Assessing degradation and recovery pathways in lakes impacted by eutrophication using the sediment record

Helen Bennion, Gavin Leslie Simpson and Ben J. Goldsmith

1   # Assessing degradation and recovery pathways in lakes impacted by
2   # eutrophication using the sediment record
3
4
5
6   **Helen Bennion[1*], Gavin L. Simpson[2,3], Ben J. Goldsmith[1]**
7
8   **1** Environmental Change Research Centre, Department of Geography, University College London, London, UK.
9   **2** Institute of Environmental Change and Society, University of Regina, Regina, Saskatchewan, Canada.
10 **3** Department of Biology, University of Regina, Regina, Saskatchewan, Canada.
11
12 *** Correspondence:** Dr Helen Bennion, Environmental Change Research Centre, Department of Geography,
13 University College London, Gower Street, London, WC1E 6BT, UK.
14 h.bennion@ucl.ac.uk
15
16
17 Keywords: diatoms, eutrophication, lakes, paleoecology, management, recovery.
18
19
20 **Word count: 8, 142**
21 **Number of figures: 9**
22 **Number of tables: 1**
23
24 **Running title: Lake degradation and recovery pathways**
25
26 **Research Topic Title: Using paleolimnology for management and restoration of lakes**

Abstract

Efforts to restore enriched lakes have increased yet there remains uncertainty about whether restoration targets can be achieved and over what timescale. Paleoecological techniques, principally diatom analyses, were used to examine the degree of impact and recovery in 13 European lakes subject to eutrophication and subsequent reduction in nutrient loading. Dissimilarity scores showed that all sites experienced progressive deviation from the reference sample (core bottom) prior to nutrient reduction, and principal curves indicated gradual compositional change with enrichment. When additive models were applied to the latter, the changes were statistically significant in 9 of the 13 sites.

Shifts in diatom composition following reduction in nutrient loading were more equivocal, with a reversal towards the reference flora seen only in four of the deep lakes and one of the shallow lakes. Of these, only two were significant (Lake Bled and Mjøsa). Alternative nutrient sources seem to explain the lack of apparent recovery in the other deep lakes. In three shallow lakes diatom assemblages were replaced by a community associated with lower productivity but not the one seen prior to enrichment. Internal loading and top down control may influence recovery in shallow lakes and climate change may have confounded recovery in several of the study sites. Hence, ecosystem recovery is not simply a reversal of the degradation pathway and may take several decades to complete. By assessing ecological change over a decadal to centennial timescale, the study highlights the important role that paleolimnology can play in establishing a benchmark against which managers can evaluate the degree to which their restoration efforts are successful.

1.   Introduction

Most lakes throughout the world have been modified to some extent by human activity. Excessive nutrient and organic matter loading resulting in eutrophication has affected numerous waterbodies, most notably since the mid-twentieth century associated with the intensification of agriculture and expansion of populations connected to sewage treatment works (Joye et al., 2006; Battarbee et al., 2011). The consequent high algal biomass leads to filtration problems for the water industry, oxygen depletion, recreational impairment, loss of biodiversity, fish mortality, and decline or loss of submerged plants (Smith et al., 1999).

Efforts to restore enriched systems have increased over the last few decades and there are now numerous examples of lakes in recovery (Jeppesen et al., 2005; Verdonschot et al., 2013). Point-source control at sewage treatment works has been particularly effective at reducing external nutrient loads but nutrient pollution from diffuse agricultural sources has proved more difficult to control as it is dispersed over large areas (Carpenter et al., 1998; Schoumanns et al., 2014). Nevertheless restoration schemes that promote use of buffer strips, good agricultural practice and wetland regeneration have all contributed to the reduction of nutrient loading from agricultural sources (Sharpley et al., 2000). In deep, well flushed lakes, eutrophication is often reversed by the reduction in phosphorus (P) inputs alone, such as in Lake Washington, USA, where P concentrations fell dramatically, phytoplankton biomass declined and there were sustained increases in transparency following effluent diversion and treatment (Edmondson and Lehman, 1981). However, in shallow lakes internal P loading can delay recovery and external P reduction is often combined with other management measures such as dredging or biomanipulation (Søndergaard et al., 2007; Jeppesen et al., 2012), and increasingly geo-engineering techniques which use P-capping agents (Spears et al., 2013; Zamparas and Zacharias, 2014).

Whilst there are many individual success stories, there remains considerable uncertainty about whether restoration targets can be achieved and over what timescales one might expect to see improvement. Recovery may be a slow process as biotic communities tend to exhibit hysteresis and time-lags, and thus ecosystems take time to re-adjust to reduced stress (e.g. Yan et al., 2003; Johnson and Angeler, 2010). In an analysis of long-term datasets from 35 restored lakes, Jeppesen et al. (2005) showed that internal nutrient loading delayed recovery, but in most lakes a new equilibrium for total P (TP) was reached after 10-15 years. Furthermore, new pressures, especially from global warming, may counter restoration strategies. Climate change in combination with land use changes is anticipated to cause increased nutrient loading in lakes, and may increase the frequency and intensity of harmful algal blooms (Jeppesen et al., 2010, 2014). Longer growth seasons, higher water temperature and more turbid conditions are likely to amplify eutrophication problems (Jeppesen et al., 2010; Moss et al., 2011). Thus the expectation that ecosystems can be returned, following remediation efforts, to conditions prior to enrichment may be a naive one and managers and policy makers may have to accept that "shifting baselines" will limit the ability to meet restoration targets (Duarte et al., 2009; Bennion et al., 2011a; Battarbee et al., 2012). Indeed the concept of "novel ecosystems" has been introduced to describe ecosystems in which the species composition and/or function have been completely transformed from the historic system (Hobbs et al., 2009). It has been argued that in these systems a refocusing of conservation and restoration practices away from existing or historical assemblages may be required though most ecologists advocate management based on the same values that we want from historical ecosystems (Higgs et al., 2014; Corlett, 2015).

Legislative programmes are now in force to reduce pollution and restore aquatic ecosystems to good health in many regions of the world. In Europe, the Water Framework

103 Directive (WFD) with its aim to restore waters to at least good status, has increased the need for
104 effective restoration programmes for all lakes (European Union, 2000). Within the WFD,
105 ecological status is based on the degree to which present day conditions deviate from those
106 expected in the absence of significant anthropogenic influence, termed reference conditions.
107 Consequently there has been a wave of research aimed at defining reference conditions and
108 development of tools for estimating deviation from them. Lake sediment analysis provides unique
109 insights into the history of freshwater ecosystems giving evidence for the nature and timing of
110 ecosystem change, and providing a record of human impact that can be indispensible in
111 developing strategies for ecosystem management (Bennion et al., 2011a). Palaeoecological
112 methods can reveal pre-impact conditions and identify any signs of recovery, and have played a
113 key role in the WFD (Bennion and Battarbee, 2007), particularly in determining pre-enrichment
114 reference conditions and degree of eutrophication (Bennion et al., 2004). Diatom records have
115 proved especially valuable in this respect, largely due to their sensitivity to shifts in trophic status
116 (Bennion and Simpson, 2011; Bennion et al., 2011b). As many restoration programmes progress,
117 there is great potential to employ a combination of limnological and sediment records to track
118 recovery using the pre-eutrophication baseline as a benchmark (Battarbee et al., 2005).

120 This paper employs palaeoecological techniques to examine the degree of impact and
121 recovery in thirteen European lakes that have been subject to eutrophication. Changes in the
122 diatom assemblages, both community composition and diatom-inferred TP (DI-TP)
123 concentrations, in sediment cores from the study lakes are assessed in response to enrichment and
124 subsequent reduction in nutrient loading. The extent to which the diatom assemblages are
125 approaching or deviating from reference conditions is explored using ordination and dissimilarity
126 scores and the identification of the floristic changes is assessed statistically using additive models.
127 The key questions being addressed are: i) Do the observed changes reflect degradation and
128 recovery?, ii) Is the recovery pathway simply a reversal of the degradation pathway?, and iii) Can
129 the lake sediment record be used to track degradation and recovery and thus inform management?

131 **2. Materials and methods**

133 **2.1. Study sites**

135 The thirteen study sites are located in European lowland catchments and represent a range of lake
136 types in terms of lake area, depth and trophic status (Table 1). The lakes are within the temperate
137 climatic zone, located in six countries across Europe from Slovenia to Norway, spanning a
138 latitudinal range from 46.4 to 60.8°. Most of the lakes lie in lowland (< 200 m) catchments, with
139 the exception of Lake Bled in Slovenia which lies at higher elevation. The dataset covers a wide
140 range of lake surface areas from <1 to 362 km^2. Similarly lakes span a broad range in maximum
141 water depth from 1.5 to 453 m. For data analyses, the sites have been classed as either deep,
142 stratifying (eight lakes) or shallow, non-stratifying (five lakes), in order to explore whether these
143 lake types respond differently to nutrient reduction measures.

145 The lakes cover a wide range of current (annual mean) TP concentrations from 4 to 476 µg
146 L^{-1}, spanning the full trophic gradient from oligotrophic to hypertrophic conditions (Table 1). The
147 catchments are largely productive with nutrient loading from either point sources such as sewage
148 treatment works and/or diffuse sources from agriculture. All of the sites have experienced
149 eutrophication within the last ~100 years and have either seen a reduction in external nutrient
150 loading from sewage treatment works since the 1970s and 1980s or, in the case of the three Polish

151 lakes, have received less diffuse pollution from the early 1990s as a result of national changes in
152 fertiliser and land use (Table 1).
153
154 **2.2.   Sediment core collection and analyses**
155
156 A sediment core was collected from the open water area of each lake as part of several different
157 previous studies and, therefore, coring methods and analytical resolution vary from site to site. At
158 least ten samples from each core spanning the last ~200 years were analysed for diatoms and,
159 while there were typically >5 samples representing the post-restoration period, in a few cases there
160 were only three samples available. Diatom analysis was carried out using standard methods
161 (Battarbee et al., 2001). A minimum of 300 valves were counted from each sample using a
162 research quality microscope with a 100x oil immersion objective and phase contrast. Krammer
163 and Lange-Bertalot (1986-1991) was the principal flora used in identification. The diatom data are
164 expressed as percentage relative abundances.
165
166   Chronologies for the cores included in this study were determined using radiometric
167 methods. Selected sediment samples were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct
168 gamma assay using the methods of Appleby et al. (1986). ^{210}Pb chronologies were calculated
169 using either Constant Rate of Supply (CRS) or Constant Initial Concentration (CIC) dating
170 models (Appleby and Oldfield, 1978), based on the method best suited to the data.
171

Table 1 Summary characteristics of the thirteen study sites

Site name	Lat	Long	Country	Alt m asl	Lake Area km^2	Max Depth m	Mean TP µg l^{-1}	Lake type	Management actions
Barton Broad	52.7	1.5	England	2	0.77	1.5	74	Shallow, non-stratifying	Reduced external P loading since late 1970s; sediment removal to reduce internal P-loading from 1995-2000
Bosherston Central Lake	51.6	-4.9	Wales	2	0.34	2.0	20	Shallow, non-stratifying	Sewage diversion since 1984, bypass pipeline construction in 1992
Loch Leven	56.2	-3.4	Scotland	106	13.7	25.5	53	Shallow, non-stratifying	Reduced P loading since 1985 but internal loading issues
Llangorse Lake	51.9	-3.3	Wales	156	1.4	9.0	118	Shallow, non-stratifying	Sewage diversion in 1981 and 1992
Marsworth Reservoir	51.8	-0.7	England	115	0.1	4.0	476	Shallow, non-stratifying	Sewage part-diversion and improved sewage treatment works in mid 1980s
Lake Bled	46.4	14.1	Slovenia	475	1.5	32.0	20	Deep, stratifying	Sewage effluent diversion in 1982
Esthwaite Water	54.4	-3.0	England	65	1	15.5	28	Deep, stratifying	Reduced P loading since 1986 but internal loading issues and fish farm present until 2009
Gjersjøens	59.8	10.8	Norway	40	2.4	64.0	15	Deep, stratifying	Sewage effluent diversion in 1971
Kiełpińskie	53.4	19.8	Poland	120	0.61	11	105	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s
Lidzbarskie	53.3	19.8	Poland	128	1.22	25.5	66	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s
Mill Loch	55.1	-3.4	Scotland	55	0.11	16.8	92	Deep, stratifying	Exact restoration measure and timing unknown
Mjøsa	60.8	11	Norway	123	362	453.0	4	Deep, stratifying	Improvements to sewage treatment works in late 1970s
Rumian	53.4	20	Poland	152	3.06	14.4	75	Deep, stratifying	Decrease in fertiliser use and change in land use in early 1990s

2.3. Data analysis

The degree of floristic change in the diatom assemblages between the bottom sample and every other sample in the core was assessed using the squared chord distance (SCD) dissimilarity coefficient (Overpeck et al., 1985) implemented in C2 (Juggins, 2003). The dissimilarity scores range from 0 to 2 whereby 0 indicates that two samples are exactly the same and 2 that they are completely different. This provides a measure of deviation from the reference assemblage. For seven cores, the records extend back to 1800 AD and, therefore, represent a time period prior to major industrialisation and/or agricultural intensification (Battarbee et al., 2011; Bennion and Simpson 2011). For the remaining sites, the cores do not extend back this far but do cover the pre-enrichment period, though the record for Rumian only represents c.25 years. It is generally considered that a shift from benthic to planktonic dominance occurs with eutrophication (Vadeboncoeur et al., 2003) and such a shift has been noted in the diatom assemblages in several palaeoecological studies (e.g. Battarbee, 1978; Sayer et al., 1999). Hence, the percentage of planktonic taxa versus non-planktonic taxa was calculated for each sample to assess whether this provides a useful metric for assessing diatom response to degradation and recovery.

