Nutrients provide a stronger control than climate on recent diatom communities in Esthwaite Water: evidence from monitoring and palaeolimnological records

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Summary

1. A long-term monitoring programme on phytoplankton and physico-chemical characteristics of Esthwaite Water (England) that started in 1945 provides a rare opportunity to understand the effects of climate and nutrients on a lake ecosystem.

2. Monitoring records show that the lake experienced nutrient enrichment from the early 1970s, particularly after 1975, associated with inputs from a local sewage treatment plant, resulting in marked increases in concentration of soluble reactive phosphorus (SRP). Climatic variables, such as air temperature (AirT) and rainfall, exhibit high variability with increasing trends after 1975.

3. Diatom analyses of an integrated ^{210}Pb-dated lake sediment core from Esthwaite Water, covering the period from 1945 to 2004, showed that fossil diatoms exhibited distinct compositional change in response to nutrient enrichment.

4. Redundancy analysis (RDA) based on diatom and environmental datasets over the past 60 years showed that the most important variables explaining diatom species composition were winter concentrations of SRP, followed by AirT, independently explaining 22% and 8% of the diatom variance, respectively.

5. Additive models showed that winter SRP was the most important factor controlling the diatom assemblages for the whole monitoring period. AirT had little effect on the diatom assemblages when nutrient levels were low prior to 1975. With the increase in nutrient availability during the eutrophication phase after 1975, climate became more important in regulating the diatom community, although SRP was still the major controlling factor.

6. The relative effects of climate and nutrients on diatom communities vary depending on the timescale. The RDA analysis and additive model revealed that climate contributed little to diatom dynamics at an annual or decadal scale.

7. The combination of monitoring and palaeolimnological records employed here offers the opportunity to explore how nutrients and climate have affected a lake ecosystem over a range of timescales. This dual approach can potentially be extended to much longer timescales (e.g. centuries), where long-term, reliable observational records exist.

Introduction

Lakes are important resources for humans, not only for supplying drinking water, but also for supporting other activities such as agriculture, industry and tourism. Nevertheless lakes face a variety of environmental pressures which greatly threaten their ecological integrity (Vorosmarty *et al.*, 2000). Lakes have undergone substantial deviations from pristine conditions over the past few centuries (e.g. Bennion, Fluin & Simpson, 2004; Taylor *et al.*, 2006; Bjerring *et al.*, 2008). One key pressure is nutrient enrichment, which has received wide attention and continues to dominate the science and policy agenda (Bennion & Battarbee, 2007). Lakes have also experienced serious pressure from climate change which in recent decades has proceeded at a rate beyond historical natural variability (IPCC, 2007; Battarbee & Binney, 2008). The changing climate may alter the structure and function of aquatic ecosystems directly, but may also exacerbate other environmental pressures such as eutrophication (George, Hurley & Hewitt, 2007; Whitehead *et al.*, 2009; Jeppesen et al, 2010).

For the purposes of restoration and lake management, knowledge of how climate change will affect lake ecosystems and how it may interfere with nutrient dynamics is required (Jeppesen *et al.*, 2010). To decipher the confounding effects of climate and nutrients on lakes, long-term monitoring datasets including ecological communities and environmental variables are needed. Such records are rare, however, or may lack consistency in methodology over different monitoring periods (Blenckner, 2005). Palaeolimnological records can augment the relatively short observed records to infer historical changes in lake ecosystems over longer timescales of several centuries or more (Smol & Cumming, 2000; Battarbee *et al.*, 2005); nevertheless, they lack direct records of historical climate and nutrient changes and may also lack good chronological resolution. Given the clearly complementary strengths and weaknesses of monitoring and palaeolimnological records, they can be integrated to conduct research on separating climate and nutrient effects on lake ecosystems (Battarbee *et al.*, 2005).

Esthwaite Water (N 54°21.56', W 002°59.15') is a well-studied site where both long-term high-resolution monitoring and numerous palaeo-environmental studies based on sediment cores have been undertaken (Bennion, Monteith & Appleby, 2000). Research initiated by the Freshwater Biology Association in 1945 and undertaken by the Centre for Ecology and Hydrology and its forerunners since 1989 offers a rare long-term and detailed record of key climate- and nutrient-related variables and biological communities (Maberly *et al.*, 1994). Importantly, this monitoring record covers both oligotrophic (prior to 1970s) and eutrophic phases (post-1970s), whereas most other monitoring records capture only the nutrient enrichment phase (Battarbee *et al.*, 2005). Consequently, this valuable record allows a direct comparison of the responses to climate forcing under different trophic conditions.

Given the complex interactions among environmental variables, statistical approaches have recently been developed to disentangle their relative effects. For example, variance partitioning (Borcard, Legendre & Drapeau, 1992) is used frequently to identify the major forcing variables and their relative effects on aquatic ecosystems over different spatio-temporal scales (e.g. Lotter & Birks, 1997; Hall *et al.*, 1999; Quinlan *et al.*, 2002; Bradshaw, Rasmussen & Odgaard, 2005; Kernan *et al.*, 2009). This method, however, can estimate only the total effect of the various covariates over the time period of interest, not answering questions about when and where the various covariates may be driving change in the response variable(s) (Simpson & Anderson, 2009). To overcome this shortcoming, Simpson & Anderson (2009) employed a flexible and powerful statistical tool, additive modeling (Wood, 2006), to elucidate the critical questions of how much, and when, do the interacting factors affect the lake ecosystems.

By combining high-resolution diatom records from a sediment core and existing long-term monitoring data for Esthwaite Water, we employ both redundancy analysis and additive models to determine how climate and nutrients have affected the lake ecosystem over the period 1945-2004. First, RDA was used to identify the major factors driving diatom community changes and eliminate insignificant and redundant collinear variables. Second, RDA was used to calculate the independent effect of each factor that can explain the main patterns of diatom variation. Finally, an additive model was employed to identify the relative importance of the main controls on the diatom community in greater temporal detail. Diatoms were selected since they have been widely used to indicate trophic changes (e.g. Sayer & Roberts, 2001; Bennion, Fluin & Simpson, 2004; Werner & Smol, 2005; Yang *et al.*, 2008) or climate-induced changes in lakes such as temperature, extent of ice cover, stratification patterns and water depth (Smol & Cumming, 2000; Battarbee, 2000; Mackay, 2007). They can, therefore, act as useful indicators of ecological change driven by both climate and nutrients.

