

Changes in phytoplankton in a boreal lake during a 14-year period

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Climate-induced changes in phytoplankton were examined over a 14-year period in a remote humic headwater lake recovering from acidification. The time series analysis revealed that the total biomass as well as the biomass of the two dominant taxa — the raphidophyte *Gonyostomum semen* and *Peridinium* dinoflagellates — decreased (changes as indicated by trends $-0.014 \text{ g m}^{-3} \text{ yr}^{-1}$ and $-0.006 \text{ g m}^{-3} \text{ yr}^{-1}$, respectively), whereas the biomass of the subdominant *Cryptomonas* spp. did not change. The timing of ice-out, the extent of the spring circulation or the length of the stratification period could not be firmly connected to the phytoplankton phenology. Concentrations of major nutrients decreased during the period, whereas the dissolved organic carbon (DOC) and water colour increased. These changes probably led to the decrease in the biomass of the dominant *G. semen* and *Peridinium* spp., and thus in the total phytoplankton biomass.

Introduction

Abundance and composition of phytoplankton is determined mainly by the light climate, temperature and nutrient concentrations in the water column, as well as by zooplankton grazing. Physical and chemical properties of lakes are modified by local weather conditions, and thus phytoplankton community composition, biomass and the timing of phytoplankton blooms are mediated by climatic forces (Moss *et al.* 2003). In lakes, the effects of climate change have most often been linked to the development

of the spring phytoplankton crop: an earlier ice-out induces an earlier phytoplankton spring bloom (Adrian *et al.* 2006). Others stress the effect of warming on phytoplankton composition; for example De Senerpont Domis *et al.* (2007) suggested that cyanophyte densities will increase following a temperature rise, whereas chlorophytes and diatoms will not benefit from warming. Moss *et al.* (2003), for their part, reported that the abundance of cyanophytes would not change, whereas certain chlorophytes would increase and some, together with cryptophytes, might decrease. Furthermore, Winder

et al. (2009) postulated that as a result of climate warming, thermal stratification in lakes will become stronger leading to increased sinking of non-motile phytoplankton species, mainly diatoms, and reshaping of phytoplankton communities towards small, flagellated species.

In the boreal zone, small lakes, which are most often humic, are typically ice-covered for 5–6 months every year. During this time, the ice — especially when covered by snow — obstructs light penetration to the water column and prevents phytoplankton photosynthesis (Tulonen et al. 1991). However, ice-out in the spring can be very rapid, making light suddenly available for photosynthesis. Consequently, the rapid recruitment of phytoplankton from resting stages commences and growth starts (Rengefors et al. 2004). Due to the absorption of solar radiation, surface temperatures rapidly increase to 10–15 °C (Eloranta 1999). This shortens the duration of the spring overturn to a few days and spring mixing is often incomplete, leaving the hypolimnion anoxic and supersaturated with carbon gases (Huotari et al. 2009). In this type of situation, nutrients are not mixed throughout the water column but remain in deeper water layers. However, nutrient reserves are replenished through the spring runoff. Summer stratification is strong, with low epilimnetic nutrient concentrations and an anoxic hypolimnion, where nutrients are released from the sediment. In these conditions, motile phytoplankton species capable of migrating vertically between the nutrient-rich hypolimnion and the illuminated epilimnion have a competitive advantage. Thus, the phytoplankton crop in humic lakes largely consists of flagellates (Lepistö and Rosenström 1998). However, if annual precipitation together with nutrient-rich runoff increases as is predicted by Jylhä et al. (2004), the non-motile phytoplankton species will profit. Nevertheless, counteracting factors such as brown-coloured organic substances in the runoff affect thermal stratification, attenuate the photosynthetically active radiation and worsen the light climate (Eloranta 1999, Arvola et al. 2010). Coloured humic substances are acid, i.e. they may lower water pH, and can also form colloids and complexes with inorganic and organic nutrients. Increasing acidity affects phytoplankton species composition

(Lepistö and Rosenström 1998), and the sequestering of nutrients can have a significant effect on the growth and reproduction of phytoplankton (Münster 1999).

Here, we report changes in the phytoplankton of a small boreal humic lake in southern Finland over the period from 1990 to 2003. The study site is a remote headwater lake in the middle of an old-growth forest and located in a nature reserve area, and is thus regarded as a true reference site (Huotari et al. 2009). The area was exposed to atmospheric acid deposition (Ruoho-Airola et al. 1998), but is now recovering (Moldan et al. 2001). It belongs to the network of Natura 2000 of the European Union (EU) and the Finnish Long Term Ecological Research (LTER) network. In this study, we focus on alterations in the total phytoplankton biomass as well as in the biomass of three phytoplankton taxa: *Gonyostomum semen*, *Peridinium* spp. and *Cryptomonas* spp. Despite differences in abundance, these taxa have some ecological and morphological similarities that are essential for successful growth in boreal humic lakes. These include resting stages for overwintering and flagella, enabling active movement in the water column (Hansson 1993, 2000). However, the chosen taxa differ in cell size (*G. semen* > 50 µm, *Peridinium* spp. 20–40 µm and *Cryptomonas* spp. 12–30 µm), i.e. they most probably differ in their rates of nutrient uptake and growth (Reynolds 2006). Moreover, the timing of their production maxima differs (Peltomaa and Ojala 2010). Thus, we assume that they respond differently to environmental changes. The chosen taxa are easy to identify, ruling out counting errors due to changes in personnel. In Finland, annual mean temperatures and precipitation have been increasing as compared with those in the baseline period of 1961–1990, and the projection is that they will increase by 1–3 °C and up to 15%, respectively, by 2020 (Jylhä et al. 2004). Our aim in this study was to connect the changes in phytoplankton to changes in temperature, i.e. in the timing of ice-out and the duration of the spring overturn as well as the length of the stratified period and the intensity of thermal stratification. We also considered changes in precipitation, and thereby the presumed increase in the concentrations of nutrients (phosphorus and nitrogen) and

dissolved organic carbon (DOC). Possible trends in water colour and pH were studied as well. We hypothesized that: (1) an earlier ice-out will advance the maxima of phytoplankton biomass; (2) as opposed to the complete spring mixing, an incomplete spring mixing leads to lower phytoplankton biomass maxima; (3) the flagellated phytoplankton species benefit from long-lasting and strong thermal stratification; (4) the increase in precipitation will increase nutrient and DOC concentrations as well as water colour; (5) increased epilimnetic nutrient concentrations will benefit the non-motile phytoplankton taxa at the expense of motile species; (6) increased DOC and colour reduce the phytoplankton biomass via decreased light penetration and (7) the increase of acidic DOC causes a decrease in pH, which induces changes in phytoplankton species composition and biomass.

