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Harnessing the potential of the multi-indicator palaeoecological approach: an assessment of the nature and causes of ecological change in a eutrophic shallow lake

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SUMMARY

1. Multi-indicator palaeoecological studies have become increasingly popular over the last decade as the need for a more complete understanding of lake ecological histories has increased. However, the true potential of the full biological record for assessing the potential drivers of observed ecological shifts in lake sediment records has rarely been demonstrated.

2. Here, we examine the remains of a range of food-web components including algae (diatoms), macrophytes (plant macrofossils), zooplankton (chitinous and ephippial Cladocera remains), invertebrates (including chironomids, bryozoans, Mollusca) and fish (fish scales and fish leech egg cocoons) in multiple sediment cores from Groby Pool, an enriched English shallow lake, to assess whole-ecosystem response to eutrophication over the last two centuries. We focus on three striking changes in the palaeorecord, namely the post-1900 increase in *Daphnia* spp., the post-1840 decline in *Cristatella mucedo* and the post-1940 increase in *Cocconeis placentula*, and utilise the multi-indicator palaeoecological data to evaluate possible explanations for these patterns.

3. Principal curves analysis revealed marked and broadly simultaneous changes in the plant macrofossils, cladocerans, diatoms and chironomids (as well as in other animal remains such as bryozoans and Mollusca), indicating an early period of enrichment most likely associated with land-use change in the late 18th century, followed by a more recent eutrophication phase coincident with the discharge of sewage effluent to the lake from 1935.

4. Ecological change, resulting from eutrophication, was shown to have progressed slowly and steadily and to have occurred at all trophic levels with a shift from a relatively diverse 'mesotrophic' macrophyte assemblage, dominance by benthic diatoms and plant-associated Chydoridae and chironomids towards a relatively species-poor, 'eutrophic' macrophyte community with dominance by planktonic algae (e.g. Cyclostephanoid diatom taxa), planktonic Cladocera (*Bosmina*, *Daphnia*) and a chironomid fauna dominated by mud-associated taxa. The inferred shift in the macrophyte community from charophyte to fine-leaved pondweed and *Callitriche truncata* suggests a reduction in the seasonal duration of plant dominance.

5. The multi-indicator analysis indicates that a combination of increased phytoplankton biomass and low zooplanktivorous fish predation is likely to explain the recent increases in *Daphnia* spp., while loss of plant habitat and increased competition for food appear to be the most likely causes of the observed decline in *C. mucedo*, and resistance to increased grazing pressure from invertebrates is the most probable driver of the *C. placentula* increase.

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6. Our study illustrates the potential of using the full array of fossil groups preserved in lake sediment cores to infer ecosystem dynamics over centennial timescales and to contribute to our understanding of the mechanisms that may link biological assemblages to a range of forcing factors. Further, this paper provides methodological guidance by demonstrating the ability of amalgamated records from three cores to reveal a strong sequence of events and coherent patterns.

Keywords: eutrophication, food web, multi-indicator, palaeoecology, shallow lake

Introduction

In shallow lakes, eutrophication is widespread and has resulted in significant shifts in biological structure, paramount of which have been changes in the abundance and diversity of aquatic vegetation (Kennison, Dunsford & Schutten, 1998; Sand-Jensen *et al*., 2000; Körner, 2002). Submerged macrophytes play a key role in the structure and function of shallow lake ecosystems, affecting a range of biological and biogeochemical patterns and processes and providing habitat and refugia for a range of animal species (Carpenter & Lodge, 1986; Scheffer *et al*., 1993; Jeppesen *et al*., 1998). Experimental work, both spatial studies along nutrient gradients and relatively short-term (<10 years) temporal studies, has demonstrated that submerged macrophytes influence trophic interactions among fish, macroinvertebrates, zooplankton, phytoplankton and periphyton in both the pelagic and littoral zones of shallow lakes (Jeppesen *et al*., 1998; Bakker *et al*., 2010). Equally, fish can play a critical structuring role in shallow lake ecosystems with 'fish effects' cascading to lower trophic levels (e.g. Carpenter, Kitchell & Hodgson, 1985). However, short-term investigations are unable to provide information on the longer term effects of vegetation and fish dynamics on trophic interactions, and laboratory and enclosure studies do not operate at the whole-system scale. Thus, an understanding of the effects of changes in aquatic vegetation and fish populations, and their subsequent impact on food-web interactions, over decadal to centennial timescales is still lacking. Such information could make an important contribution to management by characterising periods of stability versus change, allowing predictions about longer term future effects to be made, and for setting realistic restoration targets (Bennion *et al*., 2011).