Methods

Site description

Esthwaite Water is a small lake with maximum and mean depths of 15.5 m and 6.4 m, respectively. It is located in the English Lake District, northwest England, where climate is significantly affected by fluctuations in the atmospheric pressure gradient, known as the North Atlantic Oscillation (NAO) (e.g. George, Maberly & Hewitt, 2004). The small catchment (17 km^2) of Esthwaite Water receives a high rainfall, with an annual average of 1900 mm. The lake has a short residence time of *c.* 90 days and stratifies from around late April to early October (Maberly *et al.*, 1994).

Currently Esthwaite Water is eutrophic with a total P (TP) concentration of 28 µg L^{-1} (mean of fortnightly data collected in 2008), and in recent decades cyanobacteria have bloomed frequently. Nutrient loading to Esthwaite Water increased rapidly in the 1970s when a new sewage works was opened that discharged treated effluent into the main inflow (Talling & Heaney, 1988). Nutrient inputs continued to increase with the establishment of a fish farm (for rainbow trout) in the southern basin in 1981and the consequent introduction of waste from cages to the system. From 1986 the phosphorus input from sewage was reduced by tertiary chemical treatment (Talling, 1999). Nevertheless, intensive human activities, particularly tourism in the catchment, have continued to exert pressure on the lake system in recent decades.

Long-term monitoring

Weekly or fortnightly water samples were collected for the analysis of physico-chemical variables from 1945 to present. Integrated surface water samples (0-5 m) were collected using a weighted plastic tube (Lund, 1949). Chemical properties including soluble reactive P (SRP), nitrate (NO_3-N) and SiO_2 were measured according to standard methods (Sutcliffe *et al.,* 1982; Heaney *et al.,* 1988). Mean January (mid-winter) SRP concentration was used to indicate nutrient availability in this study because January SRP has been shown to provide the best measure of nutrient enrichment in the lake (Sutcliffe *et al.*, 1982; Talling & Heaney, 1988).

Meteorological data used in this study, including air temperature (AirT) and rainfall, were obtained from two weather stations in the town of Ambleside, which is within 10 km of Esthwaite Water. The first station was operated between 1931 and 1970 and the second from 1965 to 2004. The two records, exhibiting similar range and variability, were combined to form a harmonised time-series from 1945 to 2004 by taking average values for the period of overlapping measurements. Given that the NAO index is a good descriptor of regional climate forcing, winter and annual NAO index values (denoted as WNAO and ANAO, respectively) were obtained from the web site maintained by the U.S. National Centre for Atmospheric Research (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) for further analysis.

Core extraction and radiometric dating

Two sediment cores were taken from the deepest area (~15 m) of Esthwaite Water as follows: (i) ESTH1, an 86-cm core was collected using a mini-Mackereth piston corer (Mackereth, 1969) in June 1995; (ii) ESTH7, a 65-cm core was collected using a percussion piston corer (Chambers & Cameron, 2001) in April 2006. ESTH1 was sliced at 0.5 cm throughout and ESTH7 was sliced at 0.25 cm in the top 30 cm and 0.5 cm intervals thereafter. Samples were subsequently stored in polyethylene bags at 4°C in the dark.

Both cores were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay using ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. ^{210}Pb chronologies were calculated using the constant rate of ^{210}Pb supply (CRS) model (Appleby & Oldfield, 1978). Full details of the age-depth model of ESTH1 are given in Bennion *et al.* (2000).

Diatom analysis and integration of sediment cores

Fossil diatoms in each sample from both cores were analyzed following standard techniques (Battarbee *et al.*, 2001). A minimum of 300 diatom valves were enumerated for each sample. Diatom identification followed Krammer & Lange-Bertalot (1986, 1988, 1991a, b) and Håkansson & Kling (1990). The fossil diatom data were expressed as relative abundance (in percent).

Given the higher resolution of sediment accumulation for ESTH1 than ESTH7 during 1945 to 1991 and the consistency in the diatom records of the two cores, diatom records representing the period 1993-2004 in ESTH7 (2.5-8.5 cm) and 1945-1992 in ESTH1 (0.5-17 cm) were jointed to obtain a record over 1945-2004 represented by the monitoring data. The integrated core was labelled ESTH9. To match fossil records with monitoring series, estimates of sediment ages were rounded to the nearest calendar year in the monitoring record. In cases where individual years included more than one fossil observation, an arithmetic mean of the observations was used (Bunting *et al.*, 2007).

Ordination

Patterns of diatom community change were summarized using principal components analysis (PCA) of relative abundance data after Hellinger transformation (Legendre & Gallagher, 2001). The first two PCA axes were identified as explaining significant proportions of the variance in the species data when compared with those expected under the broken stick distribution (Jackson, 1993). The scores of the two axes were retained as dependent variables for subsequent modelling.

Environmental variables SRP, NO_3-N, SiO_2, Si/P, N/P, Si/N, AirT, Rainfall, Winter NAO index and Annual NAO index were transformed (log(x+1) for NO_3-N and SiO_2 and square-root transformation for all others) prior to RDA analysis. After removing redundant environmental variables (indicated by variance inflation factors (VIF) above 20) by a primary RDA, a forward manual selection RDA and Monte Carlo permutation tests identified a minimal subset of environmental variables that explained significant proportions ($P<0.05$) of the variations in the species data. Partial RDA was performed on the dataset to partition the variance explained by each variable into a number of independent components (Borcard, Legendre & Drapeau, 1992). RDA analyses were implemented in the computer program CANOCO 4.5 (ter Braak & Smilauer, 2002).

Additive models

An additive model (AM) is a semi-parametric regression in which the sum of regression coefficients × explanatory variables of a linear regression is replaced by a sum of unspecified smooth functions of the explanatory variables (Hastie & Tibshirani, 1990). To allow correlation structures in the model residuals, we use a linear mixed-model representation of the AM (Simpson & Anderson, 2009). As the data represent a time series, we allow for auto-correlation in the residuals by introducing a continuous-time, first-order autoregressive process (CAR(1)) to the model.

