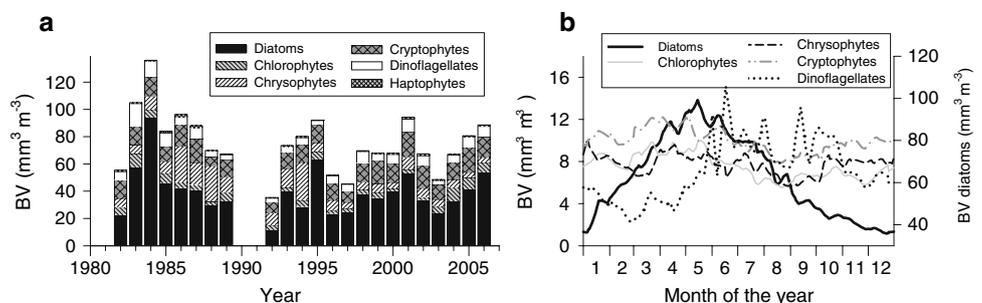
depth (Z_{Eu}) reflects the depth where photosynthetic available radiation is 1% of its surface value. **e** Brunt–Väisälä frequency (N^2) anomalies, used as an indicator of stratification strength, and **f** thermocline depth anomalies are calculated as deviations from the long-term mean between 1980 and 2006. Error bars represent SDs

variance in annual nitrate concentration in the upper 100-m water column ($P < 0.001$). Elevated annual nitrate concentrations in the upper water layers were observed with deeper spring mixing depth when high-nitrate water from deep-water layers was transported to the surface layers (Fig. 1b). Overall the dissolved nitrogen:phosphorus molar ratio increased significantly over the sampling period ($\tau = 0.28$, $P = 0.004$; Fig. 1c), indicating nitrogen limitation in the 1980s to phosphorus limitation in the 1990s and near-balanced nitrogen:phosphorus supply according to the Redfield ratio (assuming a 16:1 molar ratio) in recent years, respectively. Monthly average euphotic zone depth decreased over the sampling period ($\tau = -0.17$, $P = 0.02$) and annual averages ranged between 52 and 67 m (Fig. 1d). In addition, the strength of stratification (N^2) of the

euphotic zone depth increased ($\tau = 0.41$, $P = 0.008$) over the same period. Since the late 1990s, values of N^2 were above the average for the period 1980–2006 (except 2000) (Fig. 1e), suggesting an intensification of stratification in the 2- to 60-m depth interval. A trend of increasing stratification is further reflected in shoaling thermocline depth during the stratification period (the shoaling trend was marginally non-significant, $\tau = -0.09$, $P = 0.08$; Fig. 1f); annual average thermocline depth varied between 27.7 and 33.3 m depth.

Total annual phytoplankton biovolume was relatively consistent between 1982 and 2006 ($\tau = -0.19$, $P = 0.22$; Fig. 2a). Among the major phytoplankton groups, chrysophytes showed a significant downward trend based on monthly biovolume averages ($\tau = -0.17$, $P = 0.03$), while

Fig. 2 a Annual and **b** monthly average phytoplankton biovolume (BV) of major taxonomic phytoplankton groups in Lake Tahoe between 1982 and 2006 (no data are available for 1990 and 1991). Haptophytes are not shown in **b** because of their low abundances. Diatom BV in **b** is shown on the right-hand axis



the remaining major taxonomic groups did not exhibit a significant trend over the sampling period ($P > 0.16$). Diatoms showed a clear seasonal pattern with high abundances in spring (Fig. 2b). The diatom biovolume increased linearly from the beginning of the year and peaked in early May, soon after stratification occurred. Biovolumes of chlorophytes, chrysophytes, and cryptophytes were fairly uniform during winter and spring, and decreased slightly with stratification. Dinoflagellates displayed the opposite response, increasing noticeably after the onset of stratification in late April, peaking in June and then gradually declining through the end of the year (Fig. 2b).