Palaeoecological records afford a means of tracking centennial scale responses to environmental change and can provide relatively high-resolution data on a decadal scale beyond that usually provided by monitoring programmes (Smol, 2008). The sediment record contains the remains of a range of biotic components which can be examined individually or in combination to assess changes in biological structure and determine whole-ecosystem responses to natural and anthropogenic drivers. These so-called multi-proxy or multi-indicator studies have become increasingly popular in palaeoecology over the last decade as the need for a more complete understanding of the ecological history of aquatic systems has grown (e.g. Birks & Birks, 2006). Different fossil groups reflect different aspects of the system; hence, several groups can be used in support of one another (i.e. the weight of evidence approach), thereby strengthening palaeoenvironmental interpretations (Michelutti & Smol, 2013).

The identifiable remains of a range of biological groups, representing all aspects of the food web, are preserved in sediment cores, including *inter alia:* diatoms (Battarbee *et al*., 2001), macrophytes (Odgaard & Rasmussen, 2001; Davidson *et al*., 2005; Sayer *et al*., 2010a; Spierenburg *et al*., 2010), cladocerans (Jeppesen *et al*., 2001; Guilizzoni *et al*., 2006), Mollusca (Walker *et al*., 1993; Ayres *et al*., 2008), chironomids (Brodersen *et al*., 2001; Langdon *et al*., 2010) and fish (Davidson *et al*., 2003; Sayer *et al*., 2006), among an array of other invertebrate groups which are less frequently employed. Numerous palaeoecological studies have examined one or more of these fossil groups to assess ecological response to eutrophication (e.g. Leavitt *et al*., 1994; Miskimmin, Leavitt & Schindler, 1995; Brooks, Bennion & Birks, 2001; Taylor *et al*., 2006; Sayer *et al*., 2010a; Guilizzoni *et al*., 2012; Hobbs *et al*., 2014). However, the potential of the fuller sediment record for assessing food-web alterations and interactions between the various components of shallow lake ecosystems, over long timescales, is yet to be fully explored. Indeed, multi-indicator palaeoecological studies are more typically based on a mix of geochemical and biological analyses with only one or two organism groups represented (Birks & Birks, 2006; Michelutti & Smol, 2013).

This study examines the remains of a range of food-web components in multiple, chronologically correlated sediment cores from Groby Pool, a shallow English lake that has undergone nutrient enrichment over the last two centuries. We analysed plant macrofossils along with a range of animal groups preserved in the palaeoecological

record, namely chitinous and ephippial Cladocera remains, bryozoans, Mollusca and fish. Palaeoecological records of pollen, diatoms and chironomids already exist for this site (Sayer *et al.*, 1999), affording the possibility to explore the relationships between these groups to assess whole-ecosystem response to eutrophication over the last 200–300 years. Our central aim was to illustrate the advantages of studying multiple indicators for gaining a better understanding of the complex network of interactions throughout the ecosystem and for helping unravel the potential causes of the observed patterns. We also offer recommendations on how to best handle such data by describing a method for combining multiple cores and integrating several biological groups.