AMs containing single variables and then their combination as predictor variables, were employed to model the changes of the scores of the first two PCA axes. The optimal degree of smoothing for the model terms was determined by including the smoothing parameter (λ) in the likelihood function optimized by the model-fitting process. *P*-values based on likelihood ratio tests were used to evaluate the significance of each additional factor. Akaike's Information Criterion (AIC) and an adjusted coefficient of determination (R^2_{adjust}) were used to select the best model (with minimum AIC and highest R^2_{adjust}). Further details of the models used can be found in Simpson & Anderson (2009).

Both the PCA and AMs were performed with the R statistical software (R Development Core Team, 2009) using the vegan package (Oksanen *et al.*, 2008) and mgcv package (Wood, 2006) for R, respectively.

Results

Monitoring records of climate and nutrients

Changes in the major water chemical and climatic variables over the 60-year time series are illustrated in Fig. 1 a-f. Both AirT and the annual NAO index exhibited high variability, with decreasing trends prior to 1987 and higher values after 1987. Average temperatures for the two periods were 8.65 and 9.27 °C, respectively, indicating an overall warming trend over the monitoring period. Average annual rainfall did not show high variability over the monitoring period, but a high amount of rainfall was observed in both 1954 and 2000. There was no relationship between annual rainfall and the NAO index ($P>0.05$, $r^2=0.006$).

Winter maxima for SRP and NO_3-N remained low before 1970, with average values of 2 μg L^{-1} and 467 μg L^{-1}, respectively. After 1970, particularly after 1975, increasing trends were observed in both nutrients, with average winter values of 12 μg

L^{-1} and 797 µg L^{-1}, respectively for the period 1970-2004. Concentrations of SiO_2 changed little over the monitoring period, with the exception of two low winter concentrations (in 1953 and 1993) and one high winter concentration of 3900 µg L^{-1} in 1954.

Sedimentary diatom records

The ^{210}Pb chronology for ESTH7 using the CRS approach indicated a relatively stable sediment accumulation rate (average 5 mm $year^{-1}$) in the upper 9 cm. Calibrated dates for samples from depths (mean of top and bottom values) of 1.88, 3.88, 7.13, 8.13, 9.13 and 10.13 cm were 2004±2, 2001±2, 1995±2, 1993±2, 1991±2 and 1989±2, respectively.

Overall, 116 diatom taxa were identified in the sediment core ESTH9 (only the main species are shown in Fig. 2). Diatom assemblages were dominated by planktonic taxa and showed a typical succession found in many eutrophic lakes. The diatom stratigraphy was divided into two zones. In zone I (prior to 1975), *Asterionella formosa* Hassall and *Aulacoseira subarctica* (O. Müll.) were the dominant species, with average relative abundances of 28% in both cases. Other species typically found in relatively nutrient-poor waters, *Tabellaria flocculosa* (Roth) Kütz. and *Achnanthidium minutissimum* (Kützing) Czarnecki, were present with abundances around 10%. *Fragilaria crotonensis* Kitton, *Cyclotella comensis* Grunow and *Cyclotella radiosa* (Grun.) Lemmerman were also present but with low abundances of around 5%. A major shift occurred around 1975 (zone II), with an expansion of taxa associated with more productive waters, such as *A. formosa*, *F. crotonensis* and *Stephanodiscus binatus* Håkansson and Kling. Correspondingly, formerly abundant species such as *T. flocculosa* and *A. minutissimum* gradually declined. Zone II was subdivided into two subzones, IIa (1975-1996) and IIb (1996-2004), caused by substantial expansion of *Aulacoseira granulata* (Ehrenberg) and its subspecies *A. granulata* var. *angustissima* (O. Müller) Simonsen from ~1996.

Comparison with a broken stick distribution revealed that the first two axes of PCA summarised well the major diatom community changes (Fig. 2). Axis 1, with a distinct shift in sample scores at around 1975, accounted for 41% of the diatom variance. The scores of axis 1 were relatively stable prior to 1975 but increased gradually up the core, reflecting the progressive turnover in the assemblages. Axis 2 accounted for 16% of the diatom variance and exhibited higher variability than axis 1 and an obvious decrease after 1985. Only these two PCA axes were included in the AM analysis, since subsequent axes explained no more variance than expected under the null distribution.

Redundancy analysis

The RDA ordination biplot of samples and environmental variables (VIFs <20) shows that several variables exhibit considerable collinearity (Fig. 3a). Three groups of closely related environmental variables were detected. Nutrient factors SRP, NO_3-N and SiO_2 were correlated with each other, and were highly correlated with axis 1. The paired climate factors, AirT with annual NAO and rainfall with winter NAO, were the other two groups, explaining a considerable amount of diatom variance. Samples from the two zones defined in Fig. 2 were separated along the environmental gradients, with zone I samples negatively correlated with the nutrient variables. In contrast, zone II samples were generally positively correlated with nutrients across the whole range of climate conditions. The sample representing the year 1972, fell into zone II due to its high abundance of *A. formosa.*

Given the co-linearity among variables illustrated in Fig. 3a, a forward manual selection RDA, with Monte Carlo permutation tests, showed that SRP and AirT jointly explained 32% of the diatom variance, compared to 41% for all variables. Partial RDAs undertaken using SRP and AirT illustrated the amount of variation explained independently by each component (Fig. 3b). SRP was the most important variable and significantly explained 22% of diatom variance, while AirT explained 8%. The interaction between SRP and AirT, however, was weak, explaining only 2% of the diatom data.

Additive models

A series of AMs including smooth functions of SRP and AirT as the single covariate were fitted to both sets of axis scores, with and without a CAR(1) correlation structure. The AIC and R^2_{adjust} values for modelling the PCA axis 1 scores (denoted as PCAS1) with SRP and AirT together (with values of 18.074 and 0.704, respectively) exhibited significant improvement over those models with only the single variable SRP (21.510 and 0.623) and AirT (51.277 and 0.158). Consequently, the final model selected both

SRP and AirT as predictors. SRP and AirT did not significantly (*P*>0.05) model the PCA axis 2 scores (denoted as PCAS2) when modeled either solely or together (Table 1). Given the limited diatom variance explained by PCA axis 2, modeling was focused on PCAS1 only.