Long-term shift in phytoplankton species composition

The NMDS ordination of the phytoplankton community, based on annual average biovolume, suggested a final solution with three axes (correlation between calculated dissimilarities and ordination distance for first two dimensions $r = 0.81$); the addition of a fourth axis afforded only a slight reduction in minimum stress. Because the third axis had only low correlations with environmental

variables it will not be discussed further. The NMDS ordination indicates that community structure differed largely among years and a temporal separation based on species composition is evident (Fig. 3). Three periods of distinct phytoplankton structure were identified since 1982. Community composition differed between years during the 1980s (1982–1989) and in the early/mid 1990s (1992–1997) and since 1998 (ANOSIM contrasting the three periods, $r = 0.79$, $P < 0.001$). The pattern of temporal phytoplankton community separation is identical using cluster analysis (Fig. 4). Annual phytoplankton community was classified into two clusters with distinctive phytoplankton community structure. Cluster 2 can be split further into two sub-clusters identical to the NMDS ordination. Indicator species for the first period included genera from all functional groups, for the second period from chlorophytes and diatoms, and for the third period mainly chlorophytes, chrysophytes, cryptophytes and the diatoms *Cymbella* and *Cyclotella*. The gradient in species composition along NMDS axis 1 was most strongly associated with phosphorus concentration, euphotic zone depth, and the nitrogen:phosphorus ratio (Fig. 3; Table 1), indicating that slightly elevated phosphorus concentrations and nitrate

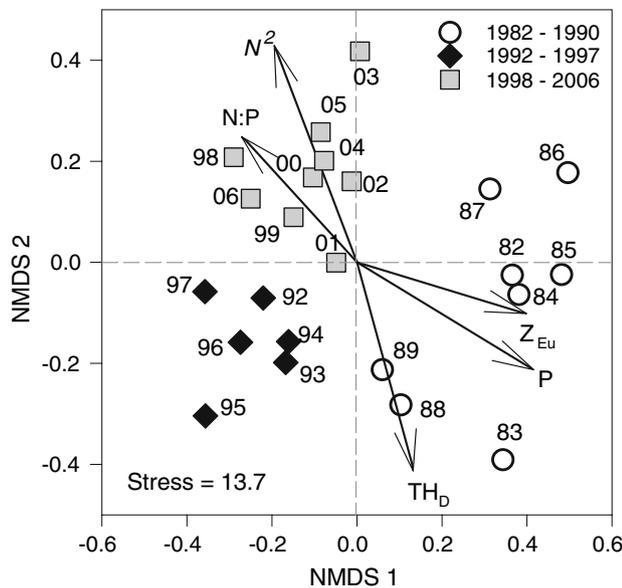


Fig. 3 Ordination and cluster analysis of the phytoplankton community from Lake Tahoe for 23 years (1982–2006; no data are available for 1990 and 1991). Non-metric multidimensional scaling (NMDS) ordination of year scores derived from annual genera BV with environmental variables overlaid [three distinct periods: 1982–1990 (circles), 1992–1997 (filled diamonds), 1998–2006 (shaded squares)]. Vector length and direction indicate correlation with the ordination and point to the direction of most rapid change in the environmental variable. Only significant vectors are shown (see Table 1). Environmental vectors are: the strength of the vertical stratification (N^2), thermocline depth (TH_D), orthophosphate concentration (P), N:P, and Z_{Eu} . For other abbreviations, see Figs. 1 and 2

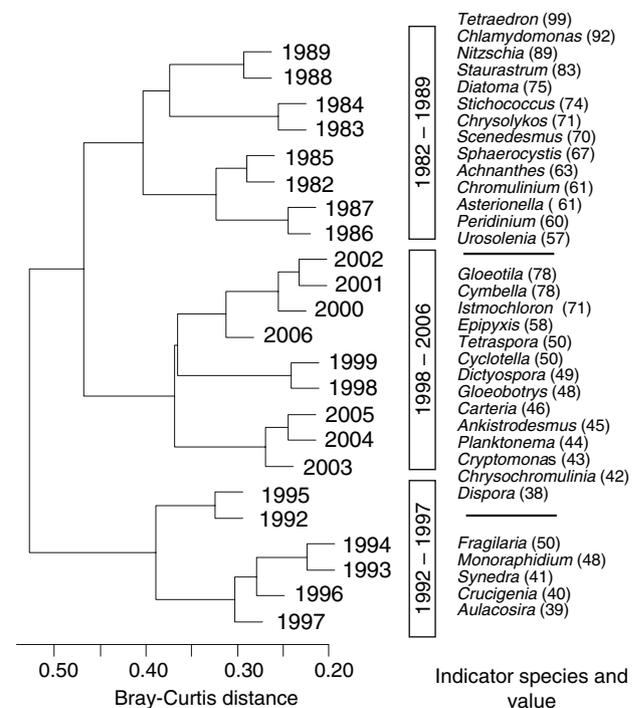


Fig. 4 Cluster dendrogram using complete-linkage method of annual BV phytoplankton genera. The horizontal axis (Bray–Curtis distance) represents the height at which each merger was made. Indicator species and their corresponding indicator value are listed for each period. Species with an indicator value >56 for the first period and >25 for subsequent periods are retained (for additional genera see Table S1 in ESM)

limitation and/or a deeper euphotic zone depth are the dominant drivers for a different phytoplankton community composition in the 1980s. The gradient of NMDS axis score 2 reflects the increasing trend in stratification strength and decreasing trend in thermocline depth, suggesting that intensified stratification affected the phytoplankton community particularly since the late 1990s. Other environmental factors considered in the analysis as well as zooplankton density showed weak association with axis scores (Table 1).