Material and methods

Site description

Valkea-Kotinen is a small (area 0.04 km², maximum depth 6.5 m, average depth 2.5 m) head-water lake located in the middle of a boreal forest in southern Finland (61°14'N, 25°04'E). It represents lakes in natural-state areas within the boreal part of the Precambrian Shield in northern Europe and North America. The water of the lake is highly humic (annual mean DOC concentration and water colour in 1990–1996 9.6–12.2 mg l⁻¹ and 103–160 mg Pt l⁻¹, respectively) and acidic (pH 5.0–5.4) (Keskitalo *et al.* 1998). The concentration of dissolved inorganic carbon (DIC) is low in the epilimnion (< 0.8 mg l⁻¹), but substantially higher in the hypolimnion (> 4.5 mg l⁻¹). Total phosphorus (P_{tot}) and total nitrogen (N_{tot}) concentrations are also lower in the epilimnion than in the hypolimnion (P_{tot} 15–22 µg l⁻¹ and 19–28 µg l⁻¹, respectively; and N_{tot} 430–560 µg l⁻¹ and 547–682 µg l⁻¹, respectively) (Keskitalo *et al.* 1998). The lake is normally steeply stratified with respect to temperature and oxygen, and the spring overturn is usually short or incomplete. The euphotic zone as well as the epilimnion reaches to the depth of 2 m (Peltomaa and Ojala 2010).

Samples

Water samples were collected weekly during the open-water periods in 1990–2003 from the central part of the lake as a part of the International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP IM) following the protocol of Keskitalo and Salonen (1994). The samples for phytoplankton studies were taken with a 7-l tube sampler (length 1 m) from the depths of 0–1 metres from two points. The two samples were pooled and preserved with acid Lugol's solution. Phytoplankton community composition was determined with inverted microscopy (total magnification 400–600×) using a settling chamber technique (sample volume 25–50 ml, settling time 24–48 h) (Utermöhl 1958). Biomass was calculated as wet weight using unpublished biovolume values of the Finnish Environment Institute for phytoplankton volumes. The calculations were based on the biovolume-to-wet weight factor of 1. Samples for the nutrient (0, 1, 2, 3 and 5 m), DOC (0 and 1 m), colour (0 m) and pH (0 m) analyses were collected with a 2.1-l Limnos tube sampler (length 0.3 m). Total phosphorus (P_{tot}) and total nitrogen (N_{tot}) were determined in 1990–1997 with an AKEA analyzer (Datex Instrumentarium, Finland) and in 1998–2003 with a Lachat Quikchem 8000 automatic FIA system (Zellweger Analytics Inc., USA). For DOC determinations, the samples were pooled and filtered through GF/C glassfiber filters (Whatman International Ltd., Maidstone, England). In 1990–1998, DOC was determined using a universal carbon analyzer (EasyQuant, Finland) equipped with a URAS infrared detector (Hartmann & Braun AG, Germany). From 1999 onwards, DOC was determined with a Shimadzu TOC 5000A carbon analyzer (Shimadzu Corporation, Australia). For measurements of water colour the samples were filtered similarly to the DOC samples, and the colour was determined with a Shimadzu UV-2100 spectrophotometer (Shimadzu Corporation, Kyoto, Japan) at 420 nm against a standard platinum solution. pH was measured with an Orion SA 720 pH-meter (Orion Research Inc., Beverly, MA, USA).

Water temperature and dissolved oxygen concentration were measured simultaneously with water sampling at 1-m intervals from 0 m

to 6 m with YSI probes (models YSI 55, YSI 57 and YSI 58; Yellow Springs Instruments Inc., USA). The completeness of the spring mixing, expressed as the thickness (m) of the mixed layer, as well as the length of the period of thermal stratification were estimated from these measurements. The strength of thermal stratification was estimated by subtracting the bottom temperature from the surface temperature. The timing of ice-in and ice-out was registered with an accuracy of one day. The lake was considered ice-free when there was only some ice near the shoreline, and frozen when it was completely covered by ice. Precipitation (monthly means in 1990–2002) was measured at the Lammi Biological Station of the University of Helsinki, ca. 30 km from the study lake.