The final AM fitted to PCAS1 (Fig. 4) includes a significant smooth term for SRP (*P*<0.0001) and AirT (*P*<0.01). The fitted relationship between PCAS1 and SRP is nonlinear (effective degrees of freedom: edf=2.57), while a linear smooth function was used for AirT (edf=1). As SRP increases the PCA scores increase, although the rate of increase is much reduced above 10 μg L^{-1}. The values of the link function for SRP increase with increasing SRP and have larger uncertainties at SRP >20 μg L^{-1} (Fig. 4a). In contrast, the smooth for AirT is much simpler with PCA scores increasing linearly with AirT (Fig. 4b). The smooth functions clearly exhibit a weak response of diatoms to changing climate and a stronger more complex response to nutrients (Fig. 4a, b). When SRP values were low (e.g. <6 μg L^{-1} in 1975), diatom communities changed steeply (nearly linearly) with increasing SRP; while the response was weaker when SRP values were higher. The CAR(1) error structure was not required, as assessed by a likelihood ratio test comparing AMs with and without the structure (*P*>0.1).

Contributions to the fitted values of the two covariates (SRP and AirT) are shown in Fig. 5. The contribution of SRP to fitted PCAS1 is much larger than that of AirT, which is clearly illustrated by the same *y*-scale in the two panels (Fig. 5a, b). A significant change occurred at around 1975 for the contribution of both SRP and AirT. Prior to 1975, SRP made a major “negative” contribution to PCAS1 (~-0.5). After this time the effect of SRP was slightly reduced but it still made a considerable "positive" contribution from 1980-2004 (0.3-0.5). AirT exhibited almost zero effect on PCAS1 prior to 1975, but afterwards there was a small contribution of around ±0.2.

Discussion

Aquatic environmental change over the past 60 years

Common to many lowland lakes in Europe and North America (see reviews in Smith, Tilman & Nekola, 1999; Schindler, 2006), monitoring records of water chemistry from Esthwaite Water indicate substantial nutrient enrichment of the lake over the past 60 years (Talling & Heaney, 1988). While improvements in wastewater treatment after 1986 reduced point source nutrient inputs, nutrients derived from catchment runoff, a fish-farm installed in 1981 and sediment-P release have negated any potential reduction in lake nutrient concentrations (May, 1997; Bennion, Monteith & Appleby, 2000). In addition, phosphorus and nitrogen accumulation from atmospheric deposition are currently important. Atmospheric input of P and N in 1986-1988 were 56 kg P km^{-2} yr^{-1} at a site in the nearby Windermere catchment, and 3500 kg N km^{-2}yr^{-1} averaged for the whole Lake District (Talling & Heaney, 1988). Current levels of nutrient deposition are expected to be higher still (Tipping *et al.*, 2008).

Esthwaite Water has also experienced considerable climate change over the past 60 years. Regionally, the winter NAO is one of the most important factors affecting Esthwaite Water's physical characteristics (George *et al.*, 2004), and factors such as lake level, ice-out time and importantly stratification are all strongly influenced by weather patterns. When the NAO is positive, the lake catchment has experienced milder and wetter conditions over the past 60 years. The long-term records also show the influence of climate change: the winter (the first ten weeks of each year) air temperature variations at Ambleside show that the average temperature recorded during 1940-1970 was 3.0 °C and that recorded during 1970-2000 was 3.6 °C, while the average winter rainfall recorded for these periods was 5.7 mm day^{-1} and 7.1 mm day^{-1}, respectively (George, Hurley & Hewitt, 2007). Several biological components of the lake ecosystem, particularly phytoplankton and zooplankton, have responded to changes in weather conditions in Esthwaite Water over intra- and inter- annual timescales (George, 2000; Talling, 2003; George, Maberly & Hewitt, 2004; Jones & Elliott, 2007).

Diatoms in the core from Esthwaite Water clearly document environmental changes over the past 60 years, particularly in lake nutrient status. Oligotrophic species such as *A. minutissimum*, *T. flocculosa*, *C. comensis*, and *C. radiosa* were present during 1945-1970 when nutrient concentrations were low (average winter SRP 2 μg L^{-1}, Fig. 1). With the slight increase in SRP during 1970-1975, the abundance of the mesotrophic species *A. formosa* increased significantly. However, the main change in the diatom community occurred after ~1977, when eutrophication accelerated (average SRP 12 μg L^{-1} during 1977-2004, Fig. 1). Species preferring eutrophic conditions, such as *S. binatus* (Findlay *et al.*, 1998) and *F. crotonensis* started to dominate and have remained abundant in the sediment ever since. The first appearance of *A. granulata* and *A. granulata* var *angustissima* (shift from zone IIa to IIb) occurred from ~1996.

The latter taxon had been first recorded in the region in the South Basin of Windermere (into which Esthwaite Water flows) in October 1991 (Canter & Haworth, 1992). These taxa commonly have high optima for silica and nitrate concentrations (Interlandi, Kilham & Theriot, 1999) and are also thermophilic species, generally associated with water temperatures in excess of 15 °C (Stoermer & Ladewski, 1976; Poulickova, 1992). Consequently, observed shifts were probably co-driven by seasonal nutrient (e.g. silica and nitrate) and climatic factors (e.g. summer temperature, wind), since annual values of these variables exhibited high variability over the period of *Aulacoseira* abundance (Fig. 1). For example, monitoring records showed that the second highest average summer temperature (16.1 °C) over the period 1980 to 2000 occurred in 1995, with relatively higher values after 1996 compared with the earlier period (George, Hurley & Hewitt, 2007). The increasing temperature under high nutrient conditions probably favoured the growth of *Aulacoseira granulata.*

RDA-based separation of nutrient and climate effects

RDA analysis revealed that SRP explained the largest amount of diatom variance of the measured environmental variables (22%), suggesting that this was the major driving factor of diatom community change over the 60 year dataset. PCAS1 accounted for 41% of diatom variance and was highly correlated to SRP (r=-0.753, p<0.01, n=39). NO_3-N was also highly correlated with SRP (r=0.69, p<0.01, n=39) and likely played an important subsidiary role in controlling diatom dynamics, whereas SiO_2 explained only a limited amount of diatom variance (Fig. 3a). Undoubtedly, all three nutrients are important to diatom growth in Esthwaite Water and elsewhere (Interlandi, Kilham & Theriot, 1999; Reynolds, 2006). However, their relative importance depends on supply rates and on the order in which they are consumed. In Esthwaite Water, the long-term data show that SRP is typically reduced to limiting concentration first, followed by SiO2 and then nitrate (Maberly *et al*., 2011). Thus our inter-annual data support this finding suggesting that SRP is of considerable importance at seasonal to decadal scales in Esthwaite Water. Air temperature, explained just 8% of diatom variance, suggesting climate conditions imposed a weaker effect on diatom change than nutrients.