The first axis scores of a principal components analysis (PCA) or a correspondence analysis (CA or detrended CA - DCA) often fail to capture a long or dominant gradient such as we might expect to be present in temporally-ordered data with progressive change in abundance or composition of organisms. As a result, the time series of axis one scores may be a poor summary of compositional change (Simpson and Birks, 2012). Principal curves (PrC; Hastie and Stuetzle, 1989; De'ath, 1999, Simpson and Birks, 2012, Simpson, in prep) is a non- or semi-parametric alternative to PCA, CA, DCA, etc that is particularly suited to the identification of single or dominant gradients within a sediment core sequence. Here we use PrCs to summarise the timing of the major compositional changes in the diatom profiles for the thirteen study lakes. We follow Simpson and Birks (2012) and allow the spline degrees of freedom to vary between species. PCA axis 1 was used as the starting curve in the principal curve fit for all sites except Mill Loch and Mjøsa, where a CA axis 1, and Gjersjøen, where PCA axis 2, were used respectively. These changes were needed to achieve a satisfactory fit with simple species response curves along the fitted PrC.

The PrC scores were extracted for each fit and arranged in time order. To determine if statistically significant change in composition (e.g. eutrophication and subsequent recovery) could be identified, we modelled the time series of PrC scores using additive models, with a continuous time first-order autoregressive process for the residuals to account for the lack of independence between observations (Simpson and Anderson, 2009). Note that here we use sample age as the sole covariate in the model and therefore, unlike the examples in Simpson and Anderson (2009), we simply wish to estimate the potentially non-linear trend in the PrC scores for each lake, to avoid over-interpretation of the time series of scores. Many of the cores were sampled with strongly-varying density in time, and often considerably more samples were available in the most recent sediments than the reference period. Therefore we chose to place knots at the deciles of the distribution of sample ages for each core. This allowed the trend splines to adapt to the data in the regions of the cores where more observations were available.

Approximate significance of the fitted trends can be achieved through the usual methods of statistical inference for additive models (Wood, 2006), however, this only provides a test against the simple null hypothesis of no change in PrC scores with time. Here, our interest is also on where in time the additive models suggest that compositional change takes place if the null hypothesis is rejected. In a linear regression, the slope of the regression line is the first derivative of that curve and, given the standard error of the estimate of the slope, one can determine if the

slope differs from 0 (i.e. no effect). With the additive model, the slope of the fitted trend is potentially changing continuously over the time series of PrC scores, and as a result we do not have a single measure of departure from zero slope. Instead, we use the first derivative of the fitted trend spline evaluated at a set of regularly spaced time points over the interval covered by each sediment core.

To estimate the first derivative of the fitted trend spline we use the method of finite differences, in which we predict from the model at the set of regularly-spaced time points and at a second set, shifted relative to the first by a very small amount. The rate of change in the predictions between the original and shifted points is an approximation to first derivative. How well the finite difference method approximates the unknown first derivative of the spline is governed by size of the shift, with smaller values producing more accurate approximations; we used a value of 0.000001 (of a year) as the shift but the results are not sensitive to a range of values around the chosen value. With each first difference estimate we also obtained its standard error and then formed a pointwise 95% confidence interval on estimate. Where this confidence interval excludes 0 (no change, zero slope) we conclude that significant change in PrC scores is observed for that time point. We indicate these periods of statistically significant change using thicker sections of the fitted trend when plotted. Colour is also used to convey meaning; blue indicates significant decrease in PrC scores whilst red indicates significant increase. In some plots, we have negated the PrC scores such that enrichment in the diatoms is associated with smaller PrC scores, and less enriched periods with larger PrC scores. This is justified as the PrC score is defined as the arc length along the fitted principal curve from one arbitrarily-chosen end of the curve (Hastie and Stuetzle, 1989). Hence the sign on the scores is arbitrary and negating the scores for some lakes improves comparison of the extracted PrC scores and the additive models fitted to them.

A diatom-TP transfer function was applied to the diatom data to reconstruct the trophic status of each site. Reconstructions of DI-TP for the deep lakes were produced using a training set of 56 relatively large, deep lakes (> 10 m maximum depth) from Scotland, Northern Ireland, Cumbria, southern Norway and central Europe with annual mean TP concentrations ranging from 1-73 μg TP L^{-1} and a median value of 22 μg TP L^{-1} (Bennion et al., 2004); the best model was generated with simple weighted averaging and inverse deshrinking (ter Braak and van Dam, 1989); this model has a coefficient of determination (r2) between observed and inferred values of 0.75 and a root mean squared error of prediction (RMSEP based on the jack-knifing cross validation method) of 0.25 log$_{10}$ μg TP L^{-1}. For the shallow lakes, a Northwest European training set of 152 relatively small, shallow lakes (< 10 m maximum depth) was used with a median value of 104 μg TP L^{-1} and a RMSEP of 0.21 log$_{10}$ μg TP L^{-1} for the weighted averaging partial least squares two-component (WA-PLS2) model (Bennion et al., 1996). All reconstructions were implemented using C^{2} (Juggins, 2003).

The samples of each core were projected passively into a PCA of samples from the modern diatom-TP training sets described above, forming so called timetrack plots. These plots allow the direction of floristic change at each site to be visualised. The sample and species scores were plotted in ordination biplots to illustrate the degree to which the recovery trajectories follow back along the enrichment trajectories. For deep lakes, only species that are present in at least two sites and with maximum abundance greater than or equal to 2% are shown and for shallow lakes, these values were five occurrences and 5% min abundance, respectively. Arrows have been added to the plots to illustrate the enrichment and post-restoration trajectories.

258

259   Unless stated otherwise, all analyses were conducted using R (version 3.1.3, R Core Team,
260   2015) with several additional packages: vegan (version 2.2-1, Oksanen et al., 2014) was used to
261   fit the ordinations, analogue (version 0.16-0, Simpson, 2007; Simpson and Oksanen, 2014) was
262   used to fit the principal curves and time tracks, and additive models were fitted using the mgcv
263   package (version 1.8.4, Wood 2004; 2006; 2011). Additional R functions written by GLS (based
264   on suggestions by Simon Wood, *pers comm.*) were used to evaluate the first derivative of the
265   trend splines and form the point-wise confidence interval. R scripts implementing the analyses
266   and reproducing the figures are available online from https://github.com/gavinsimpson/bennion-
267   frontiers-2015.

268

269

270

271   **3.   Results**

272

273   **3.1.   Dissimilarity scores**

274

275   The dissimilarity scores between core bottom and other samples in each core indicate that all sites
276   have experienced deviation from reference condition (core bottom sample) over the period
277   represented by the cores (Figure 1). All sites, with the exception of Kiełpińskie and Lidzbarskie
278   where the patterns are less clear, exhibit progressive deviation from the reference sample during
279   the period prior to nutrient reduction, indicating gradual compositional change with enrichment.
280   The diatom assemblages of some sites, most notably the deep lakes, show signs of returning
281   towards the reference flora following reduction of nutrient load. This is most apparent in Lake
282   Bled, Gjersjøen and Mjøsa. Nonetheless most are still far from reference condition with high
283   dissimilarity scores ranging from 0.38 to 1.57 between the core top and bottom samples.

284

285   **3.2.   Percentage plankton**

286

287   In four of the five shallow lakes (Barton Broad, Loch Leven, Llangorse Lake and Marsworth
288   Reservoir) the % plankton increases with enrichment but does not decline during the recovery
289   phase (Figure 2). In the other shallow lake, Bosherston Central Lake, the % plankton stays low
290   throughout the record. In the deep lakes % plankton was high throughout the cores (generally >
291   60%) but in Esthwaite Water, Gjersjøen, Mill Loch and Mjøsa slight increases in the planktonic
292   component were observed with enrichment. Only in Mjøsa, and to a lesser extent in Esthwaite
293   Water, was a slight decline in % plankton seen in the recovery period.

294

295   **3.3.   Ordination and transfer functions**

296

297   The PrC analysis shows that all sites experienced gradual yet unidirectional shifts in PrC scores
298   during the eutrophication phase (Figure 3). However, following reduction in nutrient loading, the
299   scores move in the reverse direction at only four sites (Marsworth Reservoir, Lake Bled,
300   Gjersjøen, and Mjøsa) (Figure 3). At the remaining sites, there is no clear pattern in the direction
301   of the PrC scores following restoration.

302

303   The additive model fits to the PrC scores indicate change in one direction to some
304   degree in all sites except Gjersjøen, where the rapid shifts seen across relatively few data points
305   are not well captured by the model and hence a flat line (no change, with strong residual
306   autocorrelation) is the best fitting model (Figure 4). The changes are significant (as indicated by
307   the red line in Figure 4) in all but Marsworth Reservoir, Kiełpińskie and Lidzbarskie. At
308   Marsworth Reservoir, some of the patterns in the data are explained as temporal autocorrelation

309   rather than as trend. At Kiełpińskie there are no confidence intervals on the model fit as these are
310   so large that they are off the scale. At Lidzbarskie, there is considerable scatter in the points and,
311   once temporal autocorrelation is allowed for, the uncertainty on the fitted trend is sufficiently
312   large that a statistically significant pattern cannot be extracted from the data series. For the deep
313   lakes, the first significant decrease signalling eutrophication occurs at c.1850 in Mjøsa and Mill
314   Loch, c.1930 in Esthwaite Water, c.1940 in Lake Bled, and c.1985 in Rumian. For the shallow
315   lakes, the first significant decrease occurs at c.1850 in Loch Leven, c. 1910 in Barton Broad,
316   c.1940 in Llangorse Lake, and in the early 1980s in Bosherston Central Lake. A statistically
317   significant recovery trend is observed only in Lake Bled and Mjøsa (as indicated by the blue line
318   in Figure 4), starting at c. early-1980s and mid-1970s, respectively, and in both cases is coincident
319   with restoration measures.

321   The diatom transfer functions infer an increase in TP concentrations in eight of the study
322   lakes during the enrichment period (Figure 5). Of the shallow lakes, a clear signal was not seen in
323   Barton Broad, Bosherston Central Lake or Llangorse Lake, and of the deep lakes a clear increase
324   was not apparent in Gjersjøen or Kiełpińskie. However, the diatom transfer functions infer a
325   decline in TP concentrations following a reduction in nutrient loading at 12 of the 13 study lakes,
326   the exception being Kiełpińskie where a decrease in DI-TP concentrations is not clearly seen
327   (Figure 5). This suggests that at these 12 sites there have been compositional changes towards
328   taxa associated with lower nutrient concentrations following the nutrient reductions. In the case of
329   Kiełpińskie, the shifts in the diatom assemblages were subtle and have resulted in no major
330   change in DI-TP values in recent years.

332   When the deep lake cores are plotted passively on a PCA of the large, deep lakes training
333   set samples (Figure 6) the core samples generally move from the lower right of the plot towards
334   the upper left during the enrichment period. A floristic reversal is most clearly seen in Lake Bled
335   (A), Mjøsa (G) and Gjersjøen (C), where samples move back towards the lower right following a
336   reduction in nutrient loading, and to a lesser extent in Mill Loch (F). However, the additive
337   models indicate that this reversal is statistically significant only in the former two sites. This
338   reverse pattern is not seen in Esthwaite Water (B). Nor is a clear pattern observed for the three
339   Polish lakes: at Kiełpińskie (D) samples move from right to left but there is no subsequent
340   reversal, and at Lidzbarskie (E) and Rumian (H) there is no clear direction of change. The core
341   trajectories reflect changes in the composition of the diatom flora with taxa associated with lower
342   nutrient concentrations located on the right of the diagram (e.g. *Achnanthes* spp., *Brachysira* spp.,
343   *Cymbella* spp., *Eunotia* spp., oligotrophic *Cyclotella* spp. and *Tabellaria flocculosa*), those more
344   typically found in waters with intermediate nutrient concentrations located on the upper left (e.g.
345   *Aulacoseira subarctica*, *Asterionella formosa*, *Fragilaria crotonensis* and *Cyclotella radiosa*) and
346   those commonly seen in nutrient-rich conditions located on the lower left of the plot (e.g.
347   *Aulacoseira granulata, Cyclostephanos dubius*, *Stephanodiscus hantzschii*, *Stephanodiscus*
348   *parvus*) (Figure 7).