NMDS axis score 1 is positively associated with biovolume changes of the majority of phytoplankton genera across the entire size spectrum between $7 \mu\text{m}^3$ (Flagellates) and $28,556 \mu\text{m}^3$ (*Zygnema*) cell volume or 3.5 and $332 \mu\text{m}$ maximal linear dimension (Fig. 5; Table S1 in ESM). Several chlorophyte genera including different functional and morphological characteristics showed strong association with low nitrogen:phosphorus ratios and deeper euphotic zone depth, such as the flagellate *Chlamydomonas*, the unicells *Staurastrum* and *Tetraedron*, the coenobia *Scenedesmus*, and the filamentous genera *Zygnema* and *Mougeotia* (Fig. 5a). These genera showed high indicator values for this first time period (Fig. 4) and were rarely observed in recent years, suggesting that conditions in the 1980s were favorable for these taxa. The strongest positive association of chlorophytes with axis 2 was with the coenobia *Dispora* and *Ankistrodesmus*, the coloniales *Botryococcus* and *Nephrocytium*, and the filamentous genera *Gloeotila* and *Planktonema* (Fig. 5a). These genera are representative of the third time period (Fig. 4),

indicating association with more stratified conditions. Among chrysophytes, *Ochromonas* and *Chrysolykos* indicated a positive correlation with axis 1 (Fig. 5b) and the small-sized genera *Epipyxis* and *Mallomonas* as well the colonial *Gloeobotrys* with axis 2. These taxa were indicative of the first and third time period, respectively (Fig. 4). The colonial flagellate chrysophyte *Uroglena* appeared sporadically in high densities in the lake and is strongly associated with years of greater mixing and/or phosphorus limitation. The haptophyte *Pleurochrysis*, *Bicosoeca*, and the dinoflagellates *Peridinium* indicated a strong association with axis 1, while correlations of the remaining genera within these groups and cryptophytes were generally weak with both axes (Fig. 5c). Most of the large-sized (fast-sinking) diatoms were positively associated with axis 1 such as *Suriella*, *Nitzschia*, and *Navicula* (Fig. 5d), suggesting that these diatoms were favored under low nitrogen:phosphorus ratios and stronger mixing. Among diatoms, genera associated with an intensified vertical density gradient were the relatively small-sized species *Cyclotella* and *Cymbella* and were characteristic of the third time period (Fig. 4). Additionally, these genera were negatively associated with axis 1, indicating facilitation under an increased vertical density gradient and phosphorus limitation. In contrast the large-sized genera *Fragilaria* and *Synedra* were negatively associated with axis 2 and the strength of the vertical density gradient, respectively, and indicative of the first and second time period (Fig. 4).

Several genera of the phytoplankton assemblage exhibited a trend of changing biovolume over the sampling period (for detailed trend statistics see Table S1 in ESM). Multiple regression of the phytoplankton Kendall correlation coefficient (τ) on their ordination scores were negatively associated along axis 1 and positively along axis 2 ($R = 0.81$; partial correlation coefficients, $r_{\text{NMDS1}} = -0.65$, $r_{\text{NMDS2}} = 0.32$; $P < 0.001$). This indicates that genera with positive scores along axis 1 showed a tendency of declining abundance over the sampling period (Fig. 6a), including some of the dominant taxa such as the flagellates *Chlamydomonas*, *Peridinium*, *Synura*, *Stichococcus*, the relatively large-sized cells *Asterionella*, *Synedra* and *Staurastrum*, and the small-sized unicells *Stichococcus*, *Tetraedron*, and *Urosolenia*. This association suggests a declining response to increasing nitrogen:phosphorus ratio and reduced light levels. In contrast, Fig. 6b shows that genera with high scores along axis 2 exhibited a positive trend, suggesting that these genera were particularly favored under stronger stratification and increased nitrogen:phosphorus ratio. Functional groups that contribute to this pattern include mainly filamentous (e.g., *Planktonema*, *Gloeotila*), coloniales and coenobia (e.g., *Botryococcus*, *Gloeobotrys*, *Dispora*) as well as small-sized algal cells (e.g., *Epipyxis*, *Cyclotella*).