AM-based separation of nutrient and climate effects

The smoothing functions (Fig. 4) and relative contributions (Fig. 5) derived from AM describe diatom responses to changes in SRP and AirT. SRP availability was clearly more important than AirT in regulating diatom communities when SRP concentrations were low prior to 1975. In contrast, AirT showed almost no effect on diatom communities prior to 1975 but became stronger after 1975 even though the influence of nutrients remained dominant (Fig. 5). The prevailing nutrient effect over the whole period (1945-2004) reflects the various stages of nutrient enrichment, all of which led to diatom community shifts. Furthermore, diatoms show little variation in their ability to compete for nutrients across temperature gradients from 5-20 °C (van Donk & Kilham, 1990) and any change in one of the other factors (e.g. pH, nutrients) may change the diatom composition while temperature remains constant (Anderson, 2000).

In Esthwaite Water, relatively moderate temperature variations were observed, for example, the monthly maximum and minimum air-temperature ranges were 5.4-18.7 °C and 0-10.2 °C for the period 1960-1990, respectively (data from http://www.metoffice.gov.uk/climate/uk/averages/19611990/sites/newton_rigg.html). Thus when nutrients (particularly SRP) are in a range where they are potentially limiting the growth of diatoms, competition for nutrients, rather than climatic factors, drive the community-level shifts. A similar conclusion about the importance of nutrients and physical factors linked to climate change was drawn from a modelling study on Bassenthwaite Lake, also in the English Lake District (Elliott *et al*., 2006).

Synthesis: nutrient and climate effects on diatom communities

In general, climate (including temperature, rainfall, wind, solar irradiation) and nutrients have complex and interacting effects on aquatic ecosystems. For example, increasing temperatures not only lengthen the period of thermal stratification but also bring more nitrate into lakes as higher temperatures increase soil mineralization (Whitehead *et al*., 2009). However, against a background of higher temperatures in Southern Europe, the predicted decrease in precipitation and higher evaporation will result in less runoff and, as a result, possibly lower nutrient loading to fresh waters (Jeppesen *et al*., 2009). Thus the interaction between climate change and a change in nutrient loading may vary between lake types (e.g. deep vs shallow lakes) and different trophic states (Huber, Adrian & Gerten, 2008). In small and relatively shallow lakes, climate can obscure or exaggerate the nutrient enrichment process, since the heat and energy are more easily transferred within the lake than in larger, deeper systems. Nevertheless, in Esthwaite Water it is interesting that the interaction between nutrient and climate factors was rather weak (just 2% in the partial RDA) in terms of its influence on diatom community changes over the 60-year period (Fig. 3).

The effects of climate and nutrients on diatom communities vary depending on the time-scale of the limnological records. In this study both the RDA and AM model based on the annual average data showed that climatic factors (including air temperature, rainfall, ANAO and WNAO) imposed limited effects on diatom dynamics in Esthwaite Water. However, it is undeniable that weather is one of the most important factors controlling diatom dynamics on a seasonal basis (van Donk & Kilham, 1990; Talling, 2003), a timescale normally not accessible to palaeolimnologists since most sediment records have coarser resolution. Indeed, Anderson (1995) showed that seasonal-inter-annual oscillations in diatom plankton may be smoothed out in cores which better reflect longer-term changes (e.g. decades to millennia). This is perhaps one key reason for the limited effect of climate on diatom communities in this study. In fact, temperature, with distinct seasonal cycles but relatively stable inter-annual change, controls many fundamental properties of phytoplankton and is a key factor regulating primary production in most lakes (Reynolds, 2006). This is particularly true as nutrients become less limiting for phytoplankton. Some studies have shown climate warming to have induced forward shifts in the timing of the phytoplankton spring maximum in lakes across the northern hemisphere (Gerten & Adrian, 2000; Straile *et al.*, 2003). Indeed, in Esthwaite Water, long-term monitoring records from 1945 to 2004 show that the timing of the spring bloom of *A. formosa* has been appearing progressively earlier (Patrick *et al.*, 2004). However, these phenological changes are not resolvable in the sediment record of Esthwaite Water.

Combination of RDA and AM methods

RDA analysis extracted the minimum variable combination (SRP and AirT) for further AM procedures. Given the great flexibility of AM, it can provide an excellent fit in the presence of nonlinear relationships and significant noise in predictor variables (Hastie & Tibshirani, 1990; Wood, 2006). However, caution should be exercised to avoid over-fitting of the data, i.e., application of an overly complex model (e.g. with many degrees of freedom) to data so as to produce a good fit. Unexpected results may derive from an AM based on a group of predictors with collinearity (Zuur *et al.*, 2009). The RDA including all the predictors illustrated the multi-collinearity of the environmental dataset (Fig. 3a). Consequently, a predictor selection process for complicated AMs is generally required (Wood, 2006). This study illustrates that the forward selection RDA method offers a good solution for effective predictor selection.

Combination of monitoring and palaeolimnological records

Monitoring and palaeolimnological data are highly complementary and their combination in this study makes a valuable contribution to understanding how nutrients and climate have affected Esthwaite Water. In general, observational time-series data are very limited both in space and time (Battarbee *et al.*, 2005), although they provide a precious and high-resolution description of past environmental change. Palaeolimnological data can complement monitoring data, but can also extend well beyond it, affording an important means of validating ecological hypotheses and long-term model behaviour (Anderson *et al.*, 2006, Sayer *et al.*, 2010).