350   Similarly, when the shallow lake cores are plotted passively on a PCA of the shallow lake
351   training set samples (Figure 8) the core samples of all lakes, with the exception of Bosherston
352   Central Lake (B), move from the left of the plot towards the right during the enrichment period. A
353   clear floristic reversal is apparent only at Marsworth Reservoir (E) following nutrient reduction,
354   while a slight move back towards the left of the diagram is seen at Loch Leven (C), though
355   additive models indicate that the reversal is not statistically significant in either case. At Barton
356   Broad (A), Bosherston Central Lake (B), and Llangorse Lake (D), the upper core samples move to

357   a new position within the ordination space but do not obviously track back along the enrichment
358   trajectory. As for the deep lakes, the core sample shifts during the eutrophication phase largely
359   reflect a move from taxa associated with relatively nutrient poor conditions located to the left of
360   the diagram (e.g. *Achnanthes* spp., *Brachysira* spp., *Cymbella* spp., oligotrophic *Cyclotella* spp.
361   and *Tabellaria flocculosa*) to those taxa typically found in nutrient rich waters located to the right
362   of the plot (e.g. *Cyclotella meneghiniana*, *Cyclostephanos dubius*, *Cyclostephanos tholiformis*,
363   *Stephanodiscus hantzschii*, *Stephanodiscus parvus*) (Figure 9). The benthic *Fragilaria* spp, which
364   are often abundant in shallow lakes, were positioned in the upper left of the diagram.
365
366

367   **4.   Discussion**
368

369   **4.1.   Diatom response to changes in nutrient loading**
370

371   One of the challenges for ecologists wishing to track environmental change is to find biological
372   indicators that are sufficiently sensitive to the pressure gradient of interest. Here, a range of
373   diatom metrics were explored as diatoms are sensitive to changes in water quality and are
374   particularly good indicators of lake nutrient concentrations (Hall and Smol, 2010). The most
375   striking changes were observed in diatom composition and were effectively summarised by the
376   PrC and dissimilarity (SCD) scores. The data demonstrate that progressive deviation from the
377   reference condition (here defined as the assemblage at the bottom of the core) occurred at all sites
378   during the eutrophication phase although the trends were statistically significant at only nine of
379   the 13 sites. The diatom shifts were gradual rather than abrupt, reflecting a process of relative
380   decline in taxa associated with low nutrient concentrations and their replacement with taxa
381   typically found in more nutrient-rich waters. The ordination plots illustrate that whilst the
382   reference conditions of the 13 study lakes are site specific there are some common patterns in
383   compositional change with shifts from a flora composed of *Achnanthes* spp., *Brachysira* spp.,
384   *Cymbella* spp., *Eunotia* spp., oligotrophic *Cyclotella* spp. and *Tabellaria flocculosa* to one
385   composed of *Aulacoseira subarctica*, *Aulacoseira granulata*, *Asterionella formosa*, *Fragilaria*
386   *crotonensis* and *Cyclotella radiosa* as enrichment progresses and, in the most nutrient-rich cases,
387   to an assemblage composed of small centric taxa such as *Cyclostephanos dubius*, *Stephanodiscus*
388   *hantzschii* and *Stephanodiscus parvus.* These same shifts have been observed in numerous
389   European lakes during periods of increased nutrient loading (e.g. Anderson, 1997; Lotter, 1998,
390   2001; Bennion et al., 2004; 2011b) and, therefore, provide a useful indication of ecological
391   change associated with eutrophication.
392

393   The shifts in diatom composition following reduction in nutrient loading are more
394   equivocal. A clear reversal towards the reference flora is seen only in three of the deep lakes,
395   Lake Bled, Gjersjøen, and Mjøsa, and to a lesser extent in Mill Loch, a deep lake, and Marsworth
396   Reservoir, a shallow lake, in terms of both the dissimilarity and direction of PrC scores. However,
397   the model fits indicate that the recovery trend is only statistically significant at Lake Bled and
398   Mjøsa. As for the degradation phase, the compositional changes are gradual rather than sudden
399   suggesting that ecological recovery may take several years to decades to complete. Indeed even
400   these five lakes do not exhibit a return to the pre-enrichment flora over the 20-30 year period
401   since remedial measures were introduced, as dissimilarity scores between the core bottoms and
402   tops remain relatively high, and the core trajectories illustrate that the recent assemblages have not
403   yet returned to those observed in the lower cores. The data for these five lakes suggest that, whilst
404   the diatoms have responded to nutrient reduction and are heading back along the eutrophication
405   pathway, they still have some way to go before they reach reference condition.
406

407   For the remaining lakes, the diatom response during the 'recovery' period is more difficult

408   to discern. At Esthwaite Water, P loading from a local sewage treatment works was reduced in
409   1986 but nutrients derived from catchment runoff, a fish farm established in 1981 and sediment P
410   release have negated any potential reduction in lake nutrient concentrations (Bennion et al., 2000;
411   Dong et al., 2012) and thus biological recovery is not apparent. For the three Polish lakes
412   (Kiełpińskie, Lidzbarskie, Rumian) which are relatively deep, stratifying waterbodies, the reversal
413   towards former assemblages is less striking than for the other deep sites. This may be because
414   there have been no specific restoration measures taken to reduce point sources of nutrients, and
415   any decrease in nutrient loading is due to the reduction of fertilizer use and changes in land use in
416   the catchments caused by the significant economic changes in the country in the early 1990s.
417   Diatom response is, therefore, very recent and appears to be relatively subtle.

419   The Loch Leven data point to partial recovery of the diatom flora, namely an increase in
420   *Aulacoseira subarctica* relative to *Stephanodiscus* taxa since the mid-1980s, as a result of a
421   catchment management plan introduced in 1985 (Bennion et al., 2012). Long term datasets for the
422   loch show that P concentrations have declined markedly but the trend was non-linear with a slight
423   increase in the early 1990s caused by P recycling from the sediments (Carvalho et al., 2012).
424   Additionally agriculture in the Leven catchment remains a significant diffuse source of nutrients
425   to the loch as much of the land is used for arable farming, and rural septic tanks also contribute to
426   the P load (May et al., 2012). The sediment record suggests that those diatom taxa lost during
427   enrichment have not yet returned, most likely because nutrient concentrations remain too high
428   (Bennion et al., 2012). Likewise, at Barton Broad there is little evidence of any recovery in the
429   diatom assemblages. In spite of a substantial reduction in the amount of P entering the rivers from
430   sewage treatment discharges and a consequent progressive decline in lake TP and chlorophyll *a*
431   concentrations since the late 1970s and early 1980s, the reduction in epilimnetic TP was slow due
432   to the continued release of P from the sediments (Phillips et al., 1999; 2005). Barton Broad,
433   therefore, remains dominated by phytoplankton with almost no submerged macrophyte growth
434   and it is perhaps not surprising that the diatoms show minimal response.

436   At the other two shallow lakes (Bosherston Central Lake and Llangorse Lake) there are
437   compositional changes in the diatoms following remediation efforts but the diatom floras do not
438   appear to revert back towards those seen prior to enrichment but rather move towards a different
439   assemblage. At Llangorse Lake, the effluent from the local sewage treatment works was diverted
440   from the lake in 1981, with a second smaller input diverted in 1992. While the lake appears to be
441   recovering following the remedial measures taken (Bennion and Appleby, 1999), the diatom
442   community in the upper samples is dominated by planktonic forms that were not previously
443   abundant in the record (namely *Aulacoseira subarctica*, *Aulacoseira ambigua* and *Cyclotella
444   radiosa*) and has not yet returned to the *Fragilaria* spp. dominated assemblage seen prior to
445   enrichment. One explanation for this is that algal productivity is N-limited rather than P-limited
446   for most of the summer and internal P loading from the sediments in summer remains high (May
447   et al., 2010). Furthermore, sub-surface flow has been identified at Llangorse Lake with potential
448   to bring in nutrients from outside the immediate catchment (May et al., 2010). At Bosherston
449   Central Lake monitored total phosphate concentrations have exhibited a decline since 1981
450   following various interventions including diversion of sewage since 1984 and construction of a
451   bypass pipeline in 1992 (Davidson et al., 2002). The principal change in the diatom assemblages
452   from this time, most notably since the early 1990s, has been a shift in life-forms with an overall
453   increase in epiphytic taxa relative to benthic taxa. Interpretation of the diatom species shifts is
454   difficult owing to the subtle nature of the changes and the uncertainties regarding the factors
455   which determine the composition of non-planktonic communities. Nevertheless, changes in the

nutrient concentrations, shifts in habitat availability and plant community structure and alterations in grazing pressures are all possible explanations (Davidson et al., 2002). The importance of both top down and bottom up mechanisms, the role of the trophic cascade, interactions between the pelagic and littoral environments, the potential for alternative stable states (Scheffer et al., 1993), and the numerous pathways of P recycling must all be considered in order to fully understand how shallow lake ecosystems might respond to changes in nutrient loading. It is important to bear this complexity in mind when attempting to interpret the findings for the shallow lakes in the present study.

The data suggest that the percentage of planktonic taxa may be a useful metric for tracking enrichment in shallow lakes as a shift towards higher percentage of plankton was apparent with increased nutrient loading in four of the five shallow sites. An increase was less obviously seen in the deep lakes where percentage of planktonic taxa was generally high throughout the records. The shift from benthic to planktonic production associated with eutrophication in shallow waterbodies has been well documented (e.g. Vadeboncoeur et al., 2003). Benthic algae often become light limited as planktonic forms become more abundant, and as submerged macrophytes are lost so too are potential habitats to support epiphytic taxa. However, a subsequent decline in the planktonic component of the diatom assemblages following nutrient reduction was not evident, indicating that there is a degree of 'unhelpful resilience' (Standish et al., 2014) and hysteresis in the systems and the diatom flora does not automatically revert back to that seen prior to enrichment.

Increases in DI-TP were observed in eight lakes during the enrichment period while a decline in DI-TP was seen in 12 lakes following remediation. Hence this metric, which essentially reflects shifts in diatom composition, appears to have some potential for tracking recovery. However, several studies have highlighted the shortcomings of the transfer function technique in certain situations, and this is particularly well documented for shallow lakes where non-planktonic taxa dominate the diatom assemblages. Problems include the influence of factors such as light, substrate and top-down factors in addition to water chemistry on the distribution of these taxa and their wide tolerance to nutrient concentrations, making them poor indicators of lake trophic status (e.g. Anderson et al., 1993; Bennion, 1995; Sayer, 2001; Bennion et al., 2001; Juggins et al., 2013). Nonetheless, in the absence of other techniques for hindcasting nutrient concentrations, inference models are likely to remain a valuable part of the lake manager's toolkit (Saulnier-Talbot, 2015).

4.2.   Degradation versus recovery pathways

Our palaeoecological data reveal that whilst in some cases the diatom recovery trajectories do appear to track back along the degradation pathway, in others and the shallow lakes in particular, either little sign of recovery is evident or the assemblages follow a new trajectory. Our data accord with the findings of other recovery studies in that ecosystem recovery is shown not simply to be a reversal of the degradation process. Duarte et al. (2009) examined four coastal systems demonstrating that they failed to return to the reference status upon nutrient reduction, offering alternative nutrient sources, internal loading, shifts in limiting nutrients, co-limitation effects of nutrients and light, and decreased filter-feeder activity as potential explanations for failure. Similarly riverine communities do not necessarily show the anticipated and desired signs of improvement and recovery may lead to endpoints very different from the original undisturbed state (Palmer et al., 1997). Time lags associated with the release of legacy P (the surplus P stored in soils and sediments derived from past land use activities) is one plausible explanation of why P controls may not produce expected improvements in water quality (Jarvie et al., 2013; Sharpley et al., 2013). In UK lakes, Battarbee et al. (2014) demonstrated that recovery of diatom communities

from acidification was limited when compared with the pre-acidification reference. Similarly to the current study, in a few cases the floristic composition of recent samples was different from that observed during and before the acidification phase and, while the reasons for this are not yet clear, nutrient enrichment from atmospheric N deposition and/or climate change are potential factors confounding recovery (Battarbee et al., 2014). Lake ecosystems have been reported to follow convoluted trajectories following nutrient reduction, with internal loading, changes in food webs, the impacts of climate change, and 10–15-year time lags proposed as the causes for the complex lake trajectories observed (Jeppesen et al., 2005). In a palaeoecological study of six Swiss lakes, diatoms did not switch back to the ones characteristic of the early phase of enrichment despite reductions in nutrient loading (Lotter, 2001).

Most of the existing studies on recovery pathways are based on long-term datasets but for the majority of freshwater ecosystems monitoring activities are rather short-term and do not sufficiently account for long time periods required for restoration. The longer timeframe afforded by the sediment record thus lends itself well to studies of lake recovery and by extending back several decades or even centuries is valuable for defining the reference condition against which degree of recovery can be assessed. Nonetheless, palaeoecological data are not without their limitations and in this study it is perhaps the relatively low resolution of the data for the recovery period (i.e. at some sites only two or three samples correspond to the period since nutrient reduction) that is the greatest weakness. Studies are in progress whereby sites that were cored over 20 years ago are being repeat-cored and the sediments fine-sliced to track recovery over the last few decades at a higher resolution than was possible here. Error associated with the chronologies derived from radiometric dating, albeit small in recent sediments of typically only $\pm$ 2-3 years, can cause difficulty in exactly pinpointing the timing of nutrient reduction in a core and may explain the slight offset between the management actions and diatom response observed in some of our records. Caution must also be exercised when interpreting changes seen in surface sediment samples (upper 0-1 cm) in terms of recovery as the reduced period of decomposition experienced by recently deposited diatoms can result in these being over-represented (Sayer, 2001). Varved sequences, offering an annual resolution, lend themselves particularly well to studies of degradation and recovery (e.g. Chandler Rowell et al., 2015). A combination of long-term datasets and palaeolimnological approaches provides a particularly powerful tool for assessing timescales of ecological change (Battarbee et al., 2005; Bennion et al., 2012; Dong et al., 2012).