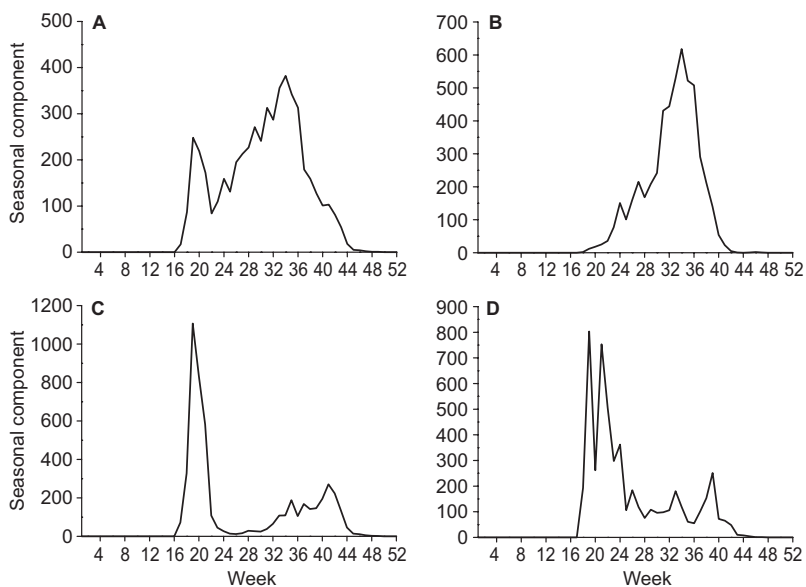
Statistical methods

Long-term changes in the total phytoplankton biomass as well as in the biomass of *Gonyostomum semen*, *Peridinium* spp. and *Cryptomonas* spp. were analyzed with a time series analysis as described in Arhonditsis *et al.* (2004), i.e. the seasonal patterns were extracted by seasonal-trend decomposition using the Census II method. This method is an extension of the classic seasonal decomposition and adjustment method (Census I), and allow successive refinements and adjustments for outliers and extreme values (Kendall and Ord 1990). Due to seasonality, there may be recurring patterns in phytoplankton dynamics and environmental data. The purpose of the seasonal decomposition method is to isolate those components, that is, to decompose the time series into three components: (1) trend, (2) seasonal, and (3) residual (i.e. remaining variability). The assumption is that each component is affected by its own set of forces, and thus they can be studied separately after the decomposition. The model form defines the functional relationship between the three components (additive or multiplicative). We chose the additive model and averaged the time series over weeks. After decomposition of the time series, we subtracted the seasonal component (centering the data) and inspected the residual values for nonstationarity problems (cf. Arhonditsis *et al.* 2004).

We used the Mann-Kendall test (MK) to evaluate the statistical significance of the trends found after deseasonalization (Sneyers 1990, Yue & Pilon 2004). A trend was considered statistically significant at $p < 0.05$.

We conducted similar time series analyses for the physical and chemical parameters, i.e. surface water temperature, precipitation and concentrations of P_{tot} , N_{tot} and DOC as well as the N to P mass ratio (N:P ratio), water colour and pH. For nutrients, we used volume-weighted means in the analysis. The lake sampling program was carried out during the open-water periods only, thus the winter values of water temperatures and phytoplankton biomass, nutrients and DOC, colour and pH could not be included in the time series analysis. Precipitation was monitored throughout the study years, we thus performed the analysis of precipitation using the whole dataset, as well as using the summer data alone. Some missing data points were extrapolated linearly using the value just before and after the missing one. For every parameter — except for precipitation — we had a dataset comprising 14 years, i.e. the total number of weeks, and thus data points, was 728. The 13-year data set for monthly means of precipitation consisted of 155 data points. We used Pearson's correlation analysis (Grafen and Hails 2002) to determine whether the date of ice-out, the spring mixing, the length of the period of thermal stratification, the intensity of thermal stratification or any of the measured environmental parameters influenced the timing or the height of the maximal phytoplankton biomass. The homogeneity of variances was tested with Levene's test and the normality of the experimental data was tested with a Kolmogorov-Smirnov goodness of fit test. When needed, \log_{10} -transformations were used to normalise the distribution of the data before the statistical analyses (Grafen and Hails 2002). In the correlation analysis, results were considered significant at $p < 0.05$. The relative effect of the different environmental parameters, i.e. water temperature, P_{tot} , N_{tot} , N:P ratio, DOC, colour and pH, on phytoplankton was examined with a partial least-square regression analysis (PLS). PLS is commonly used to find the fundamental relations between two matrices (\mathbf{x} and \mathbf{y}), where the variance x is taken to explain the vari-

Fig. 1. Seasonality of phytoplankton biomass in Valkea-Kotinen as determined by time series analysis (1990–2003, $n = 728$). The seasonal component is an index value, and thus the y -axes are not comparable. Phytoplankton biomass had two maxima (A), which mainly consisted of *Gonyostomum semen* (B), *Peridinium* spp. (C) and *Cryptomonas* spp. (D).



ance y . In PLS, x variables are ranked according to their relevance explaining y (PLS loadings). We chose the PLS analysis because it is insensitive to the x variable's interdependency and to deviations of normality (Eriksson *et al.* 1999). All the analyses, except PLS, were conducted with SPSS 15.0 for Windows (SPSS Inc.). The PAST program, version 2.12 (Hammer *et al.* 2001) was used for the PLS analysis.

Results

Seasonal succession of phytoplankton biomass in Valkea-Kotinen followed the pattern of two maxima: the first, sharper one in spring taking place in weeks 18–22 in May, and the second, wider and higher one during the strongest stratification in weeks 28–37 in July–August (Fig. 1A). It is noteworthy that there was no distinct clear-water phase, but the decline after the spring peak was followed by a sinusoidal biomass succession. The mean (\pm SE) total phytoplankton biomass in 1990–2003 was $2.09 \pm 0.01 \text{ g m}^{-3}$ (range = $1.41\text{--}2.87 \text{ g m}^{-3}$) and the community consisted of ca. 180 taxa. The species mainly belonged to the Chrysophyceae (especially the genera *Dinobryon*, *Monochrysis*, *Pedinella*, *Uroglena*), Dinophyceae (*Gymnodinium*, *Peridinium*), Diatomophyceae (*Asterionella*, *Rhizosolenia*),

Cryptophyceae (*Cryptomonas*), Chlorophyceae (*Chlorogonium*, *Chryso capsa*, *Oocystis*) and Cyanophyceae (*Cyanodictyon*, *Merismopedia*, *Snowella*). However, the bulk of the annual biomass mainly consisted of very few taxa, since most of the species appeared only occasionally and their numbers were low. Most of the biomass was in general composed of the raphidophyte *Gonyostomum semen*, which at the beginning of the research period (i.e. in 1991–1994) made up more than 95% of the total biomass.