Table 1 Pearson coefficient of determination (r) between environmental variables and phytoplankton NMDS axis scores in Lake Tahoe between 1982 and 2006 ($n = 23$)

Variables	Axis 1	Axis 2	P
Euphotic zone depth	0.63	-0.20	<0.001
Nitrate concentration	0.02	-0.03	0.73
Nitrogen:phosphorus molar ratio	-0.54	0.32	0.007
Phosphate concentration	0.74	-0.26	<0.001
Spring mixing depth	-0.07	-0.26	0.48
Stratification strength	-0.38	0.59	0.007
Thermocline depth	0.29	-0.62	0.002
Timing of stratification onset	0.14	-0.03	0.30
Zooplankton density	0.04	-0.39	0.10

Correlation coefficients indicate the strength (magnitude) and directionality (sign) of vectors to ordination axis scores 1 and 2. Positive and negative signs indicate an increase or decrease along an axis, respectively. Axis 1 is rotated to reflect the observed (decreasing) gradient in phosphorus concentration and euphotic depth. P indicates the significance of fitted vectors using permutation of environmental variables ($n = 1000$). For description of environmental variables see “Materials and methods” section. Significant variables are in bold-face type

Fig. 5a–e NMDS ordination biplots of phytoplankton genera in Lake Tahoe between 1982 and 2006. **a–d** Indicate genera within each major taxonomic group; **e** vectors of significant environmental variables are shown (with same axis scales). Environmental vectors are described in Fig. 3. Species characteristics are fast sinking (*FS*), and slow sinking (*SS*); for details see Table S1 in ESM. *Chlam* *Chlamydomonas*, *Dictyo* *Dictyosphaerium*, *Monor* *Monoraphidium*, *Neph* *Nephrocytium*, *Spon* *Spondylosium*, *Elakat* *Elakatothrix*, *Stich* *Stichococcus*, *Stau* *Staurastrum*, *Zyg* *Zygnema*, *Tetraed* *Tetraedron* (a colonial flagellate), *Oocy* *Oocystis*, *Achn* *Achnanthes*, *Masto* *Mastogloia*, *Navic* *Navicula*, *Suri* *Surirella*

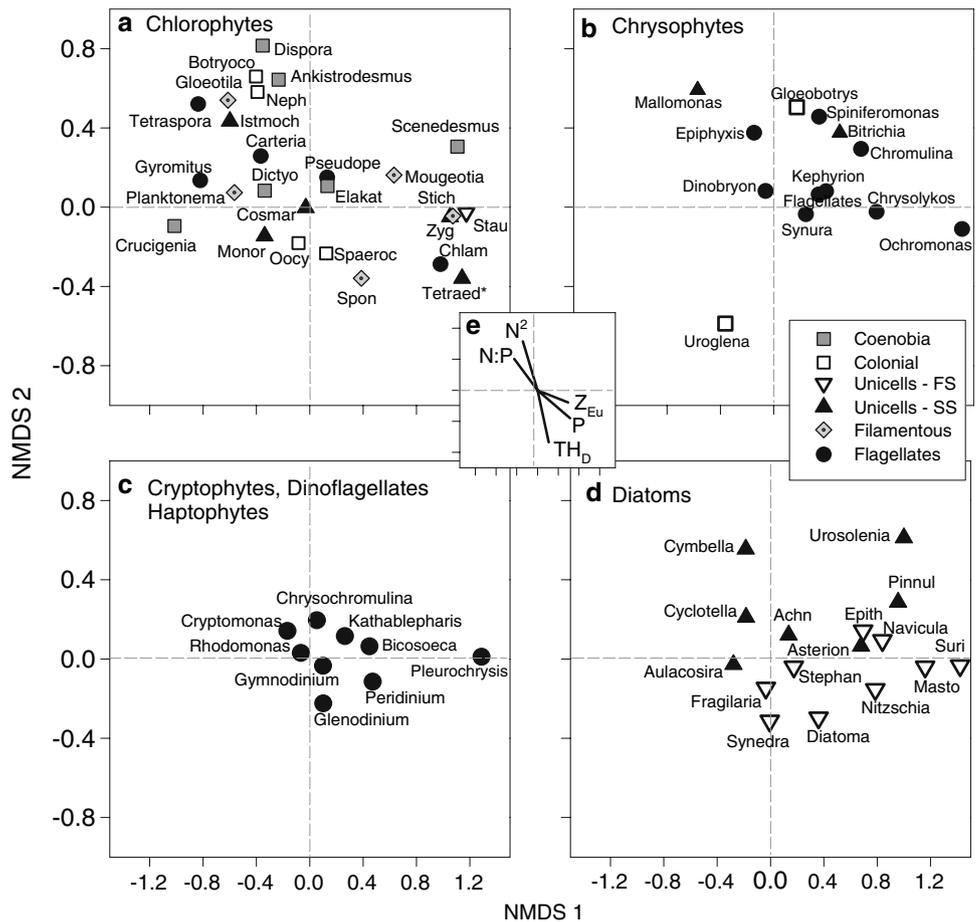
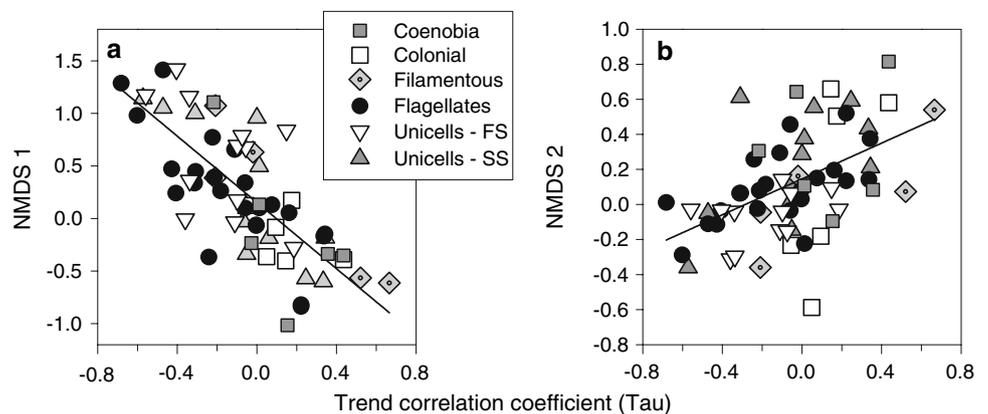