4.3.   Management implications and factors confounding recovery

Several of the study lakes exhibit signs of ecological recovery in terms of reversal in their diatom assemblages but even in these cases the assemblages are still far from reference conditions as much as two to three decades since management measures were taken to reduce nutrient loads. Our findings are in accordance with other studies which report typical timescales of recovery for lakes of 10-20 years lakes (Jeppesen et al. 2005; Jones and Schmitz, 2009; Verdonschot et al 2013). This has major implications for the WFD which requires waterbodies to be restored to at least good status, over the course of the next two river basin planning cycles in 2021 and 2027, in that the effects of any measures that have recently been introduced could take several decades to be seen. Perhaps even more importantly the data suggest that for some lake systems the assemblages following remedial action may not return back down the degradation pathway at all and, therefore, reference conditions are unlikely ever to be achieved.

In most of our study lakes, the main point source of nutrients, principally P, has been the

555 key focus of management efforts. However, in recent decades diffuse nutrient sources have
556 become relatively more significant than urban wastewater pollution and losses from agricultural
557 land are now the biggest challenge (Schoumans et al., 2014). There has been a growing literature
558 on the need to reduce nitrogen (N) loads as well as P in order to reverse eutrophication (Galloway
559 et al., 2008; Finlay et al., 2013), particularly in shallow lakes with moderate P levels where high
560 summer N concentrations stimulate algal growth and cause loss of submerged plants (e.g.
561 Jeppesen et al., 2007; Moss et al., 2013). Indeed, a recent assessment of nutrient sources to
562 Llangorse Lake revealed the importance of reducing N inputs if restoration targets are to be met
563 (May et al., 2010).

564

565   The role of climate change in exacerbating the symptoms of eutrophication and
566 confounding recovery efforts cannot be ignored. Climate change is predicted to result in higher
567 water temperatures, shorter periods of ice-cover and longer summer stratification (Jeppesen et al.,
568 2010). Models suggest that lakes with long residence times may experience higher P levels in the
569 future under warmer temperatures (Malmaeus et al*.,* 2006) and shallow lakes may be particularly
570 susceptible. Ecological consequences might include earlier appearance of spring blooming
571 phytoplankton and increased proportions of cyanobacteria. In some systems, negative effects may
572 be compensated by greater predation pressure by zooplankton which is known to be positively
573 temperature dependent. However, fish activity may also increase in warmer temperatures thereby
574 reducing zooplankton populations through increased predation (Moss et al., 2003). In addition,
575 changes in mixing may influence the availability of nutrients in the photic zone and higher
576 temperatures may enhance sediment-P release, whilst higher winter precipitation is likely to
577 enhance nutrient loss from cultivated fields (Battarbee et al., 2008).

578

579   An examination of the role of climate change in explaining the shifts in the diatom
580 assemblages of the 13 lakes is beyond the scope of this study. However, detailed studies on two of
581 the lakes, Esthwaite Water (Dong et al., 2012) and Loch Leven (Bennion et al., 2012) have
582 attempted to explore the ways in which nutrients and climate interact on decadal and inter-annual
583 timescales to affect the diatom communities. In these two lakes, the diatom response has been
584 limited despite significant decrease in external nutrient loading. Dong et al. (2012) conclude that
585 while nutrients have been important at Esthwaite Water during the entire 60-year investigation
586 period, air temperature has become a controlling factor in recent decades during a period when
587 nutrient availability was relatively high. Bennion et al. (2012) showed that at an inter-annual scale
588 the diatom data for Loch Leven exhibit high variability, yet there are several changes in species
589 composition in the recent fossil record that may be attributed to climatic controls. In both of these
590 studies the presence of *Aulacoseira granulata* and *Aulacoseira granulata* var. *angustissma* seems
591 to coincide with warmer temperatures. While the diatoms in Lake Mjøsa have experienced shifts
592 towards the pre-enrichment community, not all the pre-eutrophication taxa have reappeared, and
593 analysis of instrumental records lead Hobæk et al. (2012) to conclude that this is either because
594 nitrate concentrations remain high or because water temperature has increased. Such
595 investigations contribute to a better understanding of the effects of multiple environmental drivers
596 on aquatic ecosystems but equally illustrate the complexity of ecosystem response to synchronous
597 changes in nutrients and climate, and the difficulty of disentangling the effects of these interacting
598 pressures (Battarbee et al., 2012). Models that predict likely outcomes of climate change on
599 nutrient regimes will play a vital role in improving our understanding of future lake response and
600 in guiding management decisions (e.g. Whitehead et al., 2006). Whilst sediment records cannot be
601 used in a predictive capacity, they provide an opportunity to validate hindcasts derived from
602 dynamic models (Anderson et al*.,* 2006). They should, therefore, play an increasingly important
603 role in assessing uncertainty associated with future predictions.

604

605

606 **4.5.   Conclusions**
607
608 In terms of the original questions posed we can conclude that the observed changes in the diatom
609 records do reflect both the degradation and the recovery process. The latter has reached a different
610 stage in each of the study lakes and is more clearly seen in the deep lakes where the diatom
611 assemblages have started to revert back toward those seen prior to enrichment. In shallow lakes
612 factors such as internal loading and top down control may influence the recovery process and in
613 this study, whilst the assemblages of several shallow lakes were replaced by ones associated with
614 lower productivity following remediation, they did not track back along the enrichment pathway.
615 It can, therefore, be concluded that the deep stratified lakes tend to follow a more predictable
616 recovery pathway than the shallow lakes. Nevertheless, the recovery process has a long way to go
617 in all cases as the present assemblages remain very different from those seen in the pre-
618 enrichment samples. Dissimilarity and principal curve scores are shown to be useful measures for
619 quantifying the deviation from reference condition.
620
621   The study highlights the important role that paleolimnological approaches can play in
622 establishing a benchmark against which managers can evaluate the degree to which their
623 restoration efforts are successful. The decadal to centennial timescale adopted here provides the
624 critical temporal context to inform the difficult decisions that emerge for the management of
625 enriched waterbodies. We recognise that this study is based only on diatom responses and our
626 inferences about biological recovery may therefore be biased, especially as diatoms are arguably
627 one of the most sensitive groups in the system and have short response times relative to other
628 assemblages such as macrophytes and fish. Assessments using multiple assemblages are required
629 to evaluate wider ecosystem responses to environmental stressors, hence multi-proxy
630 palaeoecological techniques have an important role to play in future studies of degradation and
631 recovery pathways.
632

633 **5.   Acknowledgements**
634
642
643
644
645

646 **Author contributors**
647
648 HB led the writing of the paper with contributions from GLS and BG. HB and BG counted the
649 diatoms in most of the cores and discussed interpretations. GLS carried out the numerical
650 analyses. All authors reviewed and edited the manuscript.
651
652
653
654

6.   References

Anderson, N. J. (1997). Historical changes in epilimnetic phosphorus concentrations in six rural lakes in Northern Ireland. *Freshwat. Biol.* 5, 427–440. doi: 10.1046/j.1365-2427.1997.00249.x

Anderson, N. J., Rippey, B., and Gibson, C. E. (1993). A comparison of sedimentary and diatom-inferred phosphorus profiles: implications for defining pre-disturbance nutrient conditions. *Hydrobiologia* 253, 357-366. doi: 10.1007/BF00050761

Anderson, N. J., Bugmann, H., Dearing, J. A., and Gaillard, M. J. (2006). Linking palaeoenvironmental data and models to understand the past and to predict the future *Trends Ecol. Evol.* 21, 696-704. doi: 10.1016/j.tree.2006.09.005).

Appleby, P. G., and Oldfield F. (1978). The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. *Catena* 5, 1-8. doi: 10.1016/S0341-8162(78)80002-2.

Appleby, P. G., Nolan, P. J., Gifford, D. W., Godfrey, M. J., Oldfield, F., Anderson, N. J., et al. (1986). ^{210}Pb dating by low background gamma counting. *Hydrobiologia* 141, 21-27. doi: 10.1007/978-94-009-4047-5_4

Battarbee, R. W. (1978). Observations on the recent history of Lough Neagh and its drainage basin. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 281, 303-345. doi: 10.1098/rstb.1978.0001

Battarbee, R. W., Jones, V. J., Flower, R. J., Cameron, N. G., Bennion, H., Carvalho, L., et al. (2001). "Diatoms," in *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators* eds. J. P. Smol, H. J. B. Birks, and W. M. Last (Dordrecht, The Netherlands: Kluwer Academic Publishers), 155-202.

Battarbee, R. W., Anderson, N. J., Jeppesen, E., and Leavitt, P. R. (2005). Combining palaeolimnological and limnological approaches in assessing lake ecosystem response to nutrient reduction. *Freshwat. Biol.* 50, 1772-1780. doi: 10.1111/j.1365-2427.2005.01427.x

Battarbee, R. W., Kernan, M., Livingstone, D., Nickus, U., Verdonschot, P., Hering, D., et al. (2008) "Freshwater ecosystem responses to climate change: the Euro-limpacs project," in *The Water Framework Directive - Ecological and Chemical Status Monitoring (Water Quality Measurements),* eds. P. Quevauviller, U. Borchers, C. Thompson, and T. Simonart (London: John Wiley and Sons), 313-354.

Battarbee, R. W., Morley, D., Bennion, H., Simpson, G. L., Hughes, M., and Bauere V. (2011). A palaeolimnological meta-database for assessing the ecological status of lakes. *J. Paleolimnol.* 45, 405-414. doi: 10.1007/s10933-010-9417-5

Battarbee R. W. Anderson N. J. Bennion H., and Simpson, G. L. (2012) Combining limnological and palaeolimnological data to disentangle the effects of nutrient pollution and climate change on lake ecosystems: problems and potential. *Freshwat.Biol.* 57, 2091-2106. doi: 10.1111/j.1365-2427.2012.02860.x

703   Battarbee, R. W., Simpson, G. L., Shilland, E. M., Flower, R .J., Kreiser, A., Yang, H., et al.
704   (2014). Recovery of UK lakes from acidification: An assessment using combined
705   palaeoecological and contemporary diatom assemblage data. *Ecol. Indicators* 37, 365-380. Doi:
706   10.1016/j.ecolind.2012.10.024

708   Bennion, H. (1995). Surface-sediment diatom assemblages in shallow, artificial, enriched ponds,
709   and implications for reconstructing trophic status. *Diatom Res.* 10, 1-19. doi:
710   10.1080/0269249X.1995.9705326

712   Bennion, H., and Appleby, P. G. (1999). An assessment of recent environmental change in Llangorse
713   Lake using palaeolimnology. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* 9, 361-375.
714   DOI: 10.1002/(SICI)1099-0755

716   Bennion, H., and Battarbee, R. (2007). The European Union Water Framework Directive:
717   opportunities for palaeolimnology. *J. Paleolim.* 38, 285-295. doi: 10.1007/s10933-007-9108-z

719   Bennion, H., and Simpson G. L. (2011). The use of diatom records to establish reference
720   conditions for UK lakes subject to eutrophication. *J. Paleolim.* 45, 469-488. doi: 10.1007/s10933-
721   010-9422-8

722   Bennion, H., Juggins, S., and Anderson, N. J. (1996). Predicting epilimnetic phosphorus
723   concentrations using an improved diatom-based transfer function and its application to lake
724   eutrophication management. *Environ. Sci. Technol.* 30, 2004-2007. doi: 10.1021/es9508030

726   Bennion, H., Monteith, D., and Appleby, P. (2000). Temporal and geographical variation in lake
727   trophic status in the English Lake District: evidence from (sub)fossil diatoms and aquatic
728   macrophytes. *Freshwat. Biol.* 45, 394-412. doi: 10.1046/j.1365-2427.2000.00626.x

730   Bennion, H., Appleby, P. G., and Phillips, G.L. (2001), Reconstructing nutrient histories in the
731   Norfolk Broads: implications for the application of diatom-phosphorus transfer functions to
732   shallow lake management. *J. Paleolim.* 26, 181- 204. doi: 10.1023/A:1011137625746

734   Bennion, H., Fluin, J., and Simpson, G. L. (2004). Assessing eutrophication and reference
735   conditions for Scottish freshwater lochs using subfossil diatoms. *J. Appl. Ecol.* 41, 124-138.
736   doi: 10.1111/j.1365-2664.2004.00874.x

738   Bennion, H., Battarbee, R. W., Sayer, C. D., Simpson, G. L., and Davidson, T. A. (2011a).
739   Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology:
740   a synthesis. *J. Paleolim.* 45, 533-544. doi: 10.1007/s10933-010-9419-3

742   Bennion, H., Simpson, G. L., Anderson, N. J., Dong, X., Hobaeck, A., Guilizzoni, P., et al.
743   (2011b). Defining ecological and chemical reference conditions and restoration targets for nine
744   European lakes. *J. Paleolim.* 45, 415-431. doi: 10.1007/s10933-010-9418-4

746   Bennion, H., Carvalho, L., Sayer, C., Simpson, G. L., and Wischnewski, J. (2012). Identifying
747   from recent sediment records the effects of nutrients and climate on diatom dynamics in Loch
748   Leven. *Freshwat. Biol.* **57**, 2015-2029. doi: 10.1111/j.1365-2427.2011.02651.x

750   Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., and Smith, V. H.
751   (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* 8, 559-
752   568. doi: 10.1890/1051-0761

753

754 Carvalho, L., Miller, C., Spears, B., Gunn, I., Bennion, H., Kirika A., et al. (2012) Water quality
755 of Loch Leven: responses to enrichment, restoration and climate change. *Hydrobiologia* 681, 35-
756 47. doi: 10.1007/s10750-011-0923-x

757

758 Chandler Rowell, H., Bopp, R.F., Peng, F., Velinsky, D. J., and Bloomfield, J.A. (2015).
759 Annually laminated sediments from Onondaga Lake, New York (USA) provide a basis for high-
760 resolution studies of lake degradation and recovery. *J. Paleolim.* 53, 107–12. doi:
761 10.1007/s10933-014-9811-5

762

763 Corlett, R.C. (2015). The Anthropocene concept in ecology and conservation. *Trends Ecol. Evol.*
764 30, 36-41. doi: 10.1016/j.tree.2014.10.007

765

766 Davidson, T., Bennion, H., Yang, H., Appleby, P. G., and Luckes, S. (2002) *Investigation of*
767 *environmental change at the Bosherston Lakes, Pembrokeshire.* CCW Contract Science Report
768 No. 496.