The seasonal-component analysis revealed clear differences among the studied three taxa; the differences were so clear that they were already visible in the raw data (Fig. 2). *Cryptomonas* spp., which apparently comprised three species (size-range $12\text{--}30 \mu\text{m}$), had its maximum at the beginning of the summer (May–June: weeks 19–23 in), whereas the maximum biomass of *G. semen* was detected later in the summer (August: week 34), concomitantly with the maximum total biomass (Fig. 1). The mean (\pm SE) summer biomass of *G. semen* in 1990–2003 was $1.00 \pm 0.004 \text{ g m}^{-3}$ (range = $0.37\text{--}2.41 \text{ g m}^{-3}$), and during the study period it made up on average 48% of the total phytoplankton biomass. *Peridinium* spp. consisted of four species (size-range $20\text{--}40 \mu\text{m}$) and had two maxima, i.e. a large, short-lasting one in May (weeks 19–21) during the spring overturn and a much smaller one in September–October

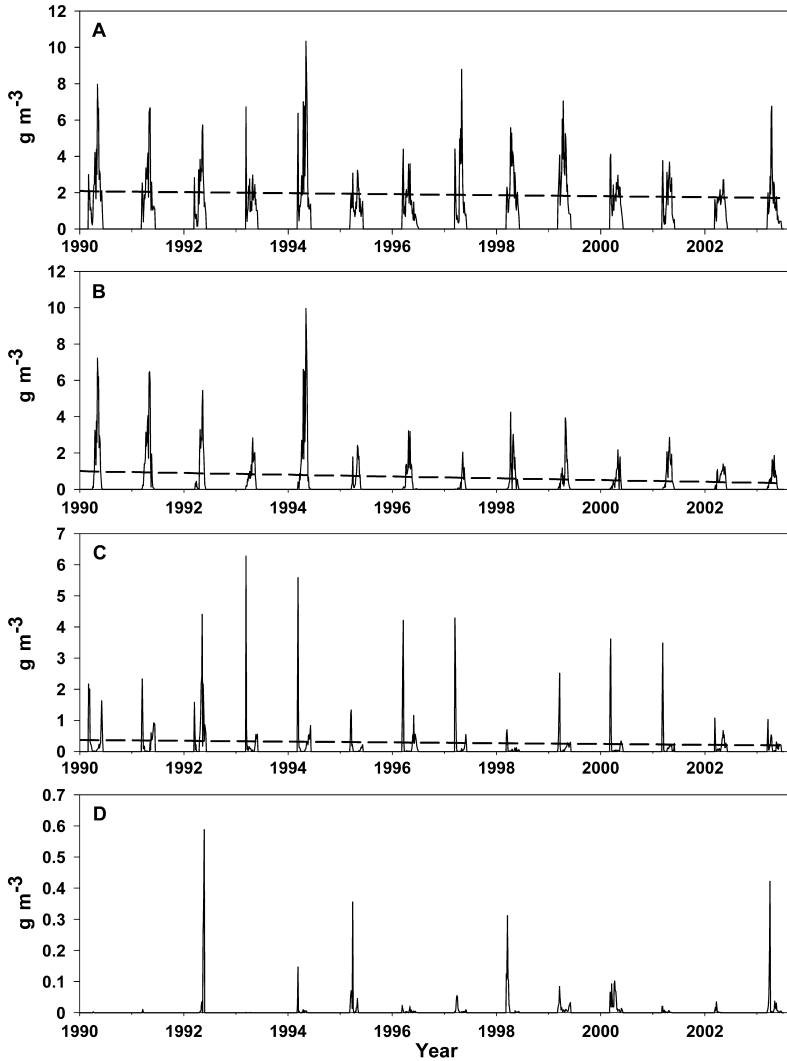


Fig. 2. Phytoplankton biomass (solid lines) and the trends (dashed lines) during 1990–2003 in Valkea-Kotinen ($n = 728$). **(A)** Total phytoplankton (trend equation $y = -0.003x + 0.025$, change $-0.014 \text{ g m}^{-3} \text{ yr}^{-1}$, $p < 0.05$), **(B)** *Gonyostomum semen* (trend equation $y = -0.0005x - 0.508$, change $-0.024 \text{ g m}^{-3} \text{ yr}^{-1}$, $p < 0.001$), **(C)** *Peridinium* spp. (trend equation $y = -0.0001x - 0.818$, change $-0.006 \text{ g m}^{-3} \text{ yr}^{-1}$, $p < 0.02$), and **(D)** *Cryptomonas* spp. (no trend, $p = 0.29$).

(weeks 36–43), when the lake was undergoing the autumn overturn (Fig. 1C). It is noteworthy that the three *Cryptomonas* species had very similar seasonal abundance patterns, as did the four species of the *Peridinium*-group (data not shown). The mean (\pm SE) biomass of *Peridinium* spp. was $0.37 \pm 0.002 \text{ g m}^{-3}$ (range = 0.10–0.87 g m^{-3}), and these dinoflagellates made up 18% of the total biomass. *Cryptomonas* spp., although among the most abundant taxa in Valkea-Kotinen, had a mean (\pm SE) biomass of only $0.02 \pm 0.0002 \text{ g m}^{-3}$ (range = 0.0001–0.06 g m^{-3}), and they were responsible for 1% of the total biomass.

There was a decreasing trend in the total biomass, indicating a change of $0.014 \text{ g m}^{-3} \text{ yr}^{-1}$

(see Fig. 2A). A similar trend was revealed for *G. semen*, but the change was even steeper ($-0.024 \text{ g m}^{-3} \text{ yr}^{-1}$; see Fig. 2B). The biomass of *Peridinium* spp. also decreased, but the rate of the decline was slower ($-0.006 \text{ g m}^{-3} \text{ yr}^{-1}$; see Fig. 2C). Unlike for *G. semen* and *Peridinium* spp., there was no clear trend in the total biomass of cryptophytes. We calculated that at these slow but constant rates, *G. semen* and *Peridinium* spp. would disappear in 42 and 62 years, respectively. However, the amplitudes of the residual components were high (Fig. 3), and other, unknown factors besides seasonality and long-term changes were thus also behind the variations in the biomasses.