Methods

Study site

Groby Pool is a small (0.12 km^2), shallow (1.1 m mean depth, 1.8 m maximum depth) lake with a largely rural, lowland catchment (lake altitude 95 m above sea level, catchment area 8.6 km^2) located in Leicestershire, England (Latitude: 52.6667N, Longitude: 1.2167W). The origin is uncertain, but the lake is thought to result either from damming of a stream in the 12th/13th century or flooding of an abandoned clay pit. The lake is currently alkaline (mean pH 8.4, mean alkalinity 192 mg L^{-1}) and eutrophic (mean TP 683 μg TP L^{-1}, range 179–1470 μg TP L^{-1}) but remains in a clear water, vegetated state with relatively low chlorophyll-*a* concentrations (mean 10 μg TP L^{-1}) (Environment Agency 2010 data, unpublished). Recent aquatic plant surveys report *Potamogeton pectinatus* and *Elodea nuttallii* as abundant and *Ceratophyllum demersum* and *Callitriche truncata* as frequent (Environment Agency 2013 data, unpublished). Previous palaeoecological studies of the lake, combining botanical data and pollen records, have demonstrated a dynamic sequence of vegetation change over the last 250 years in response to eutrophication (Sayer *et al.*, 1999; Davidson *et al.*, 2005). Land enclosure took place in 1789 resulting in the ploughing up of large tracts of pasture for arable farming, and by 1925 *c.* 30% had been converted to arable (David & Roberts, 1990; David, 1991). A sewage works was installed in 1935, from which time treated effluent was discharged to the Slate Brook inflow. The geology, chemistry, ecology, history and palaeolimnology of the lake are further documented in David & Roberts (1990), David, Dearing & Roberts (1998), Sayer *et al.* (1999) and Davidson *et al.* (2005).

Sediment coring, dating and core correlation

For macrofossil analyses, two wide diameter (7.4 cm) piston cores, GROB2, 73 cm in length and GROB4, 92 cm in length, were taken from the littoral zone in July 2000 in a water depth of 90 and 70 cm, respectively, along with an open water core, GROB5, 85 cm in length, in a water depth of 129 cm. The latter core was analysed for both macrofossils and Cladocera. The cores were extruded in the field at 1-cm intervals and any changes in lithology noted. Diatom and chironomid analyses were undertaken on a mini-Mackereth core (GR95B) (Mackereth, 1969), 103 cm in length, taken from the centre of the lake in June 1995 (Sayer *et al.*, 1999). Pollen data referred to briefly in this paper are from the upper section of a 4-m Livingstone piston core (C31) (Livingstone, 1955), taken from the centre of the lake in 1985 (David *et al.*, 1998).

Core GROB4 was dated radiometrically (^{210}Pb, ^{226}Ra, ^{137}Cs, ^{241}Am) by direct gamma assay in the University of Liverpool Environmental Radioactivity Laboratory, using standard procedures (Appleby *et al.*, 1986; Appleby, Richardson & Nolan, 1992). Subsamples from GROB2, GROB4 and GROB5 were analysed for spheroidal carbonaceous particles (SCPs) using the method described in Rose (1994). These data were used to provide supplementary dates to those available from the radiometric analyses for GROB4 and to allow correlation of GROB2 and GROB5 with GROB4. Dates were allocated using an SCP dating model for southern and central England (Rose & Appleby, 2005) whereby the cumulative percentage SCP profiles (with 100% set to the SCP concentration peak) provide eleven calibrated dates from the start of the SCP record (0%; 1850 ± 25 years) to the SCP concentration peak (100%; 1970 ± 5 years). This model is based on independently dated SCP profiles from 15 sediment cores from across the region including a previous Groby Pool core. The chronologies of core GR95B and C31 were derived from correlation with a radiometrically dated central lake core, as detailed in Sayer (1997) and David *et al.* (1998), respectively. In the former, cross-correlation was primarily by means of matching loss-on-ignition profiles and in the latter was based on strong similarities in pollen concentration and percentage data.

Analysis of fossil remains

A total of 21, 26 and 13 subsamples of between 20 and 30 cm^3 from cores GROB2, GROB4 and GROB5, respectively, were analysed for macrofossils, the exact volume

determined using water displacement (Birks, 2001). Samples were washed through a 350-μm sieve, and the entire retent was examined under a stereo-microscope at ×10–40 magnification and identifiable remains enumerated. A subsample, approximately a quarter of the total sample, was subsequently washed through a 150-μm sieve and analysed at a higher magnification for smaller remains. Plant macrofossils consisting of seeds, fruiting bodies, oospores, turions, leaves, spines and trichoscleroids (star-shaped leaf hairs of Nymphaeaceae) were identified with reference to herbarium material held at the Environmental Change Research Centre, University College London. Various animal macrofossil remains were separated and enumerated at the same time as the plant macrofossils including zooplankton ephippia, Mollusca, bryozoan statoblasts, testate amoebae, fish leech egg cocoons and fish scales (see examples in Fig. 1). All macrofossil data are expressed as numbers per 100 cm^3 of fresh sediment.