One possible disadvantage of using palaeolimnological records to extend monitoring data is that they may suffer from taphonomic biases and occasionally from uncertain chronology (Battarbee *et al.*, 2005). Fortunately, increasing research has demonstrated that shifts in many biological components of aquatic ecosystems can be reliably recorded in the lake sediments (e.g. Cameron, 1995). In Esthwaite Water, there was also good agreement between the 60-year monitoring diatom data and corresponding fossil diatom assemblages, indicating that sediment records for this site are reliable (unpublished results). Furthermore, sediment records provide more comprehensive diatom habitats (including epiphytic and benthic species) than phytoplankton data and, importantly, the analysis based on the 60-year dataset can be used "experimentally" to test the practicability of using the sediment record for interpreting longer term changes.

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Table 1 Summary for the additive model fitted to diatom PCA axis 1 and 2 scores.

	PCA axis 1			**PCA axis 2**		
Variable	edf*	F	*P*	edf*	F	*P*
SRP	2.57	31.7	1.92×10^{-9}	1	0.29	0.58
Air Temperature	1	7.68	0.008	1	0.00	0.97

* edf = effective degrees of freedom

Figure legends

Fig. 1 Annual averages for climatic (a-c) and January nutrient (d-f) variables over the monitoring period in Esthwaite Water, respectively.

Fig. 2 Diatom assemblage changes over the past 60 years in core ESTH9 from Esthwaite Water. Diatom data are expressed as % relative abundance and PCA axis 1 and 2 sample scores are shown. Zones of major compositional change are indicated by horizontal lines with dashed lines for subzones.

Fig. 3 (a) Ordination biplot showing environmental variables and samples plotted against RDA axes 1 and 2 for the 60-year sedimentary diatom record. Samples are labelled with the last two numbers of their dates. (b) Variance partitioning of diatom composition, explained by SRP and AirT. See methods for the abbreviations of environmental variables.

Fig. 4 The fitted smooth functions for SRP (a) and air temperature (b) from the final AM for the PCAS1. The dashed lines are approximate 95% confidence intervals on the fitted functions. The tick marks inside the panels on the x-axis show the distribution of observed values for the two covariates. The numbers in brackets on the y-axis (2.57 and 1 for SRP and AirT, respectively) are the effective degrees of freedom for each smoother.

Fig. 5 The contribution of (a) SRP and (b) air temperature to the fitted diatom PCA axis 1 scores. The dashed lines are approximate 95% confidence interval on the contribution.

Fig. 1

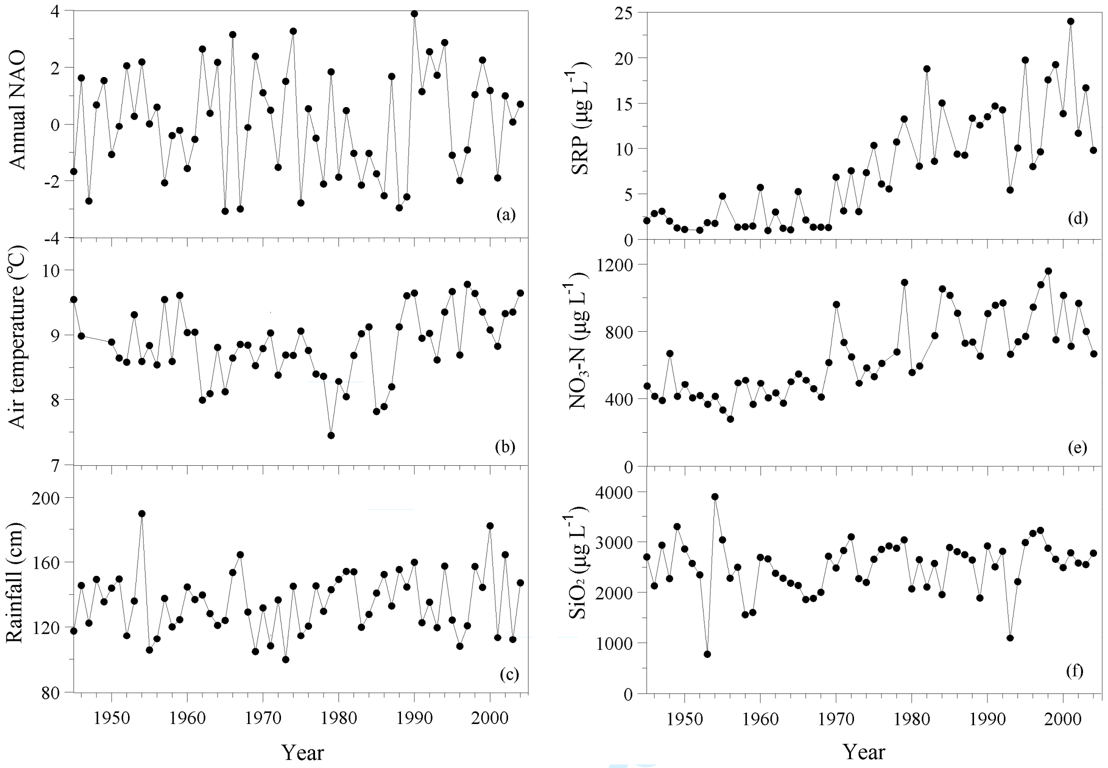

Annual NAO
4
2
0
-2
-4
(a)
Air temperature (℃)
10
9
8
7
(b)
Rainfall (cm)
200
160
120
80
(c)
1950
1960
1970
1980
1990
2000
Year
SRP (μg L^{-1})
25
20
15
10
5
0
(d)
NO$_3$-N (μg L^{-1})
1200
800
400
0
(e)
SiO$_2$ (μg L^{-1})
4000
3000
2000
1000
0
(f)
1950
1960
1970
1980
1990
2000
Year