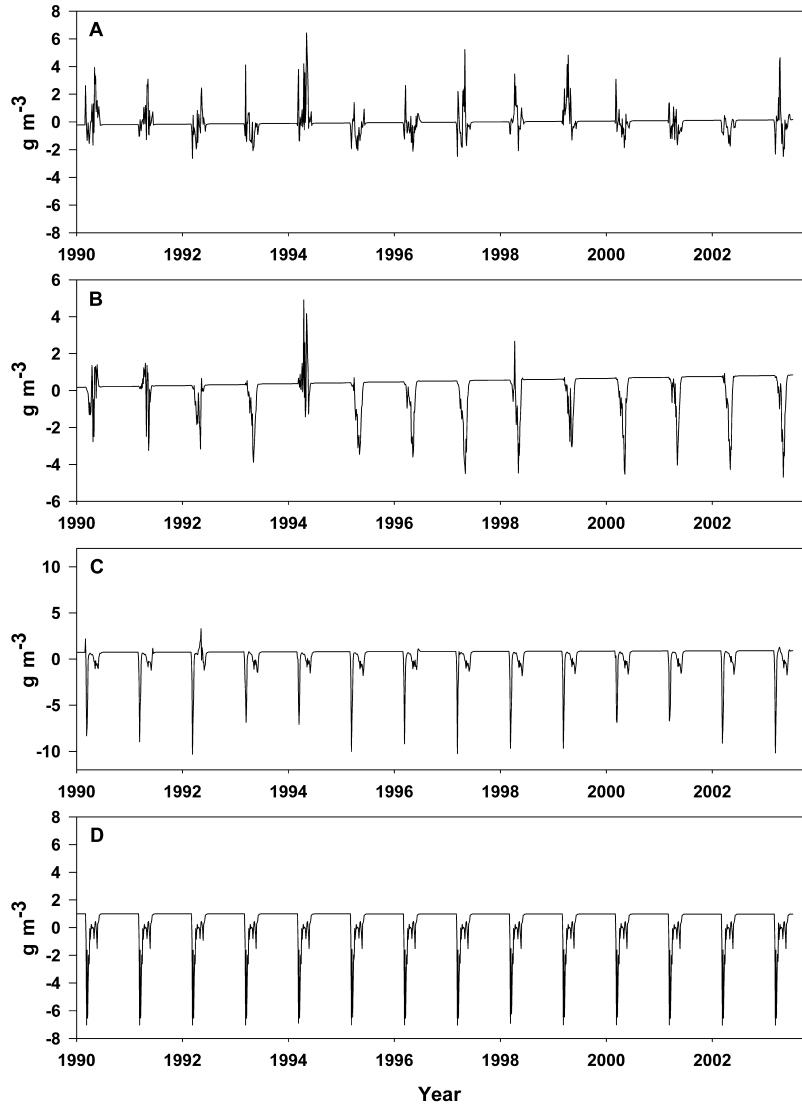


Fig. 3. Residual components indicating considerable random variations in (A) the total phytoplankton biomass, (B) the *Gonyostomum semen* biomass, (C) the *Peridinium* spp. biomass, and (D) the *Cryptomonas* spp. biomass in Valkea-Kotinen during 1990–2003 ($n = 728$).

Ice-out took place in late April or at the beginning of May, but there was no tendency

towards an earlier ice-out during the study period ($r_p = 0.008$, $p = 0.98$). The timing of ice-

Table 1. Pearson's correlations (r_p) between the phytoplankton biomass and selected parameters ($n = 14$). Existing correlations are set in boldface.

| Parameter | Biomass | | | |
|-------------------------------------|-----------------------------|-----------------------------|------------------------|-------------------------|
| | Total | <i>G. semen</i> | <i>Peridinium</i> spp. | <i>Cryptomonas</i> spp. |
| Ice-out | -0.14 (n.s.) | -0.06 (n.s.) | 0.52 (n.s.) | 0.35 (n.s.) |
| Duration of mixing | 0.02 (n.s.) | 0.24 (n.s.) | 0.09 (n.s.) | -0.12 (n.s.) |
| Thickness of mixed layer | 0.00 (n.s.) | 0.28 (n.s.) | 0.27 (n.s.) | -0.16 (n.s.) |
| Length of stratified period | -0.11 (n.s.) | 0.42 (n.s.) | 0.37 (n.s.) | 0.03 (n.s.) |
| Intensity of thermal stratification | 0.22 ($p < 0.001$) | 0.26 ($p < 0.001$) | -0.10 (n.s.) | 0.05 (n.s.) |

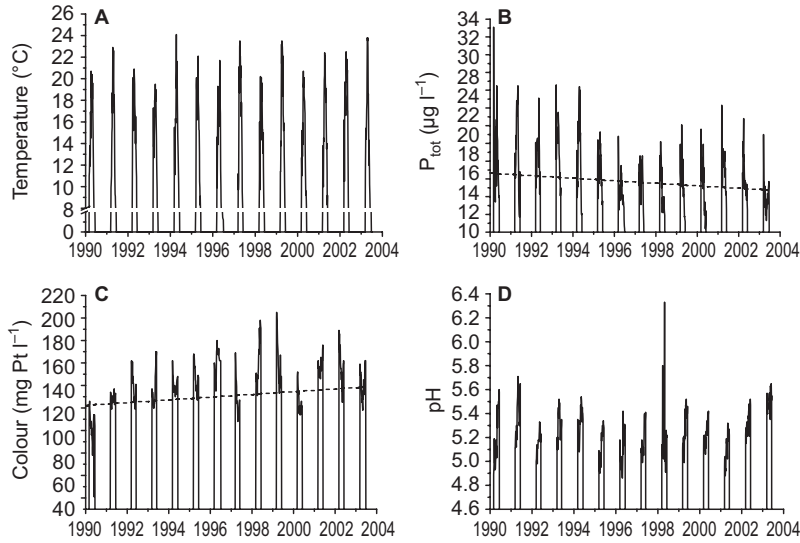


Fig. 4. Data (solid lines) and trends (dashed lines) in (A) temperature (no trend, $p = 0.48$), (B) Total phosphorus (P_{tot}) (trend equation $y = -0.0014x + 7.17$, change $-0.071 \mu\text{g l}^{-1} \text{yr}^{-1}$, $p < 0.001$), (C) water colour (trend equation $y = 0.0235x + 144$, change $1.22 \text{ mg Pt l}^{-1} \text{yr}^{-1}$, $p < 0.001$), and (D) pH (no trend, $p = 1.0$) in Valkeakotinen during open water-periods in 1990–2003 ($n = 728$).

out had no effect on the timing of the maximum of *Cryptomonas* spp., *Peridinium* spp., *G. semen* or the total biomass (Table 1). The latter finding is logical, since *G. semen* and also *Peridinium* spp. made up the bulk of the phytoplankton biomass. The spring overturn typically lasted for a week, but in 1994 and 1995 it continued for two and three weeks, respectively. In 4 out of 14 years, the spring overturn was incomplete: in 1998 the mixing only extended to two meters, in 2003 to three meters and in 1993 and 1999 to four meters. The duration of the mixing period correlated strongly with the variation in mixing depth ($r_p = 0.60$, $p = 0.02$), but neither the duration nor the thickness of the mixed layer affected the height of the phytoplankton biomass maxima (Table 1). The length of the period of thermal stratification did not affect the total biomass or the biomasses of the studied taxa; however, *G. semen* and total phytoplankton biomass were weakly and positively correlated with the strong thermal stratification ($r_p = 0.26$, $p < 0.001$ and $r_p = 0.22$, $p < 0.001$, respectively; Table 1).