Fig. 6 Correlation between **a** NMDS axis scores 1 and **b** NMDS axis scores 2 and trend statistic of phytoplankton genera between 1982 and 2006. The trend is calculated according to the Kendall τ -test (*Tau*). Morphological characteristics of genera are represented by symbols (*FS*, *SS*; for species classification see Table S1 in ESM). For abbreviations, see Figs. 3 and 5



Vertical distribution patterns

The bulk phytoplankton biomass in Lake Tahoe is observed between 45 and 65 m depth and concentrated around the depth region where phosphorus and nitrogen increase (Fig. 7). Compared to the 1980s, mean depth of diatoms was about 10 m shallower in most recent years (mean depth between 1983 and 1986 was 59 ± 3 m and between 2002 and 2006 50 ± 4.6 m; ANOVA contrasting

the two periods, $F_{(2,11)} = 8.9$, $P = 0.004$; Fig. 7). In addition, maximum mean diatom depth was at about 75 m in the 1980s compared to 60 m in more recent years, suggesting that a larger fraction of diatom biomass was present at shallower depths and a smaller fraction at deeper depth in more recent years. The trend of higher diatom biovolume in shallower depths cannot be explained by changes in the euphotic zone depth (correlation coefficient between Z_{Eu} and mean diatom depth, $r^2 = 0.28$, $P = 0.11$,

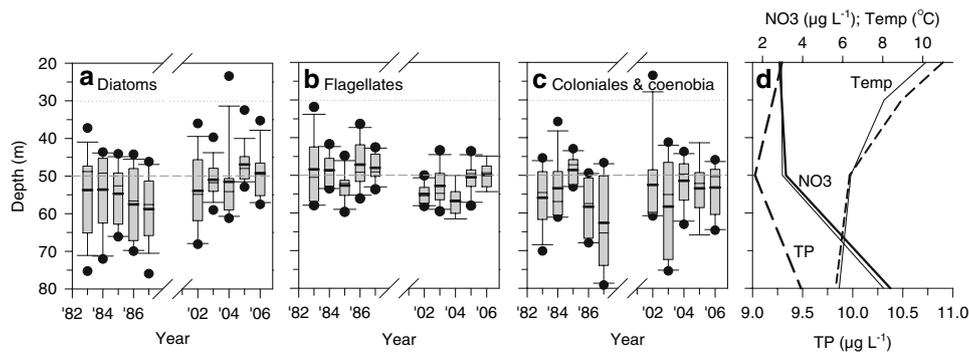


Fig. 7 Monthly values of the center of gravity (mean depth) of the vertical distribution of **a** diatoms, **b** flagellates, **c** colonial and coenobia cell types shown as annual box plots. *Heavy lines* indicate annual means, *dots* indicate outliers. **d** Average values of vertical temperature (*Temp*) and nitrate concentration (*NO3*) are shown for the

$n = 10$). In comparison, flagellates displayed a slightly deeper and narrower depth distribution in more recent years although the difference was marginally significant between the early and recent time periods (ANOVA, $F_{(2,11)} = 3.5$, $P = 0.06$), whereas coloniales and coenobia did not exhibit a different vertical distribution pattern between the two time periods (ANOVA, $F_{(2,11)} = 0.03$, $P = 0.9$; Fig. 7).