769

770 De'ath, G. (1999). Principal Curves: A New Technique for Indirect and Direct Gradient Analysis.
771 *Ecology* 80, 2237–2253. doi: 10.2307/176906

772

773 Dong, X., Bennion, H., Maberly, S. Sayer, C. D., Simpson, G. L, and Battarbee, R. W. (2012).
774 Nutrients exert a stronger control than climate on recent diatom communities in Esthwaite Water:
775 evidence from monitoring and palaeolimnological records. *Freshwat.Biol.* 57, 2044-2056.
776 doi: 10.1111/j.1365-2427.2011.02670.x

777

778 Duarte, C. M., Conley, D. J., Carstensen, J., and Sánchez-Camacho, M. (2009). Return to
779 Neverland: shifting baselines affect eutrophication restoration targets. *Estuaries and Coasts* 32,
780 29–36. doi: 10.1007/s12237-008-9111-2

781

782 Edmondson, W. T., and Lehman, J. T. (1981). The effect of changes in the nutrient income on the
783 condition of Lake Washington *Limnol. .Oceanogr.* 26, 1–29. doi*:* 10.4319/lo.1981.26.1.0001

784

785 European Union (2000). Directive 2000/60/EC of the European Parliament and of the Council of
786 23 October 2000 establishing a framework for Community action in the field of water policy.
787 *Official Journal of the European Communities* L327, 1–73.

788

789 Finlay, J. C., Small, G. E., and Sterner R.W. (2013). Human influences on nitrogen removal in
790 lakes. *Science* 342, 247-250. doi: 10.1126/science.1242575

791

792 Galloway, J. A., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. F., et al.
793 (2008). Transformation of the nitrogen cycle: recent trends, questions, and potential solutions.
794 Science 320, No. 5878, 889-892. doi: 10.1126/science.1136674

795

796 Hall R. I., and Smol, J. P. (2010). "Diatoms as indicators of eutrophication," in *The Diatoms:*
797 *Applications for the Environmental and Earth Sciences*, 2nd edition, eds. E. F. Stoermer, and J. P.
798 Smol (Cambridge: Cambridge University Press), 122-151.

799

800 Hastie, T., and Stuetzle, W. (1989). Principal Curves. *J. Am. Stat. Assoc.* 84, 502–516. doi:

801   10.2307/2289936

803   Heinsalu, A., and Alliksaar T. (2009). Palaeolimnological assessment of the reference conditions
804   and ecological status of lakes in Estonia: implications for the European Union Water Framework
805   Directive. *Est. J. Earth Sci.* 58, 4, 334-341. doi: 10.3176/earth.2009.4.11

807   Higgs, E., Falk, D.A., Guerrini, A., Hall, M., Harris, J., Hobbs, R.J., et al. (2014). The changing
808   role of history in restoration ecology. *Front. Ecol. Environ.* 12, 499–506. doi: 10.1890/110267

810   Hobæk, A., Løvik, J. E., Rohrlack, T., Moe, S. J., Grung, M., Bennion, H., et al. (2012).
811   Eutrophication, recovery, and temperature in Lake Mjøsa: Detecting trends with monitoring data
812   and sediment records. *Freshwat. Biol.* 57, 1998-2014. doi: 10.1111/j.1365-2427.2012.02832.x

814   Hobbs R. J., Higgs E., and Harris J. A. (2009). Novel ecosystems: implications for conservation
815   and restoration. *Trends Ecol. Evol.* 24, 599–605. doi: 10.1016/j.tree.2009.05.012

817   Jarvie H. P,. Sharpley, A. N., Withers, P. J. A., Scott, J. T., Haggard, B. E., and Neal, C. (2013).
818   Phosphorus mitigation to control river eutrophication: murky waters, inconvenient truths, and
819   "postnormal" science *J. Environ. Qual.* 42, 295–304. doi:10.2134/jeq2012.0085

821   Jeppesen, E., Søndergaard, M., Jensen, J. P., Havens, K., Anneville, O., Carvalho, L., et al.
822   (2005). Lake responses to reduced nutrient loading – an analysis of contemporary long-term data
823   from 35 case studies *Freshwat. Biol.* 50, 1747–1771. doi: 10.1111/j.1365-2427.2005.01415.x

825   Jeppesen, E., Søndergaard, M., Meerhoff, M., Lauridsen, T..L., and Jensen, J. P. (2007). Shallow
826   lake restoration by nutrient loading reduction—some recent findings and challenges ahead.
827   *Hydrobiologia* 584, 239–252. doi: 10.1007/978-1-4020-6399-2_22

829   Jeppesen, E., Moss, B., Bennion, H., Carvalho, L., DeMeester, L., Feuchtmayr, H., et al. (2010).
830   "Chapter 6 Interaction of climate change and eutrophication," in *Climate Change Impacts on*
831   *Freshwater Ecosystems,* eds. M. Kernan, R. W. Battarbee, and B. Moss, (Chichester: Wiley,
832   Blackwell), 119-151.

834   Jeppesen E., Sondergaard, M., Lauridsen, T. L., Davidson, T. A., Liu, Z. W., Mazzeo, N., et al..
835   (2012). Biomanipulation as a restoration tool to combat eutrophication: recent advances and
836   future challenges. *Adv. Ecol. Res*. 47, 411-488. doi: 10.1016/B978-0-12-398315-2.00006-5

838   Jeppesen E., Meerhoff, M., Davidson, T. A., Trolle, D., Søndergaard, M., Lauridsen, T. L., et al.
839   (2014). Climate change impacts on lakes: an integrated ecological perspective based on a multi-
840   faceted approach, with special focus on shallow lakes. J. .Limnol. 73, 84-107.
841   doi: 10.4081/jlimnol.2014.844

843   Johnson, R. K., and Angeler, D. G. (2010). Tracing recovery under changing climate: response of
844   phytoplankton and invertebrate assemblages to decreased acidification. *J. N. Am. Benthol. Soc.*
845   29, 1472–1490. doi: http://dx.doi.org/10.1899/09-171.1

847   Jones, H P., and Schmitz, O. J. (2009). Rapid recovery of damaged ecosystems. Plos One 4,
848   e5653. doi:10.1371/journal.pone.0005653

850   Joye, S. B., Smith, V. H., and Howarth R. W. (2006). Eutrophication of freshwater and marine
851   ecosystems. *Limnol. Oceanogr*. 51, 351–800. doi: 10.4319/lo.2006.51.1_part_2.0351

852

853 Juggins, S. (2003). *C^2 User guide. Software for ecological and palaeoecological data analysis*
854 *and visualisation.* University of Newcastle, Newcastle upon Tyne, UK. 69 pp.

855

856 Juggins, S., Anderson, N. J., Ramstack Hobbs, J. M., and Heathcote, A. J. (2013). Reconstructing
857 epilimnetic total phosphorus using diatoms: statistical and ecological constraints *J. Paleolimnol.*
858 49, 373–390. doi: 10.1007/s10933-013-9678-x

859

860 Krammer, K., and Lange-Bertalot, H. (1986-1991). Bacillariophyceae. 1-4 Teil. *Süsswasserflora*
861 *von Mitteleuropa,* eds. H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer. (Stuttgart: Gustav Fischer
862 Verlag).

863

864 Lotter, A. F. (1998). The recent eutrophication of Baldeggersee (Switzerland) as assessed by
865 fossil diatom assemblages. *Holocene* 8, 395–405. doi: 10.1191/095968398674589725

866

867 Lotter, A. F. (2001). "The effect of eutrophication on diatom diversity: examples from six Swiss
868 lakes," in *Lange-Bertalot-Festschrift*, eds. R. Jahn, J. P. Kociolek, A. Witkowski, and P. Compere
869 (Ganter Ruggell), 417–432.

870

871 Malmaeus, J. M., Blenckner, T., Markensten, H., and Persson, I. (2006). Lake phosphorus
872 dynamics and climate warming: A mechanistic model approach. *Ecol. Model.* 190, 1-14.
873 doi:10.1016/j.ecolmodel.2005.03.017

874

875 May, L., Spears, B. M., Dudley, B. J., and Hatton-Ellis, T. W. (2010). The importance of nitrogen
876 limitation in the restoration of Llangorse Lake,Wales, UK. *J. .Environ. Monit*, 12, 338–346. doi:
877 10.1039/b912827a

878

879 May, L., Defew, L. H., Bennion, H., and Kirika, A. (2012). Historical changes (1905-2005) in
880 external phosphorus loads to Loch Leven, Scotland, UK. *Hydrobiologia* 681, 11-21. doi:
881 10.1007/s10750-011-0922-y

882

883 Moss, B., McKee, D., Atkinson, D., Collings, S. E., Eaton, J. W., Gill, A. B., et al. (2003). How
884 important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow
885 lake microcosms. *J. Appl. Ecol.* 40, 782-792. doi: 10.1046/j.1365-2664.2003.00839.x

886

887 Moss, B., Kosten, S., Meerhoff, M., Battarbee. R. W., Jeppesen, E., Mazzeo. N., et al. (2011).
888 Allied attack: climate change and eutrophication. *Inland Waters* 1, 101-105. doi: 10.5268/iw-
889 1.2.359

890

891 Moss, B., Jeppesen, E., Søndergaard, M., Lauridsen, T. L., and Liu, Z. (2013). Nitrogen,
892 macrophytes, shallow lakes and nutrient limitation: resolution of a current controversy?
893 *Hydrobiologia* 710, 3–21. doi: 10.1007/s10750

894

895 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., et al. (2014).
896 vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-
897 project.org/package=vegan

898

899 Overpeck, J. T., Webb, T., and Prentice, I.C. (1985). Quantitative interpretation of fossil pollen

900 spectra - dissimilarity coefficients and the method of modern analogs. *Quartern. Res.,* 23, 87-108.
901 doi: 10.1016/0033-5894(85)90074-2

903 Palmer, M. A., Ambrose, R. F., and Poff, N. L. (1997). Ecological theory and community
904 restoration ecology. *Restor. Ecol.* 5, 291–300. doi: 10.1046/j.1526-100X.1997.00543.x

906 Phillips, G. L., Bramwell, A., Pitt, J. A, Stansfield, J., and Perrow, M. (1999). Practical
907 application of 25 years' research in the management of shallow lakes. *Hydrobiologia* 395/396,
908 61–76. doi: 10.1023/A:1017059031741

910 Phillips, G. L, Kelly, A., Pitt, J. A., Sanderson, R., and Taylor, E. (2005). The recovery of a very
911 shallow eutrophic lake, 20 years after the control of effluent derived phosphorus. *Freshwat. Biol.*
912 50, 1628-1638. doi: 10.1111/j.1365-2427.2005.01434.x

914 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
915 Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

917 Saulnier-Talbot, É. (2015). Overcoming the disconnect: are paleolimnologists doing enough to
918 make their science accessible to aquatic managers and conservationists? *Front. Ecol. Evol.* 3, 32.
919 doi: 10.3389/fevo.2015.00032

921 Sayer, C. D. (2001). Problems with the application of diatom-total phosphorus transfer functions:
922 examples from a shallow English lake. *Freshwat. Biol.* 46, 743-757. doi: 10.1046/j.1365-
923 2427.2001.00714.x

925 Sayer, C. D., Roberts, N., Sadler, J., David, C., & Wade, M. (1999). Biodiversity changes in a
926 shallow lake ecosystem: a multi-proxy palaeolimnological analysis. *J. Biogeogr.* 26, 97-114.
927 doi: 10.1111/j.1365-2699.1999.00298.x

929 Scheffer, M., Hosper, A. H., Meijer, M-L., Moss, B., and Jeppesen, E. (1993). Alternative
930 equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275-279. doi: 10.1016/0169-5347(93)90254-M

932 Schoumans, O. F., Chardon, W. J., Bechmann, M. E., Gascuel-Odoux, C., Hofman, G., Kronvang,
933 B., et al. (2014). Mitigation options to reduce phosphorus losses from the agricultural sector and
934 improve surface water quality: A review. *Sci. Total Environ.*468–469, 1255–1266. doi*:*
935 10.1016/j.scitotenv.2013.08.061

937 Sharpley, A., Foy, B., and Withers, P. (2000). Practical and innovative measures for the control of
938 agricultural phosphorus losses to water: an overview. *J. Environ. Qual.* 29, 1-9.
939 doi: 10.2134/jeq2000.00472425002900010001x

941 Sharpley, A., Jarvie, H. P., Buda, A., May, L., Spears, B., and Kleinman, P. (2013). Phosphorus
942 legacy: overcoming the effects of past management practices to mitigate future water quality
943 impairment. *J. Environ. Qual.* 42, 1308–1326. doi: 10.2134/jeq2013.03.0098