Several studies have demonstrated that, while it cannot provide a complete inventory of historically recorded species, plant macrofossil analysis can provide a reliable indication of temporal change in the dominant components of the aquatic vegetation of shallow lakes (Davidson *et al.*, 2005; Salgado *et al.*, 2010; Clarke *et al.*, 2014; Leví *et al.*, 2014). Nonetheless, there is large spatial variation in macrofossil remains within a lake (Davidson *et al.*, 2005), and to account for this, a novel approach was employed whereby the macrofossil data from all three cores were combined. Firstly, data from samples (between 1 and 5) were aggregated into 20-year time intervals (e.g. 1700–20, 1720–40, etc.) for each core, and the mean abundance for each taxon in that time period was calculated. Secondly, the resulting data from each core were combined to give an overall mean for each taxon in each 20-year time period.

Analysis of the chitinous remains of Cladocera was carried out on 10 samples from core GROB5 as outlined in Davidson *et al.* (2007). This is an adaptation of more standard methods (Jeppesen *et al.*, 2001; Korhola & Rautio, 2001). The sample was heated in a deflocculating agent (KOH) and sieved with 150- and 50-μm meshes. The remains retained by the two sieves were then washed into separate pots and stained with safranin. Subsamples were analysed using a compound microscope at ×40–400 magnification and the chitinous remains of the Cladocera were identified with reference to Flössner (1972), Frey (1958) and Alonso (1996). Carapaces, head shields and post-abdomens were recorded separately, and the minimum possible number of individuals was calculated. Cladoceran ephippia were enumerated as part of the macrofossil analysis from GROB2, GROB4 and GROB5. The combination of chitinous and ephippial remains provides a more complete picture of the Cladocera community than either in isolation, the former better reflecting the benthic community and the

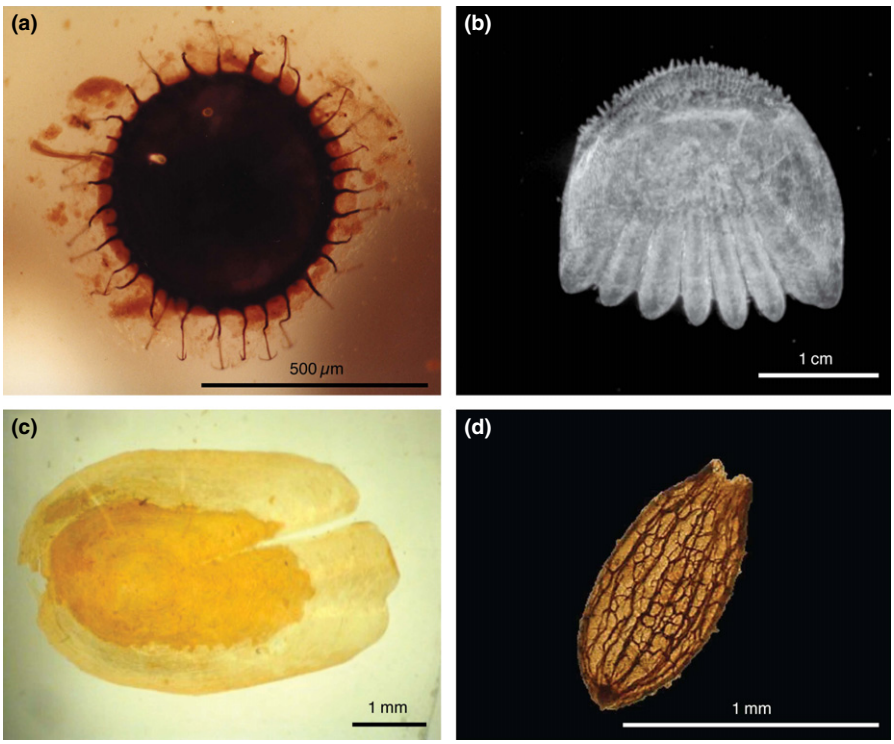

Fig. 1 Examples of animal remains found in samples from Groby Pool: (a) *Cristatella mucedo* statoblast, (b) Percid scale, (c) Pike (*Esox lucius*) scale, (d) *Piscicola geometra* egg cocoon (Photos a, b, c by Tom Davidson and d by Ruth Rawcliffe).

latter the pelagic community. As chitinous and ephippial remains are differentially produced and their total abundance is not comparable, for GROB5, they were converted to relative abundance and weighted relative abundance, respectively. In brief, ephippial relative abundance was weighted by that sample's total ephippial abundance (see Davidson *et al.*, 2007 for details).