Changes in the surface water temperature did not follow any clear trend (Fig. 4A). The total phytoplankton biomass and the biomass of *G. semen* were positively correlated with temperature ($r_p = 0.35$, $p < 0.001$ and $r_p = 0.31$, $p < 0.001$, respectively), whereas the biomass of *Peridinium* spp. was negatively correlated with temperature ($r_p = -0.25$, $p < 0.001$), and

no such correlation was found for *Cryptomonas* spp. (Table 2). Precipitation (annual and monthly means \pm SEs: 623 ± 0.18 mm and 52 ± 0.09 mm, respectively) significantly decreased (change as indicated by the trend -0.066 mm yr^{-1} , $p < 0.001$), which most apparently resulted from the decrease in snowfall, since the summer precipitation (seasonal and monthly means \pm SEs: 444 ± 0.2 mm and 56 ± 0.1 mm, respectively) was increasing at the rate of 0.055 mm yr^{-1} ($p < 0.001$).

Neither the maximum phytoplankton biomass nor nutrient concentrations correlated with annual or summer precipitation (Table 2). Nutrient concentrations either could not be linked to precipitation. Furthermore, the N_{tot} (mean \pm SE = $492 \pm 0.15 \mu\text{g l}^{-1}$) and P_{tot} (mean \pm SE = $16.7 \pm 0.01 \mu\text{g l}^{-1}$) concentrations did not increase, but declined at the rates of $-0.149 \mu\text{g l}^{-1} \text{yr}^{-1}$ ($p < 0.001$) and $-0.071 \mu\text{g l}^{-1} \text{yr}^{-1}$ ($p < 0.001$), respectively (Fig. 4B and Table 2). Since the absolute values of N_{tot} were higher than those of P_{tot} , N_{tot} was declining more slowly than P_{tot} , and the N:P ratio (mean \pm SE = 31 ± 0.02) was increasing (change as indicated by the trend 0.150 yr^{-1} , $p < 0.001$). In terms of the Redfield ratio of 7:1, phytoplankton was slowly becoming more phosphorus-limited (Redfield 1958) (Table 2). Neither the decreasing N_{tot} nor the increasing N:P ratio affected the maximal phytoplankton biomass or the biomass of *Peridinium*

spp., *G. semen* or *Cryptomonas* spp. (Table 2). However, the biomass of *Peridinium* spp. and *G. semen* correlated positively with P_{tot} ($r_p = 0.54$, $p = 0.05$ and $r_p = 0.69$, $p = 0.01$, respectively), and thus were probably negatively affected by the decrease in P_{tot} (Table 2). Unlike the nutrients, the DOC concentration (mean \pm SE = 13.0 ± 0.004 mg l⁻¹) and water colour (mean \pm SE = 142 ± 0.06 mg Pt l⁻¹) increased at the rates of 0.046 mg l⁻¹ yr⁻¹ ($p < 0.02$) and 1.22 mg Pt l⁻¹ yr⁻¹ ($p < 0.001$; see Fig. 4C), respectively. Similar to nutrients, the changes in DOC and colour were not affected by precipitation ($r_p = 0.04$, $p = 0.72$ and $r_p = 0.12$, $p = 0.31$, respectively). Phytoplankton biomass did not correlate with DOC (Table 2); however, had the increase in the DOC concentration been significant, considering the low rate of changes it would have taken more than two hundred years for the concentration to double. Total phytoplankton biomass and *G. semen* were weakly and negatively correlated with water colour ($r_p = -0.21$, $p < 0.001$ and $r_p = -0.29$, $p < 0.001$, respectively), but there was no correlation between the colour and the biomass of *Peridinium* spp. or *Cryptomonas* spp. (Table 2). The lake pH did not change (mean \pm SE = 5.25 ± 0.002 ; Table 2 and Fig. 4D), and no influence of pH on *Peridinium* spp. or *Cryptomonas* spp. was detected (Table 2). Because pH did not change during the study period, it could not explain the decrease in the biomass of *G. semen*, although a low positive correlation was detected between *G. semen* and pH ($r_p = 0.24$, $p < 0.001$; Table 2).

In the PLS analysis, water temperature and P_{tot} were most strongly related to the first and second PLS vectors, whereas the N:P ratio and water colour were related to the third vector, and N_{tot} , DOC and pH to the fourth vector (Fig. 5). The first two vectors of the PLS model explained 99.8% of the phytoplankton variation. The PLS analysis supported our results from the correlation analysis, i.e. the total phytoplankton biomass and the biomass of *G. semen* were related to the first and third vectors indicating the importance of temperature and P_{tot} , but also the N:P ratio and water colour. *Peridinium* dinoflagellates were related to the second and third vectors and thus they were also affected by water temperature, P_{tot} , N:P ratio and water colour. *Cryptomonas* spp. was related to the fourth vector, i.e. N_{tot} , DOC and pH were the most important predictors of their biomass (Fig. 5).