Discussion

The present study demonstrates that in addition to nutrient alterations (Anneville et al. 2005), changes in thermal stratification processes affect the temporal organization and vertical positioning of natural phytoplankton assemblages. In Lake Tahoe, a long-term warming trend was observed over the last decades (Coats et al. 2006). As a result, water-column stability increased and thermocline depth became shallower, indicative of stronger vertical thermal gradients and reduction in turbulent diffusion (King et al. 1999; Winder and Schindler 2004b). In addition, deep spring mixing events have not occurred since 1999, with concurrent effects on nitrate availability in the upper water column, while phosphorus concentrations were at a relatively constant level since the 1990s. Lake Tahoe's phytoplankton composition is strongly coupled with the vertical mixing regime (Carney et al. 1988; Tilzer and Goldman 1978); consequently alterations in physical (mixing) conditions affected phytoplankton dynamics likely by altering resource competition and species sinking rates (Bopp et al. 2005; Huisman et al. 2006; Ptacnik et al. 2003), and ultimately the expansion of species and morphological cell types best adapted to conditions associated with intensified stratification.

Mixing processes operate on phytoplankton through an effect on sinking velocities of non-motile species and on

periods 1983–1987 (*thin lines*) and 2002–2006 (*heavy lines*), and total phosphorus (*TP*) concentration for 2002–2006. *Dotted horizontal lines* indicate thermocline depth, *dashed horizontal lines* indicate nitrocline depth

nutrient exchange rate between deep and surface water layers (Behrenfeld et al. 2006; Verburg et al. 2003). In Lake Tahoe, much of the interannual nitrate variability is due to the variable depth of spring mixing (Jassby et al. 1995). In contrast phosphate concentrations were unaffected by mixing intensity. Reasons for this independency are likely due to depletion by phytoplankton assimilation of this growth-limiting resource, insufficient measurements of the total bioavailability phosphorus pool, and improved watershed management constrained external phosphorus loadings (Jassby et al. 1995, 1994). Overall nitrate concentrations were not depleted in surface waters despite increasing stratification, which is probably due to intensive internal spring loadings in the late 1990s, increasing atmospheric deposition (Jassby et al. 1995, 1994), and in addition, an exhausted phosphate concentration may have restricted extensive algal growth and thus nitrogen uptake. On the other hand, high interannual variability may mask a long-term trend. However, high year-to-year nitrate variability and low consistent phosphorus levels resulted in increasing nitrogen:phosphorus ratios, indicating that phosphorus has become the primarily limiting resource (Goldman et al. 1993). This demonstrates that mixing affects primarily the variability of nutrients (nutrient ratios), which are as important for phytoplankton as their absolute concentrations (Elser et al. 2007; Makulla and Sommer 1993; Tilman et al. 1982).

In response to altering resource availability and mixing a temporal gradient in phytoplankton structure was observed in Lake Tahoe between 1982 and 2006, whereas phytoplankton biomass did not exhibit a significant change, probably because of compensatory species dynamics (Vinebrooke et al. 2003). The ordination analysis captured two main correlates of phytoplankton community structure–resource availability (nitrogen:phosphorus ratio, phosphorus, light) along the first and the strength of thermal stratification along the second axis. The majority of

algal species across a wide size range and different motility characteristics were positively associated with the first axis, indicating resource variability as a dominant driver for phytoplankton growth (Anneville et al. 2005; Guildford and Hecky 2000; Lehman et al. 2004) and that low nitrogen:phosphorus ratios, i.e., N limitation, in the 1980s favored certain species from all functional groups. Some large-sized flagellates (e.g., *Chlamydomonas*), including mixotrophic species such as *Peridinium* and *Ochromonas* were associated with low nitrogen:phosphorus ratios in the 1980s. Overall mixotrophic species did not increase in Lake Tahoe ($\tau = -0.21$, $P = 0.16$) despite a critical phosphorus concentration (Goldman et al. 1993). This observation is in contrast to studies reporting an increase in large-size flagellates and a dominance of mixotrophic species with phosphorus reduction (Dokulil and Teubner 2005; Findlay et al. 2001; Gaedke and Schweizer 1993; Sommer et al. 1993). A lack of an increase in these functional groups in Lake Tahoe is likely owing to relatively small changes in phosphorus concentration compared to the other studies. Generally, species that are most strongly associated with the first axis and thus the resource gradient, and indicative of the 1980s, showed a declining trend over the sampling period, indicating a response to changing nutrient availability. In later years, phosphorus became the nutrient limiting resource in Lake Tahoe and together with increasing stratification resulted in the expansion of a different phytoplankton community.