945 Simpson, G. L. (2007). Analogue Methods in Palaeoecology: Using the analogue Package.
946 *Journal of Statistical Software* 22, 1–29. Retrieved from http://www.jstatsoft.org/v22/i02

948 Simpson, G. L., and Anderson, N. J. (2009). Deciphering the effect of climate change and
949 separating the influence of confounding factors in sediment core records using additive models.
950 *Limnol. Oceanogr.* 54, 2529–2541. doi:10.4319/lo.2009.54.6_part_2.2529

951

952 Simpson, G. L., and Birks, H. J. B. (2012). "Statistical Learning in Palaeolimnology," in *Tracking*
953 *Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques* Vol. 5,
954 eds. H. J. B. Birks, A. F. Lotter, S. Juggins, and J. P. Smol (Netherlands: Springer), pp. 249–327.
955 doi:10.1007/978-94-007-2745-8_9

956

957 Simpson, G. L., and Oksanen, J. (2014). analogue: Analogue matching and Modern Analogue
958 Technique transfer function models. R package version 0.16-0. http://cran.r-
959 project.org/package=analogue

960

961 Smith, V. H., Tilman, G. D., and Nekola, J. C. (1999). Eutrophication: impacts of excess nutrient
962 inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* 100, 179–96.
963 doi: 10.1016/S0269-7491(99)00091-3

964

965 Søndergaard, M., Jeppesen, E., Lauridsen, T., Van Nes, S. C. H., Roijackers, R., Lammens, E., et
966 al. (2007) Lake restoration: successes, failures and long-term effects. *J. Appl. Ecol.* 44, 1095–
967 1105. doi: 10.1111/j.1365-2664.2007.01363.x

968

969 Spears, B. M., Lürling, M., Yasseri, S., Castro-Castellon, A. T., Gibbs, M., Meis, S., et al. (2013).
970 Lake responses following lanthanum-modified bentonite clay (Phoslock®) application: an
971 analysis of water column lanthanum data from 16 case study lakes. *Water Res*. 47, 5930−5942.
972 doi: 10.1016/j.watres.2013.07.016

973

974 Standish, R.J. , Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T. Suding, K. N., Battaglia, L. L.,
975 et al. (2014) Resilience in ecology: Abstraction, distraction, or where the action is? *Biol.Conserv*.
976 177, 43–51. doi: 10.1016/j.biocon.2014.06.008

977

978 ter Braak, C .J. F., and van Dam, H. (1989). Inferring pH from diatoms: a comparison of old and
979 new calibration methods. *Hydrobiologia* 178, 209-223. doi: 10.1007/BF00006028

980

981 Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M. J., Schierup, H. H., Christoffersen, K., and
982 Lodge, D.M. (2003). From Greenland to Green Lakes: cultural eutrophication and the loss of
983 benthic pathways in lakes. *Limnol. .Oceanogr.* 48, 1408-1418. doi: 10.4319/lo.2003.48.4.1408

984

985 Verdonschot, P. F. M., Spears, B. M., Feld, C. K., Brucet, S., Keizer-Vlek, H., Borja, A., et al.
986 (2013). A comparative review of recovery processes in rivers, lakes, estuarine and coastal waters.
987 *Hydrobiologia* 704, 453–474. doi: 10.1007/s10750-012-1294-7

988

989 Whitehead, P. G., Wilby, R. L., Butterfield, D., and Wade, A. J. (2006). Impacts of climate
990 change on in-stream nitrogen in a lowland chalk stream: an appraisal of adaptation strategies. *Sci.*
991 *Total Environ.* 365, 260–273. doi*:* 10.1016/j.scitotenv.2006.02.040

992

993 Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized
994 additive models. *J. Am. Stat. Assoc.* 99, 673–686. doi:10.2307/27590439

995

996 Wood, S. N. (2006). *Generalized Additive Models: An Introduction with R*. Chapman and
997 Hall/CRC.

998

999   Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation
1000 of semiparametric generalized linear models. *J. Roy. Stat. Soc. Ser. B. (Stat. Method.)* 73, 3–36.
1001 doi:10.1111/j.1467-9868.2010.00749.x
1002
1003 Yan, N.D., Leung, B., Keller, B., Arnott, S. E., Gunn, J. M., and Raddum, G.G. (2003).
1004 Developing conceptual frameworks for the recovery of aquatic biota from acidification. *Ambio*
1005 32,165–169. doi: 10.1579/0044-7447-32.3.165
1006
1007 Zamparas, M., and Zacharias, I. (2014). Restoration of eutrophic freshwater by managing internal
1008 nutrient loads. A review. *Sci. Total Environ.*496, 551–562. doi: 10.1016/j.scitotenv.2014.07.076

1009 **7. Figure legends**
1010

1011 **Figure 1 Dissimilarity scores for the thirteen study sites.** The degree of floristic change in the
1012 diatom assemblages between the bottom sample and every other sample in the core; timing of
1013 nutrient reduction is shown by the arrow.

1014 **Figure 2 Percentage plankton in the thirteen study sites.** Timing of nutrient reduction is shown
1015 by the arrow.

1016 **Figure 3 Principal curve scores for the thirteen study sites.** Timing of nutrient reduction is
1017 shown by the arrow.

1018 **Figure 4 Principal curve fits with derivatives for A) shallow lakes and B) deep lakes.** Red and
1019 blue lines indicate significant decrease and significant increase in PrC scores, respectively.
1020 Dashed lines are 95% confidence intervals.

1021 **Figure 5 Diatom-inferred TP (DI-TP) reconstructions for the thirteen study sites.** Timing of
1022 nutrient reduction is shown by the arrow.

1023 **Figure 6 Deep lake cores plotted passively on a PCA of training set samples.** The direction of
1024 change over time is shown by the arrows. **(A)** Lake Bled, **(B)** Esthwaite Water, **(C)** Gjersjøen, **(D)**
1025 Kielpinskie, **(E)** Lidzbarskie, **(F)** Mill Loch, **(G)** Mjøsa, **(H)** Rumian.

1026 **Figure 7 Species plot on a PCA of training set samples for the deep lake cores.** (A) All taxa
1027 present in at least two sites and with maximum abundance greater than or equal to 2% , (B)
1028 zoomed in section as indicated by the inset in (A). See Supplementary material, Appendix 1 for
1029 diatom codes and names.

1030 **Figure 8 Shallow lake cores plotted passively on a PCA of training set samples.** The direction
1031 of change over time is shown by the arrows. **(A)** Barton Broad, **(B)** Bosherston Central Lake, **(C)**
1032 Loch Leven, **(D)** Llangorse Lake, **(E)** Marsworth Reservoir.

1033 **Figure 9 Species plot on a PCA of training set samples for the shallow lake cores.** (A) All
1034 taxa present in at least five sites and with maximum abundance greater than or equal to 5%, (B)
1035 zoomed in section as indicated by the inset in (A). See Supplementary material, Appendix 1 for
1036 diatom codes and names.

Supplementary material – Appendix 1 is presented in a separate Word file

Appendix 1 List of diatom taxa included in the data analyses with codes and names