Discussion

Climate-driven changes in the physical and chemical characteristics of a lake induce taxon-specific responses of phytoplankton, as well as other organisms (Moss *et al.* 2003, Adrian *et al.* 2006, Thackeray *et al.* 2008), and thus we intentionally chose for our study three taxa that presumably respond differently to environmental changes. We detected long-term trends in the biomass of some studied taxa (*Gonyostomum semen* and *Peridinium* spp.), but the rates of

Table 2. Changes as indicated by the trends in the studied environmental parameters as well as Pearson's correlation coefficients (r_p) between the environmental parameters and phytoplankton biomass. $n = 728$, except for precipitation ($n = 155$). Significances of the trends are indicated as follows: # $p < 0.05$, * $p < 0.02$, ** $p < 0.01$, *** $p < 0.001$.

| Parameter | Change (yr ⁻¹) | Total biomass | <i>G. semen</i> | <i>Peridinium</i> spp. | <i>Cryptomonas</i> spp. |
|--|----------------------------|---------------|-----------------|------------------------|-------------------------|
| Temperature (°C) | +0.029 (n.s.) | 0.35*** | 0.31*** | -0.25*** | 0.03 (n.s.) |
| Precipitation | | | | | |
| annual (mm) | -0.066*** | 0.12 (n.s.) | 0.05 (n.s.) | -0.08 (n.s.) | 0.52 (n.s.) |
| summer (mm) | +0.055*** | -0.10 (n.s.) | 0.09 (n.s.) | 0.11 (n.s.) | 0.46 (n.s.) |
| P_{tot} (μg l ⁻¹) | -0.071*** | 0.31 (n.s.) | 0.69** | 0.54# | 0.26 (n.s.) |
| N_{tot} (μg l ⁻¹) | -0.149*** | 0.03 (n.s.) | 0.26 (n.s.) | 0.02 (n.s.) | 0.04 (n.s.) |
| N:P ratio | +0.150*** | -0.20 (n.s.) | -0.44 (n.s.) | -0.46 (n.s.) | 0.22 (n.s.) |
| DOC (mg l ⁻¹) | +0.046* | -0.23 (n.s.) | -0.08 (n.s.) | 0.09 (n.s.) | 0.26 (n.s.) |
| Water colour (mg Pt l ⁻¹) | +1.219*** | -0.21*** | -0.29*** | 0.10 (n.s.) | 0.02 (n.s.) |
| pH | +0.001 (n.s.) | 0.16** | 0.24*** | -0.08 (n.s.) | 0.02 (n.s.) |

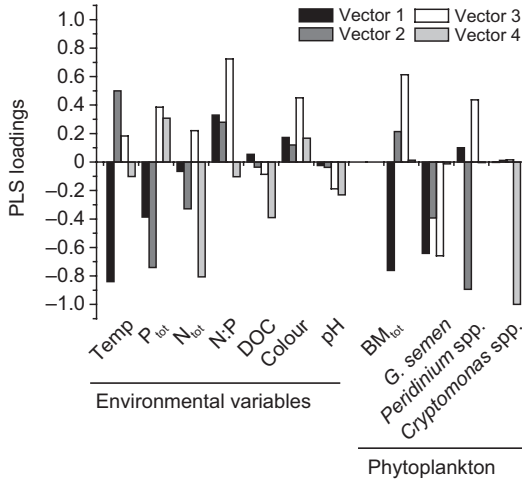


Fig. 5. The partial least-square-regression (PLS) loadings for water temperature (Temp.), P_{tot} , N_{tot} , N:P ratio, DOC, water colour and pH and total phytoplankton biomass (BM_{tot}) as well as the biomass of *G. semen*, *Peridinium* spp. and *Cryptomonas* spp. The first two vectors of the PLS model explain 99.8% of the variation in phytoplankton ($n = 728$).

change were slow and decreasing. Most interestingly, the raphidophyte *G. semen*, a nuisance alga found to be increasing in Scandinavian lakes (Cronberg *et al.* 1988, Lepistö *et al.* 1994 and references therein), decreased in biomass. In Valkea-Kotinen, *G. semen* dominated the phytoplankton in the early years of the study. However, because the total phytoplankton biomass had not decreased by the end of the study period as much as that of *G. semen*, this species must have been replaced by several, but less abundant species. The list of species and biomasses (E. Peltomaa unpubl. data) also confirmed the absence of any new strongly dominant taxa. The residual components in the time series analysis were considerable, indicating that random variations can be high and occasionally even more important for the development of phytoplankton than the long-term trends. In general, the large residuals complicate the interpretation of the long-term monitoring data. They should never be ignored, since these neither systematic nor predictable changes could stem from chaotic fluctuations that are typical of plankton communities (Benincà *et al.* 2008).

Increase in nutrient concentrations due to climate change is suggested to explain the observed

changes in phytoplankton communities better than a temperature rise alone (Thackeray *et al.* 2008). In our study lake, the nutrient concentrations were declining, but still the importance of these two variables came out in the PLS models. Nevertheless, we believe that the temperature rise itself was not a real driver for the trends of phytoplankton. The detected positive effect of temperature on *G. semen* and total biomass in fact reflects the annual increase in solar radiation, which enhances phytoplankton growth but also raises water temperature. The increase in temperature could have caused the decline of *Peridinium* dinoflagellates, some of which thrive at low temperatures (Grigorsky *et al.* 2003). However, dinoflagellates tend to be absent when epilimnetic PO_4 -P concentrations are low (Berman *et al.* 1992, Peltomaa and Ojala 2010) and thus, the decline in phosphorus concentration during the stratification is the more likely cause.

In accordance with the study of Meis *et al.* (2009), the timing of ice-out does not clearly affect the build-up of total biomass or the biomass of any of the studied taxa. Similarly to ice-out, an incomplete spring mixing did not affect the phenology of the phytoplankton. The temperature and oxygen concentration were always measured from the deepest part of the lake (6.5 m), and the interpretation of the completeness of the spring mixing was based on these results. The deep area in Valkea-Kotinen is small, and mixing in the shallower areas was probably sufficient for the recruitment of phytoplankton. Since all the three studied taxa are flagellated and capable of vertical migrations (Hansson 1993), we hypothesized that the long thermal stratification period would favour these species over the non-motile ones. However, we found no evidence on that, but the biomass of the dominant *G. semen* — and thus also the total phytoplankton biomass — was highest during the strongest thermal stratification. This indicates that *G. semen* can migrate through steep chemical and physical gradients to maximize nutrient uptake and photosynthesis, as documented by Salonen and Rosenberg (2000).