The gradient of the second NMDS axis, which was most strongly correlated with thermal stratification, was formed by distinctive phytoplankton cell types. Among chlorophytes, colonial, coenobial, and filamentous forms showed a strong positive linkage with this axis, indicating facilitation under reduced vertical mixing. Particularly filamentous ($\tau = 0.18$, $P = 0.05$) and coenobial cell types ($\tau = 0.21$, $P = 0.02$) increased in Lake Tahoe. The filamentous *Planktonema lauterbornii*, which is a cosmopolitan species that seems to prefer warmer waters (Noges and Viirret 2001) was recorded for the first time in Lake Tahoe in 1986 (Buerger et al. 1993). Further, the filamentous chlorophyte *Gloeotila* sp. had not been recorded in surveys before 1989 and was a constant representative thereafter, and the coenobia *Dispora* sp. was first observed in 2003. Similarly, the colonial species *Botryococcus braunii* was only recorded once in low abundance before 1994 and blooms were increasingly observed in subsequent years. Reduced mixing and warmer water temperature may have favored the invasion and contributed to the success of these chlorophytes (Reynolds 2006; Tilman et al. 1986). These algal cell types have several adaptations to reduce their sinking rates, including form resistance in filamentous species (Padisák et al. 2003) or a mucilaginous sheath and oil inclusion in *Botryococcus* (Belcher 1968; Wehr and

Sheath 2003). Indeed, filaments can reach high abundance in stratified water columns (Leitao et al. 2003; Reynolds et al. 2002; Salmaso 2003). These characteristics give them buoyancy and competitive advantage over species with higher sinking velocities at reduced mixing (Reynolds 2006). In addition, many of these chlorophytes are chlorococcales, which tend to increase at high nitrogen:phosphorus ratios (Makulla and Sommer 1993) and increasing phosphorus limitation in Lake Tahoe may have further contributed to their success. Filamentous blue-greens, which have similar morphological adaptations to reduce sinking velocities (Reynolds 2006) usually dominate under reduced mixing conditions in nutrient-enriched environments (Harris and Baxter 1996; Huisman et al. 2004; Visser et al. 1996). The present study suggests that intensified stratification will likely increase the incidence of filamentous and coenobial chlorophytes, which can adapt to chronically oligotrophic conditions (Makulla and Sommer 1993), in lakes where large-sized cyanobacteria are under-represented.

Chrysophytes, which are generally considered to be good competitors at a low phosphorus concentration (Lehman and Sandgren 1985; Siver 2003), are the only taxonomic group that showed a significant decline in Lake Tahoe despite increased nitrogen:phosphorus ratios. These ecophysiological requirements cannot explain the declining trend of this group relative to others, although their resource physiologies can be quite diverse (Nicholls and Wujek 2003). The small-sized genus *Epipyxis* is the only chrysophyte that showed a significant increase and was most strongly associated with increased stratification. Whether the lack of deep spring mixing events in recent years and increase in stability are responsible for the loss of re-suspension of viable chrysophytes resting stages and the causes for the declining abundance remains a hypothesis to be tested. Indeed, viable phytoplankton communities can survive in deep-water layers in Lake Tahoe (Kiefer et al. 1972; Tilzer et al. 1977; Vincent 1983) and reduced spring mixing may not provide enough of an initial inoculum for the population to flourish.