Fig. 2

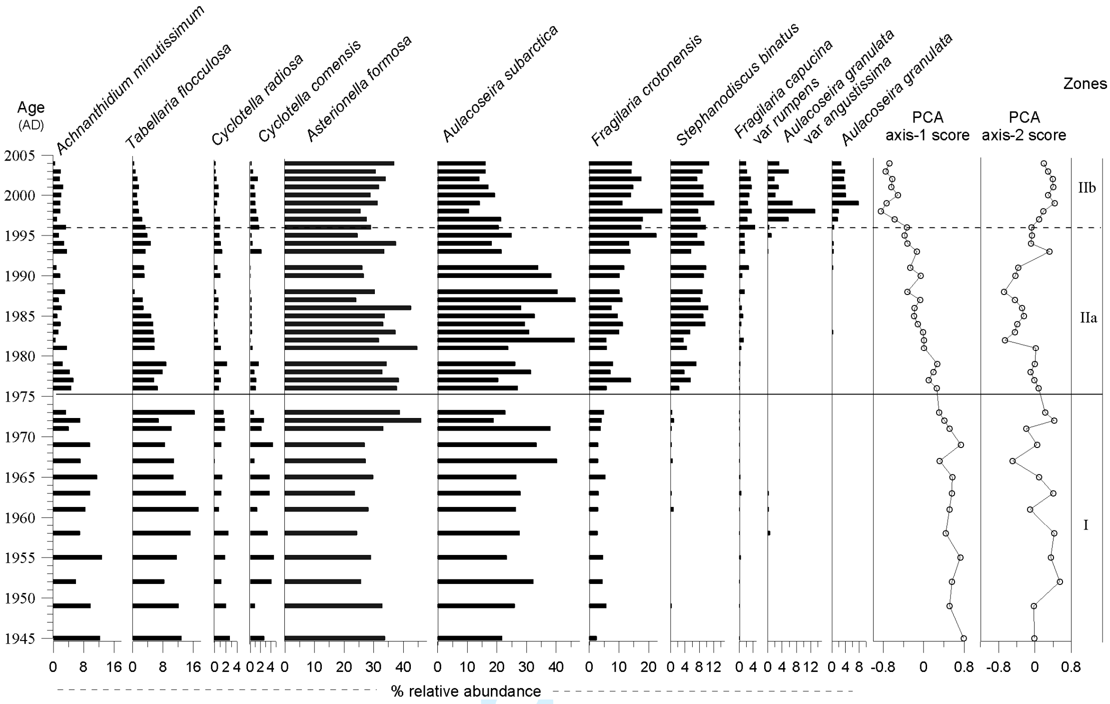

Age
(AD)
Achnanthidium minutissimum
Tabellaria flocculosa
Cyclotella radiosa
Cyclotella comensis
Asterionella formosa
Aulacoseira subarctica
Fragilaria crotonensis
Stephanodiscus binatus
Fragilaria capucina var rumpens
Aulacoseira granulata var angustissima
Aulacoseira granulata
PCA axis-1 score
PCA axis-2 score
Zones
IIb
IIa
I
2005
2000
1995
1990
1985
1980
1975
1970
1965
1960
1955
1950
1945
0 8 16
0 8 16
0 2 4
0 2 4
0 10 20 30 40
0 10 20 30 40
0 10 20
0 4 8 12
0 4
0 4 8 12
0 4 8
-0.8 0 0.8
-0.8 0 0.8
% relative abundance

Fig. 3

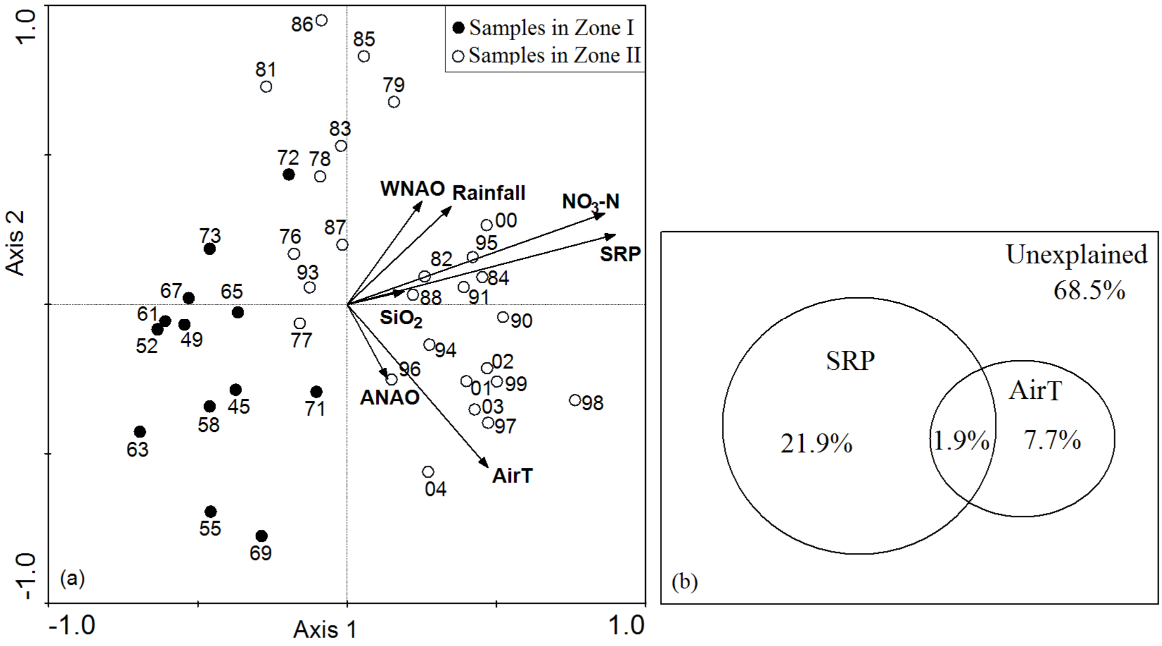

● Samples in Zone I
○ Samples in Zone II
Axis 2
1.0
-1.0
Axis 1
-1.0
1.0
(a)
WNAO
Rainfall
NO_3-N
SRP
SiO_2
ANAO
AirT
86
85
81
79
83
72
78
73
76
87
93
67
65
61
52
49
77
45
58
71
63
55
69
00
95
82
84
88
91
90
94
96
02
01
99
03
97
98
04
(b)
Unexplained
68.5%
SRP
21.9%
1.9%
AirT
7.7%