Figure 1.TIF
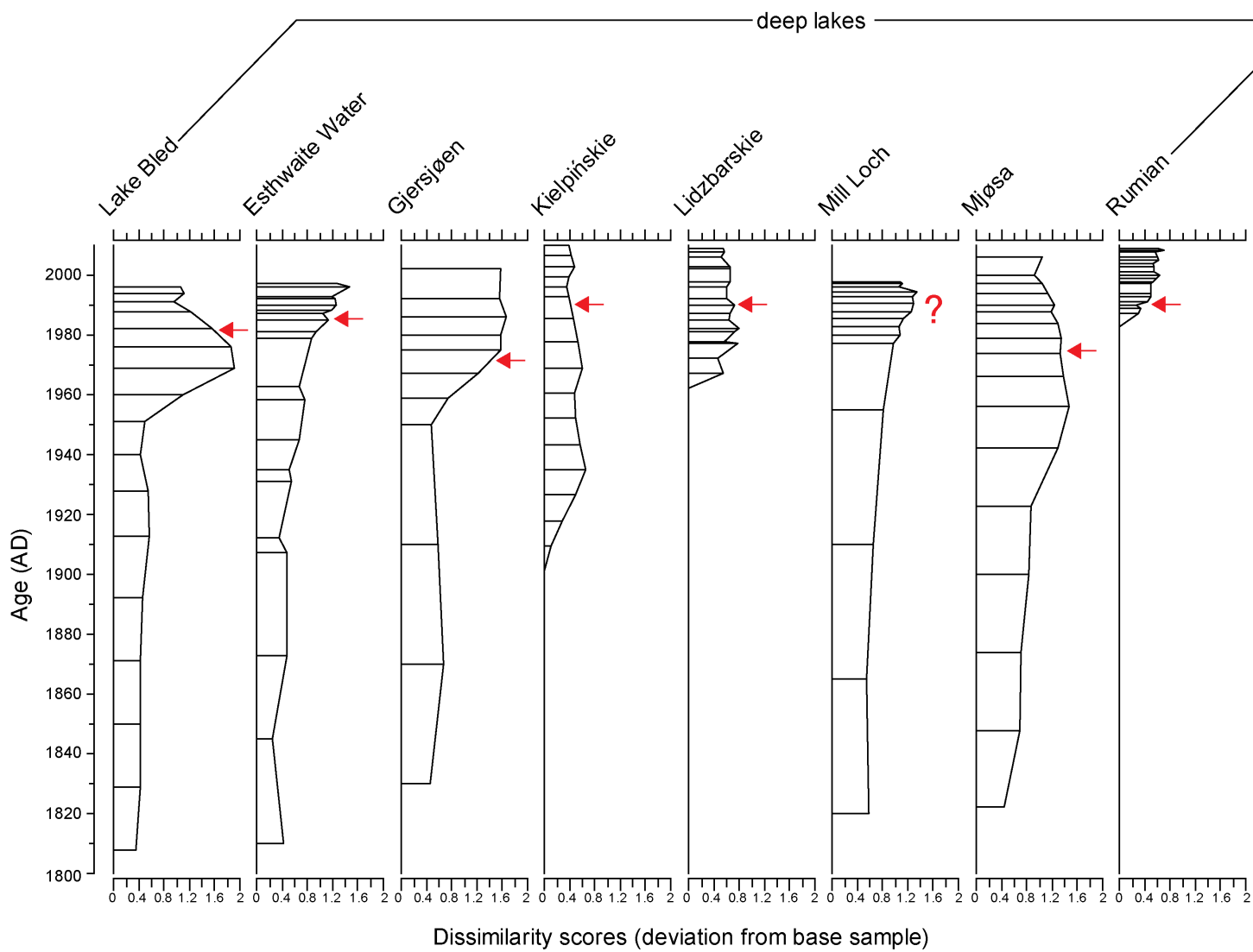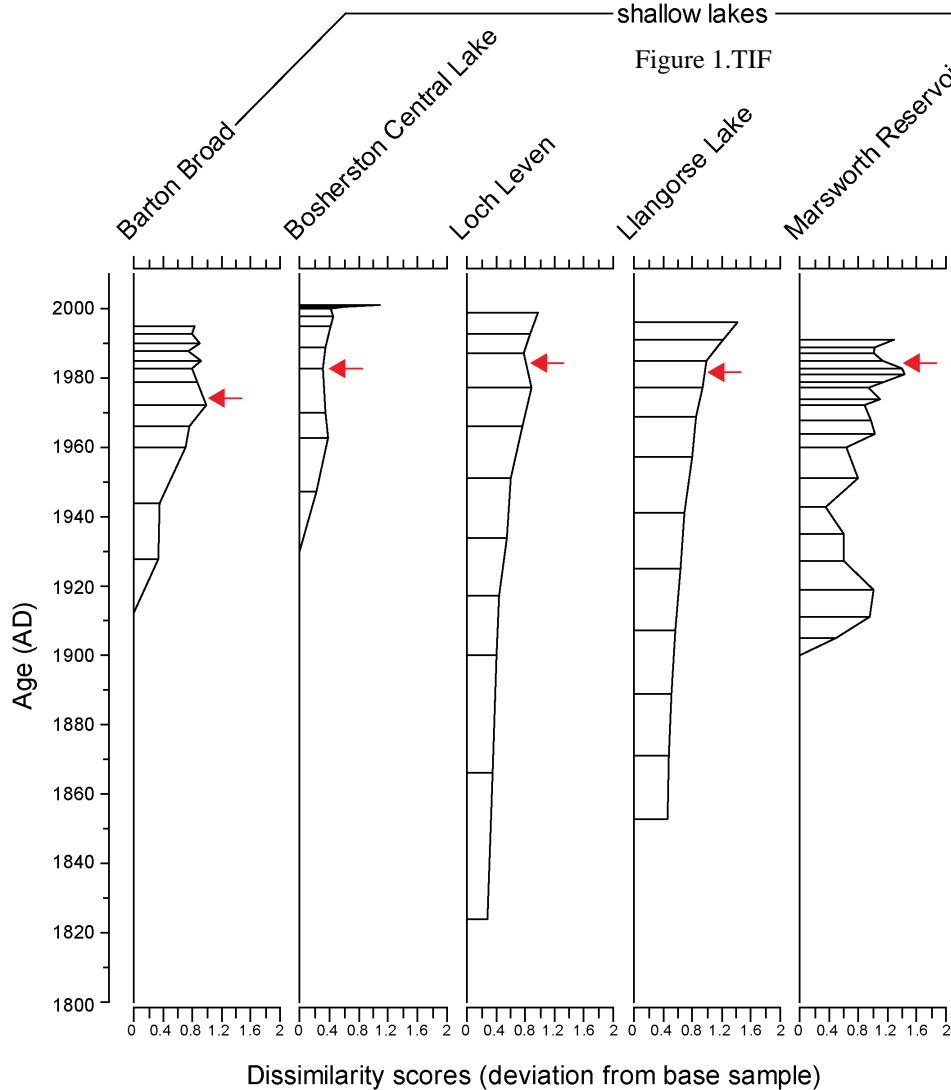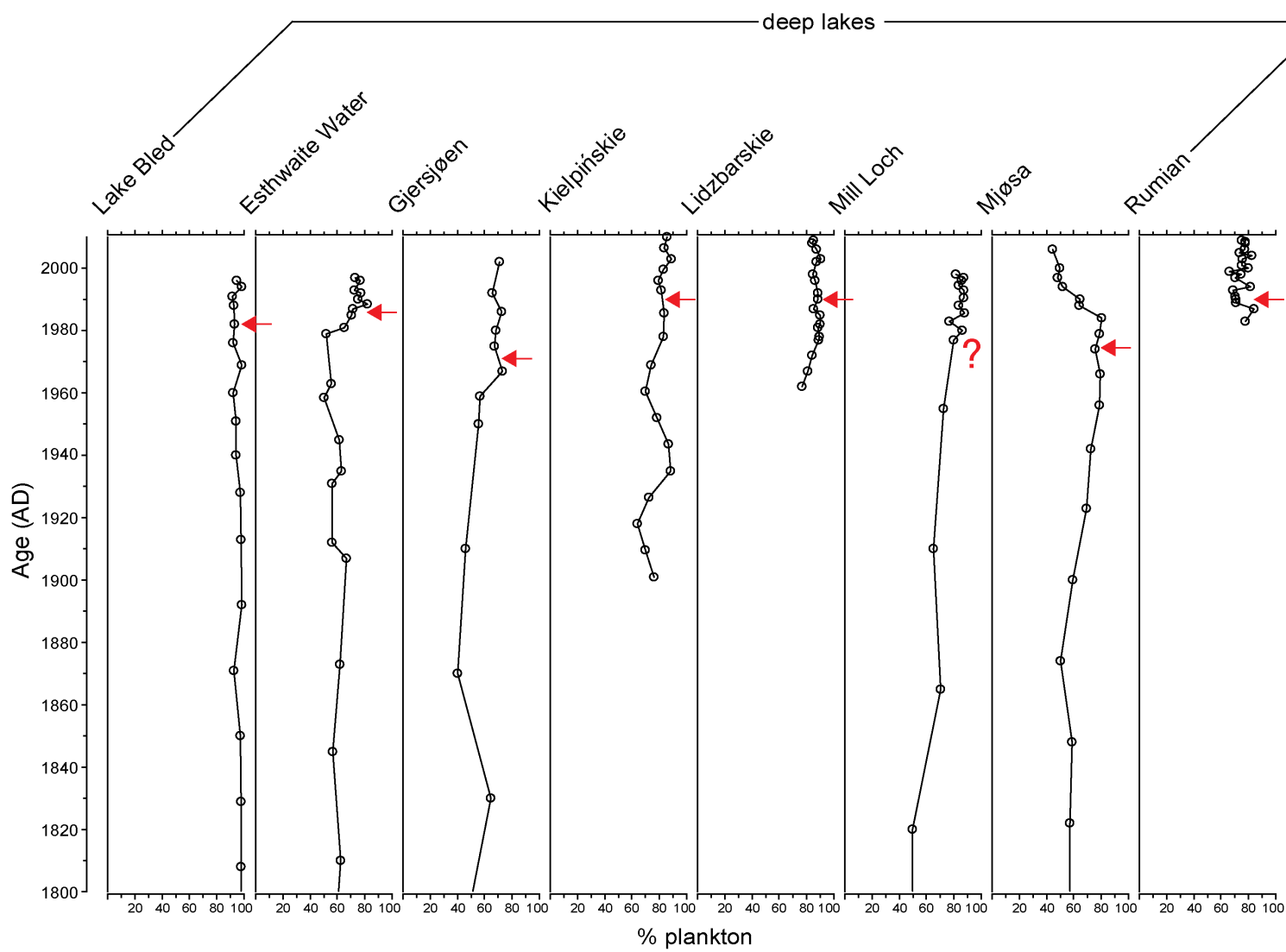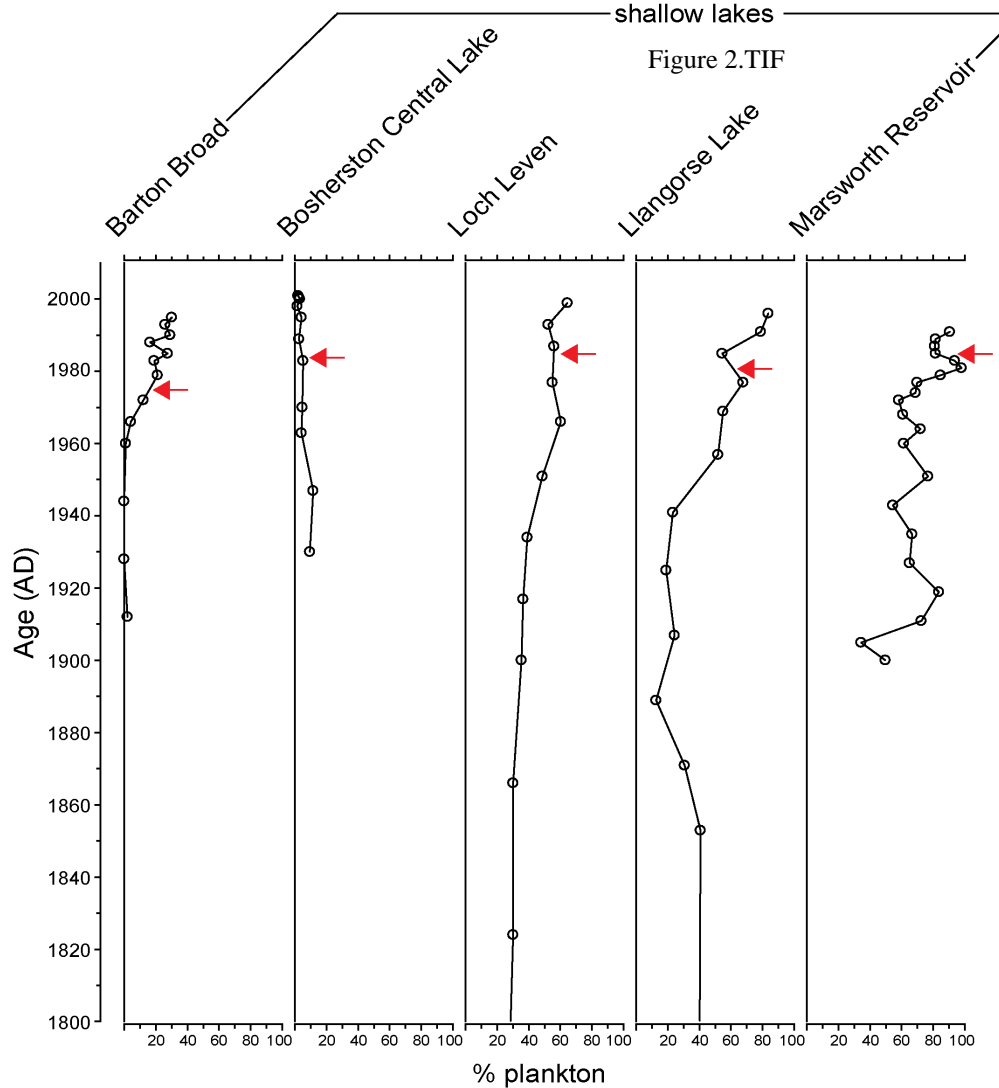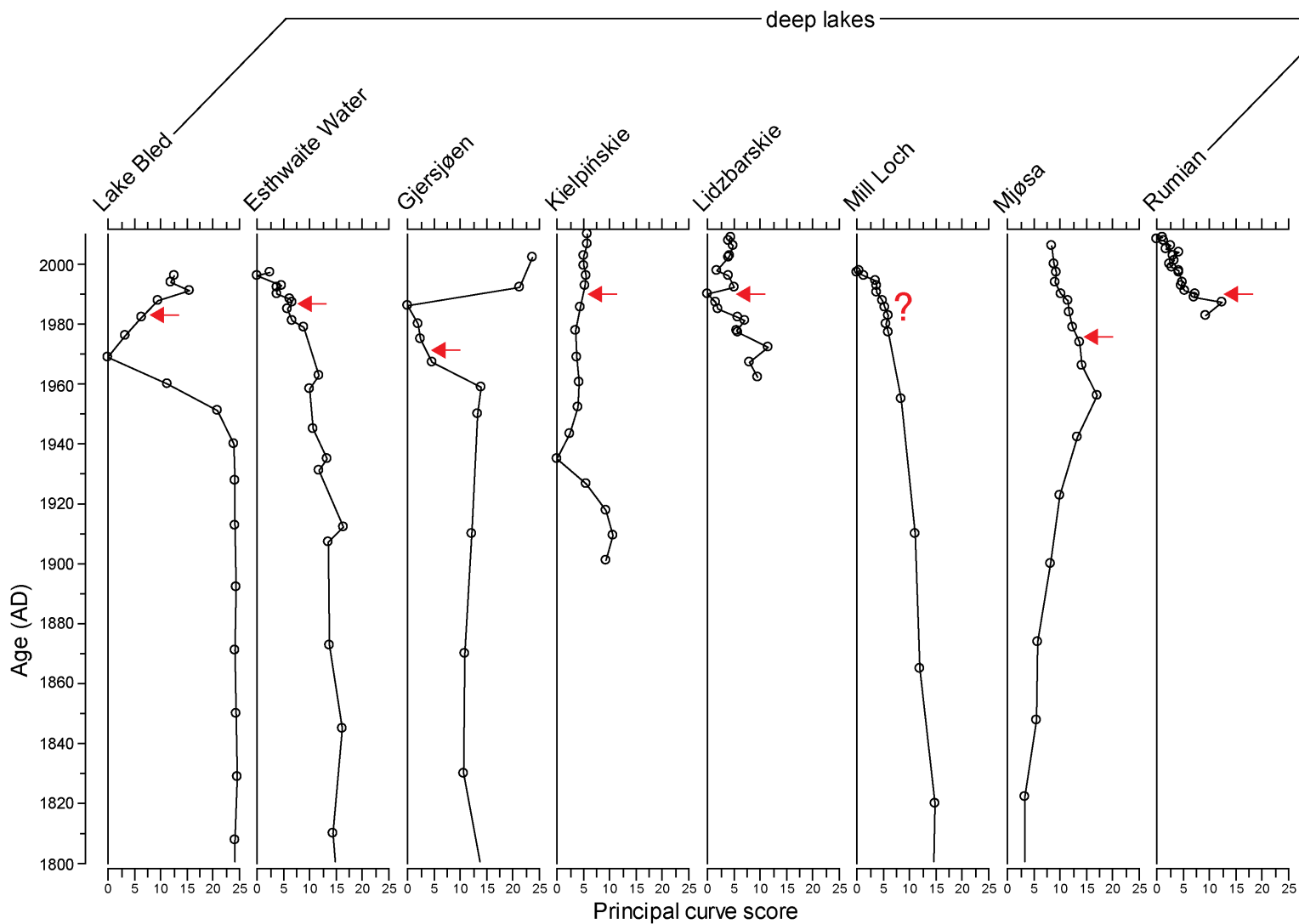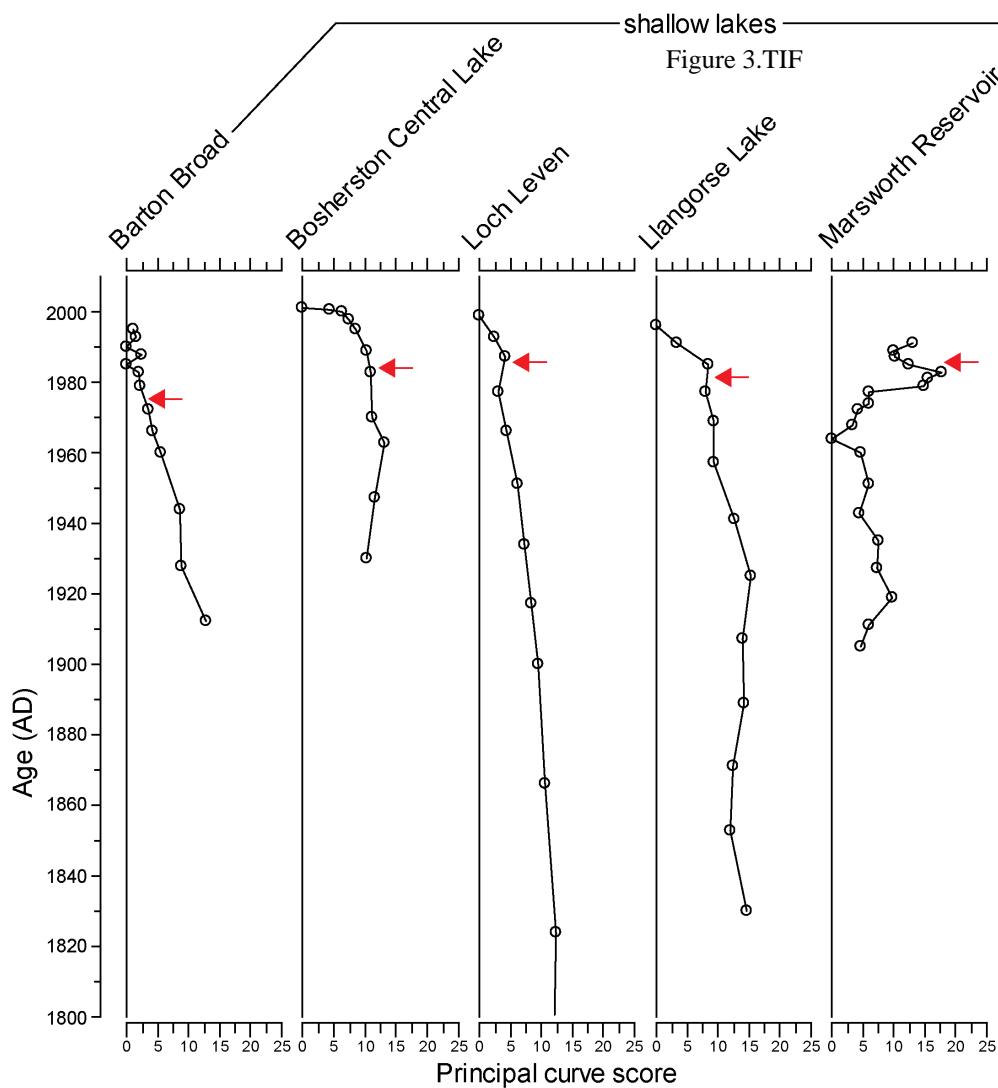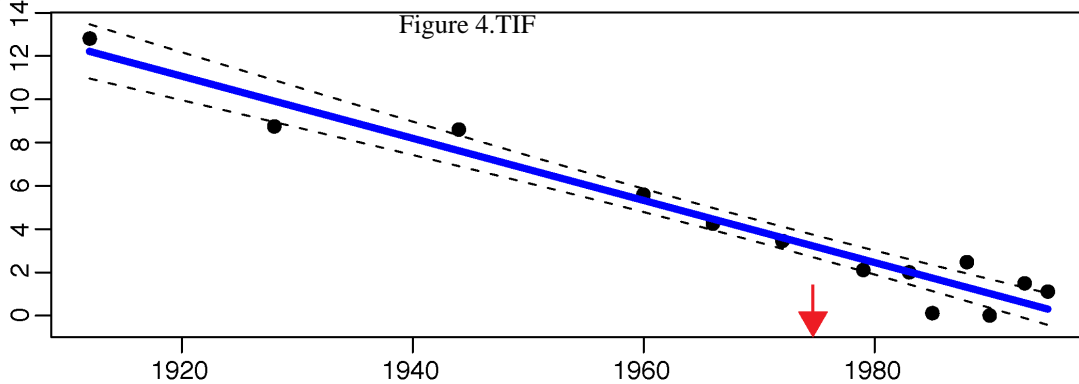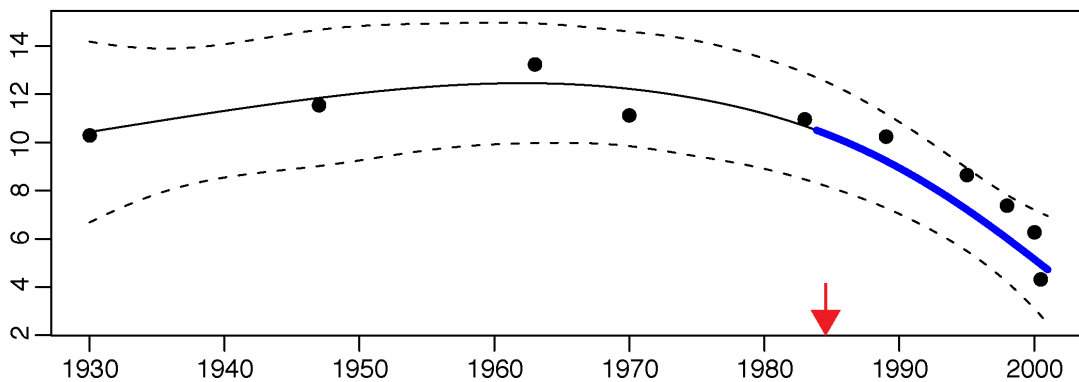
shallow lakes — Barton Broad, Bosherston Central Lake, Loch Leven, Llangorse Lake, Marsworth Reservoir
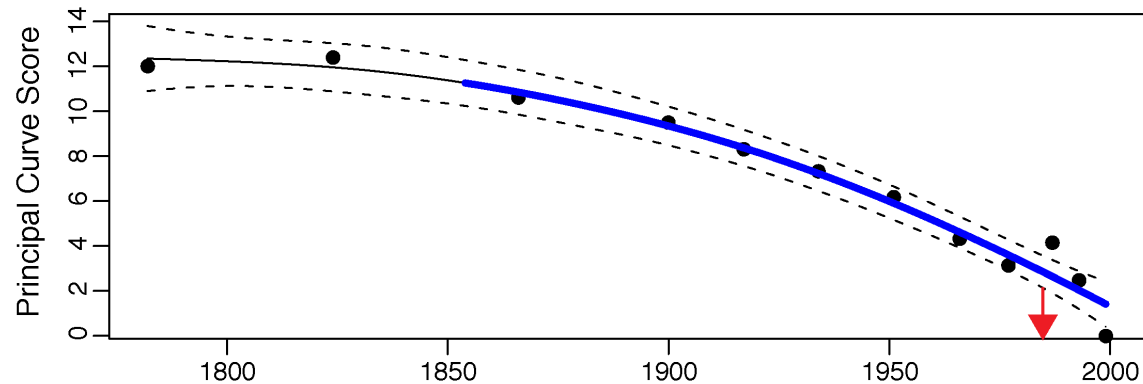
deep lakes — Lake Bled, Esthwaite Water, Gjersjøen, Kielpińskie, Lidzbarskie, Mill Loch, Mjøsa, Rumian