Among diatoms, the dominant taxonomic group in Lake Tahoe, *Cyclotella*, is the only genus that increased significantly over the last few decades. This small-sized ($180 \mu\text{m}^3$ average cell volume) centric genus showed a positive association with the second NMDS axis, while larger-sized genera such as *Synedra* ($367 \mu\text{m}^3$), *Fragilaria* ($430 \mu\text{m}^3$), and *Stephanodiscus* ($4,309 \mu\text{m}^3$) showed negative correlations with NMDS axis 2, indicating a response to the changing mixing regime. For diatoms, sinking velocities increase with size (Diehl et al. 2002; Ptacnik et al. 2003; Reynolds 2006). These siliceous algae require well-mixed conditions to remain suspended in the water column (Reynolds 1984) and some cells dominate under

isothermal mixing (e.g., *Stephanodiscus*) (Sommer 1985). The competitive increase in *Cyclotella* in Lake Tahoe may be due to their small cell size, which reduces sinking velocities and gives them buoyancy at periods of stronger thermal stratification. *Cyclotella* contributes more than 60% of the total diatom biovolume (data not shown), and *Cyclotella ocellata*, with an average diameter of $\sim 12 \mu\text{m}$ accounts for over 80% of total *Cyclotella* biovolume (data not shown). The increasing trend in *Cyclotella* is largely attributed to this species, and overall small-sized slow-sinking diatoms exhibited an increasing trend in Lake Tahoe ($\tau = 0.27$, $P = 0.006$) compared to a decreasing trend of large-sized fast-sinking cells ($\tau = -0.22$, $P = 0.05$) (for cell size see Table S1 in ESM). *Cyclotella* is characteristic of a lower nutrient concentration during times of stable stratification in surface waters in Lake Tahoe (Carney et al. 1988). In addition, this species is a good competitor for nitrogen and has high light requirements (Carney 1987; Interlandi and Kilham 2001). These ecophysiological characteristics are inconsistent with increasing nitrogen:phosphorus ratio and decreasing clarity in Lake Tahoe (Jassby et al. 2003) and cannot be responsible for their expansion. However, the physical and chemical changes may have a synergistic effect on this small-sized species because a large surface to volume ratio allows rapid nutrient uptake. A geographically widespread increase in *Cyclotella* species has been documented in palaeoecological records (Kilham et al. 1996; Ruehland and Smol 2005; Saros et al. 2003; Sorvari et al. 2002) and their success has been linked to an extended growing season and enhanced thermal stratification (Smol et al. 2005). While paleolimnological studies do not explain the detailed processes and mechanisms of the observed changes, the present study suggests that in deep lakes the driving mechanism for the success of small-sized diatom species is linked to thermal stratification.

Increased water-column stability in Lake Tahoe has favored particularly diatom taxa that are less prone to sinking. The selection for small-sized diatoms is further supported by the shoaling trend in their vertical position in the water column. Compared to the 1980s, a larger fraction of total diatom biomass was observed at about 10 m shallower depths in recent years. The deep-chlorophyll maximum in Lake Tahoe may be due to cells sinking out of the mixed layer (Kiefer et al. 1972), and indeed peak phytoplankton production occurred in the upper 20- to 40-m water layer (Finger et al., in preparation). The vertical displacement of diatoms cannot be attributed to a temporal trend in total phytoplankton biovolume nor to changing light levels, and are likely a result of smaller sizes, which suffer lower sedimentation rates (Ptacnik et al. 2003). A shoaling trend of maximal biovolume with decreasing cell size and thus sinking

velocity is in agreement with theoretical work (Huisman and Sommeijer 2002). In contrast to diatoms, mean depth of flagellates increased slightly in recent years. These motile plankters have the ability to search for optimal growth conditions (Reynolds 2006), and the affinity for deeper depth strata suggests a spatial shift of optimum nutrient and light conditions. Lake Tahoe's deep chlorophyll maximum is located in the vicinity of the nitrocline, and a deeper flagellate depth positioning is likely due to reduced re-submission of nutrients from deep-water layer resulting in a deepening of the nitrocline. Unfortunately depth resolutions of nutrient data are not high enough in Lake Tahoe (see "Materials and methods") to track nitrocline changes at this scale during the stratification period.

The present results demonstrate that reorganizations within the phytoplankton community likely occur with changing thermal structure of the water column (Bopp et al. 2005; Findlay et al. 2001; Huisman et al. 2004; Smol et al. 2005; Strecker et al. 2004). Moreover, the present study suggests that species best adapted to increasing stratification, such as small-sized algal cells and species that are able to regulate their buoyancy, are able to expand. Intensified stratification is expected with climate warming (Schmittner 2005; Winder and Schindler 2004a), and our study indicates that this change will be accompanied by altering phytoplankton structure, which also affects their positioning in the water column. This suggests that the capability of phytoplankton to adapt to intensified stratification should be considered in biogeochemical models used to predict global warming impacts. These changes in primary producers are crucial for entire ecosystems and will have associated effects on primary production, biogeochemical cycling of carbon and other elements, and will determine energy transfer to higher trophic levels through microbial or herbivore pathways (Legendre and Le Fèvre 1989; Sommer et al. 2002).

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