The average N:P ratio (31:1) of Valkea-Kotinen indicates that in terms of nutrients the phytoplankton production is phosphorus- rather

than nitrogen-limited. Furthermore, the upward trend of the N:P ratio, the positive correlation between P_{tot} and *Peridinium* spp. as well as *G. semen*, and the N:P and P_{tot} results from the PLS models support the notion of phosphorus limitation and indicate that the limitation is becoming more severe. Normally, epilimnetic nutrient depletion should not be a problem for flagellates, since they are able to migrate to the nutrient-rich hypolimnion, where inorganic phosphorus is continuously released from the sediments to the water column. However, in Valkea-Kotinen, inorganic phosphorus accumulates only in the hypolimnion during the winter and is depleted from the whole waterbody in the summer (Keskitalo *et al.* 1998). When the spring circulation is incomplete, as every fourth year in Valkea-Kotinen, the importance of spring runoff as a way of replenishing nutrient reserves is emphasized. However, the decreasing trend in snowfall in the Valkea-Kotinen area indicates that the spring load from the catchment is declining. The combination of incomplete mixing and decline in snowfall will result in a lower amount of available phosphorus, and could be the underlying cause of the declining trend in *Peridinium* spp. In particular, an incomplete spring mixing can lead to phosphorus deprivation and thus lower the spring biomass of *Peridinium* spp. The importance of phosphorus in Valkea-Kotinen is reflected in the annual succession of the dinoflagellate biomass, which shows a large maximum in spring during and right after the circulation, when phosphorus reserves in the water column are replenished after hypolimnetic accumulation in winter. The second biomass peak during the autumn mixing is smaller and can be explained by smaller reserves of phosphorus due to the lack of phosphorus accumulation in the hypolimnion in summer (Berman *et al.* 1992, Peltomaa and Ojala 2010). The decrease in the phosphorus concentration may also explain the decline in *G. semen*, which has been observed to thrive when phosphorus is plentiful (Lepistö *et al.* 1994). The fairly large size of both taxa probably makes them less competitive in nutrient-poor conditions than cryptophytes (Reynolds 2006), which in Valkea-Kotinen are substantially smaller.

Arvola *et al.* (2006) showed that high summer precipitation enhances DOC load from the catch-

ment and results in increases in the concentration of DOC in rivers. The increase in summer precipitation could not be connected with increased loading of organic matter to Valkea-Kotinen, probably because Valkea-Kotinen is the uppermost lake in a lake chain, and thus without a visible inflow. However, we detected an ascending trend in the surface water DOC concentration and in water colour. Similar findings have earlier been reported for Valkea-Kotinen by Vuorenmaa *et al.* (2006) and Arvola *et al.* (2007). Mobilization of organic carbon increased probably as a consequence of ecosystem recovery following a reduction in sulphur emissions (Vuorenmaa *et al.* 2006, Keskitalo *et al.* 1998) or through changes in soil microbial activity (Goodale *et al.* 2005). DOC came out as an important variable for *Cryptomonas* spp. in the PLS model, and water colour was among the most important variables for *G. semen*, *Peridinium* spp. and the total phytoplankton biomass. As we hypothesized, the increase in DOC and especially in water colour decreased light availability and probably caused the decline in phytoplankton biomass, since primary production in Valkea-Kotinen and in small lakes with a high DOC concentration in general is light-limited (Karlsson *et al.* 2009, Peltomaa and Ojala 2010). Elevated DOC concentrations in soil water could also have affected nutrient availability already in the catchment and thus, despite increased precipitation, the nutrient concentrations in Valkea-Kotinen did not increase, but instead the levels of nitrogen as well as phosphorus slowly decreased. This was against our expectations and therefore we could not test our fifth hypothesis on epilimnetic nutrient concentrations. Similar findings for nitrogen are nowadays common in northern forest areas, and it has been suggested that they stem from changes in atmospheric chemistry or enhanced microbial activity caused by increased DOC concentrations (Wright *et al.* 2001, Goodale *et al.* 2005). Overall, we suggest that the *Cryptomonas* spp., which had seasonal dynamics very similar to *Peridinium* spp. but unlike these dinoflagellates or *G. semen* did not show any decreasing trend, were less vulnerable to the changing environmental conditions than these two other taxa. Cryptophytes have been reported to be more efficient at nutrient uptake when little light is avail-

able (Weng *et al.* 2009), which could explain their different response as compared with that of *G. semen* and *Peridinium* spp. Despite the increase in DOC concentration, pH in Valkea-Kotinen was not decreasing, which indicates a neutralization effect between the acidity of DOC and lake recovery from acidification (Arvola *et al.* 2010). Since the change in pH was negligible, we could not detect any pH induced changes in phytoplankton.

Gonyostomum semen, which was by far the most abundant taxon in Valkea-Kotinen, has only recently been reported to form mass blooms in northern lakes, and it can thus be considered an invasive species (Lepistö *et al.* 1994 and references therein). The invasive species are said to be resistant to grazing (Strayer *et al.* 2006), and *G. semen* as well as *Peridinium* spp. are indeed large as prey items. Besides, *G. semen* possesses potential defensive structures, i.e. trichocysts (Chadefaud 1937). Because the biomass of the only taxon that is well suited for zooplankton as food, i.e. cryptophytes (Sterner 1989), was increasing, it is improbable that changes in grazing pressure are behind the decline of *G. semen*. Studies on stable isotopes of carbon in Valkea-Kotinen have also shown that *G. semen* is not grazed at all (Jones *et al.* 1999). The invasive species are able to displace native species in abnormal environmental conditions (Strayer *et al.* 2006), but in Valkea-Kotinen the cause of the initial expansion of *G. semen* is uncertain; however, eutrophication and acidification have been suggested as possible causes (Cronberg *et al.* 1988, Lepistö *et al.* 1994, Hehmann *et al.* 2001, Findlay *et al.* 2005, Rengefors *et al.* 2008). There are no limnological data from Valkea-Kotinen prior to 1990, and thus we are unable to compare the chemistry or phytoplankton composition before and after the appearance of *G. semen*. Valkea-Kotinen is a true reference site in the middle of an old forest and recovering from anthropogenic acidification. Human-induced eutrophication is impossible, since the surrounding forest has not been fertilized (Ruoho-Airola *et al.* 1998, Vuorenmaa *et al.* 2006). Thus, in Valkea-Kotinen the decline in the biomass of certain phytoplankton taxa as well as the increase of some others could ultimately stem from acidification recovery processes in the catchment.

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