Fig. 4

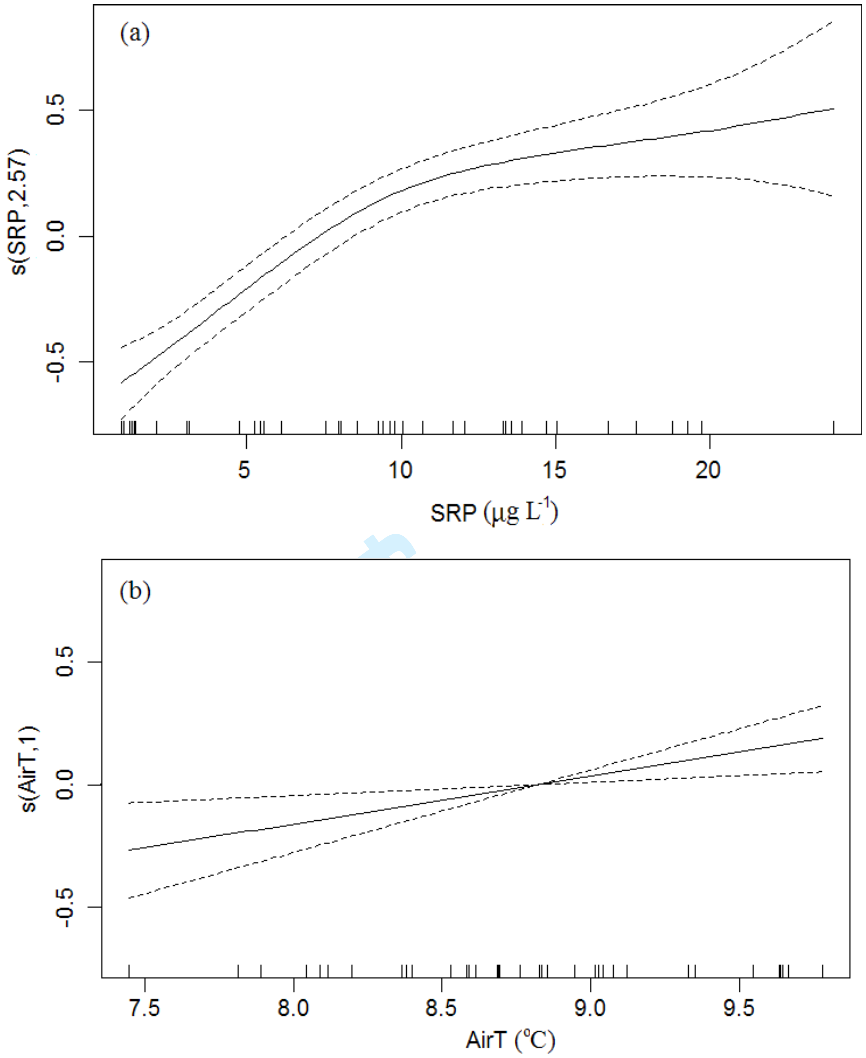
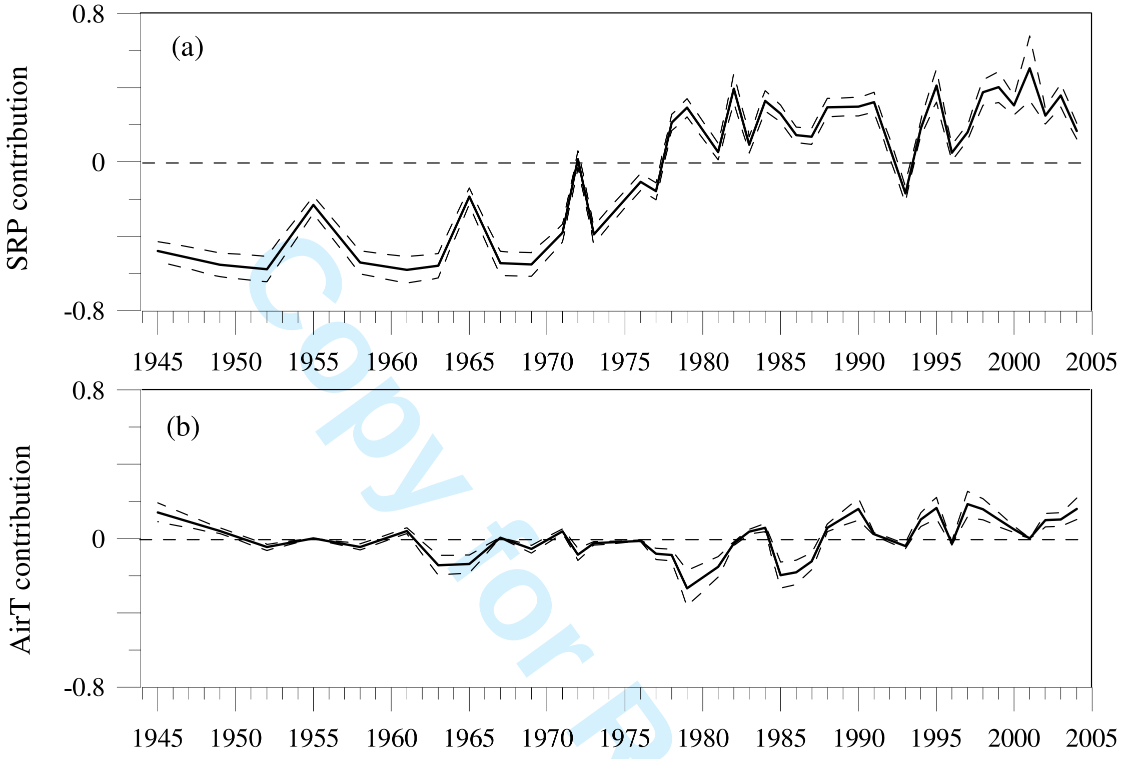

(a)
s(SRP,2.57)
0.5
0.0
-0.5
5
10
15
20
SRP (μg L-1)
(b)
s(AirT,1)
0.5
0.0
-0.5
7.5
8.0
8.5
9.0
9.5
AirT (°C)

Fig. 5


0.8
0
-0.8
SRP contribution
(a)
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
0.8
0
-0.8
AirT contribution
(b)
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005