Dissimilarity scores (deviation from base sample)

Age (AD)

Figure 2.TIF

Figure 3.TIF

Figure 4.TIF
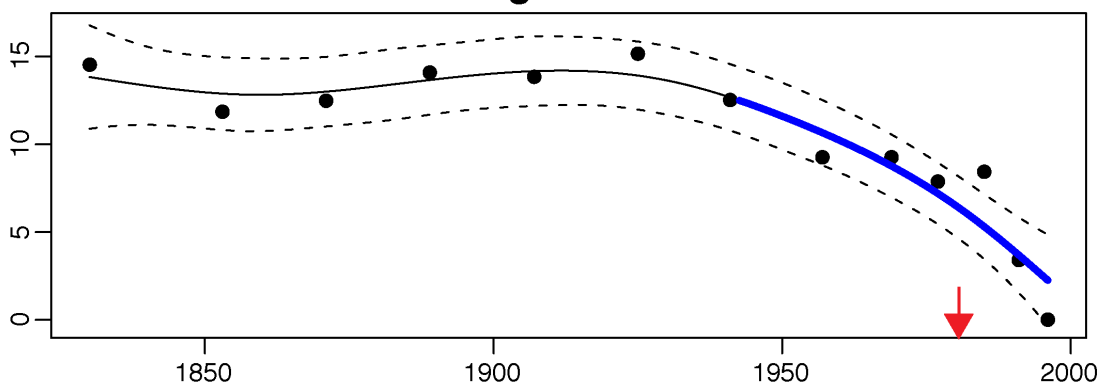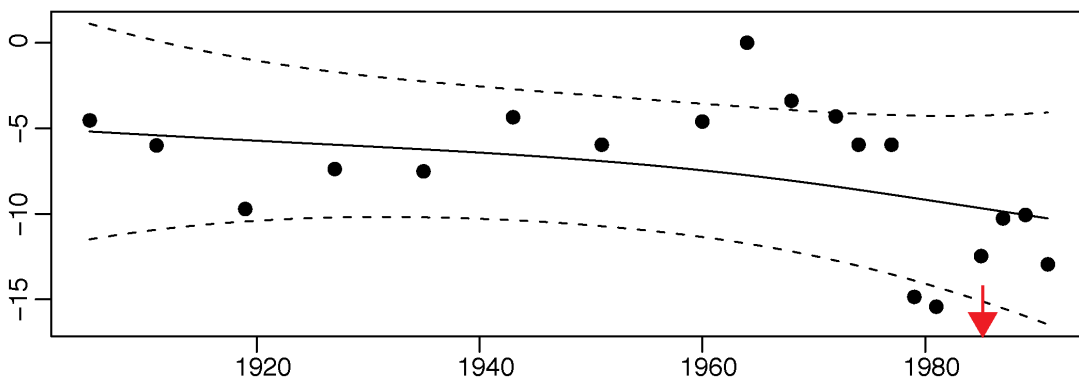
Figure 5.TIF
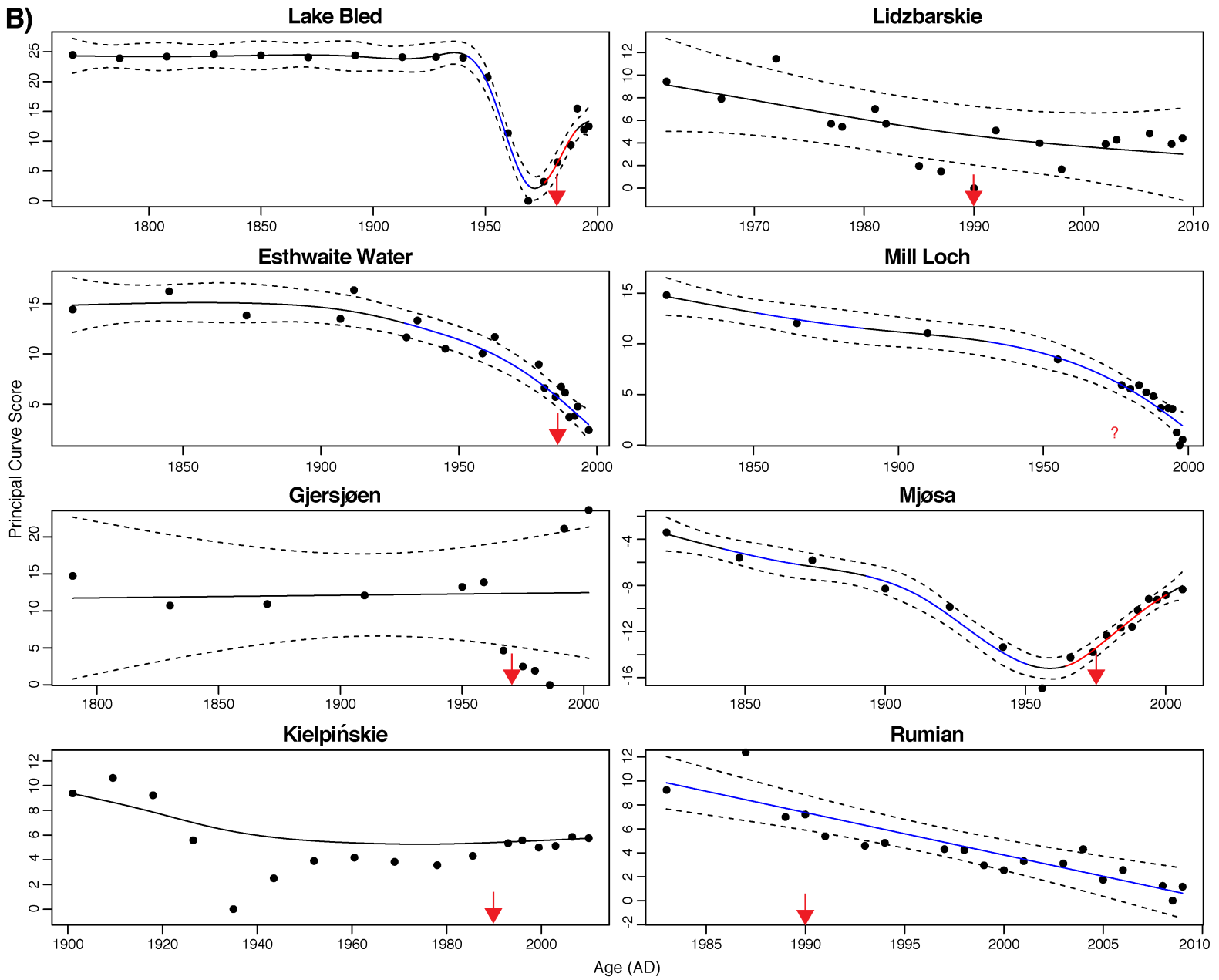
Figure 6.TIF

Figure 7.TIF

Figure 8.TIF

Figure 10.TIF

A)

Figure 11.TIF

Benthic
Fragilaria spp.

Cymbella spp.

Brachysira spp.

Stephanodiscus /
Cyclostephanos spp.

Achnanthes spp.

Tabellaria
flocculosa

Fragilaria crotonesis

Cyclotella spp.

Aulacoseira ambigua

Aulacoseira
subarctica

Asterionella
formosa

B)