Diatom analysis was carried out on 35 samples from core GR95B using standard procedures (Battarbee *et al.*, 2001) and chironomid (head capsule) analysis of 16 samples from the same core followed the methods of Walker (1987). Here, summary diatom and chironomid data are expressed as percentage relative abundance, and the full data sets were reported in Sayer *et al.* (1999).

Numerical analyses

To identify the major zones in the palaeoecological records and facilitate description of the main compositional changes, constrained clustering analysis CONISS (Grimm, 1987) was carried out on the fossil assemblage data of each biological group using Tilia v. 1.7.16 (Grimm, 2011). Stratigraphic diagrams were produced in C2 (Juggins, 2003). As a summary of palaeoecological data, the first axis scores of a principal components analysis (PCA) or a correspondence analysis (CA) 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 and composition of organisms (Simpson & Birks, 2012). Principal curves (PrC; Hastie & Stuetzle, 1989; De'ath, 1999; Simpson & Birks, 2012; G. L. Simpson, in prep.) are a non- or semi-parametric alternative to PCA and CA that are amenable to the identification of data sets with a single or dominant gradient. Here, we use PrCs to summarise and compare timing of the major compositional changes in the different biological groups: plant macrofossils in the combination of GROB2, GROB4 and GROB5; Cladocera ephippial and chitinous remains in GROB5; Cladocera ephippial remains in the combination of GROB2, GROB4 and GROB5; and existing diatom and chironomid records from core GR95B. Nymphaeaceae trichosclereids, which include both *Nuphar* and *Nymphaea*, were removed from the plant macrofossil data set prior to analysis owing to the exceptionally high numbers of remains and hence their undue influence. PrC analysis was not applied to the other animal macrofossil data (bryozoans, Mollusca, fish scales) owing to scarcity of macrofossils in a few samples and hence irregularity in the abundance data. In the case of Cladocera ephippia, the data exhibited two gradients of similar magnitudes and thus are not well modelled via PrCs. In this instance, we used the first two principal components (PCs) to summarise changes in ephippial remains. We expressed the variation explained by the PrCs or PCs, and thus summaries of change over time, as distances along each PrC or PC after normalising the scores to the unit interval (to remove the variation in magnitude of the scores arising from the differing units of measure inherent to each species group). We then scaled the normalised scores relative to the proportion of variance explained by each PrC or PC. This has the effect of giving greater visual emphasis to changes in PrC or PC scores that represent greater amounts of variation explained.

To explore community-level change across groups, we employed a novel approach using a principal coordinates analysis (PCoA) of a fused dissimilarity matrix. Samples were aggregated into 20-year time intervals, yielding ten samples spanning 1740–2000 for which data from all fossil groups were available. The absence of chironomid data precluded the inclusion of samples before 1740 and from the time intervals 1760–80 and 1800–40. The macrofossil data set included all aquatic plant taxa except Nymphaeaceae trichosclereids as above, animal taxa (bryozoans, insects, Mollusca, testate amoebae) and Cladocera ephippia from the combination of GROB2, GROB4 and GROB5. Chitinous remains of Cladocera were not included in PCoA owing to the low number of samples once data were aggregated into 20-year time slices. This was chiefly caused by poor preservation in the pre-1780 period which led to a low number (<100) of individuals in the samples, with a relatively large proportion being unidentifiable. Such low numbers have been shown to poorly reflect the subfossil cladoceran assemblages (Kurek *et al.*, 2010). The poor preservation is most likely due to the change in sediment structure at *c.* 1780 AD and the fact that the sediments had been dried prior to sample preparation. The process of drying the clay-rich sediments appears to have distorted and damaged the chitin of the cladoceran body parts. Diatom and chironomid percentage data from GR95B for all taxa with >2% occurrence were included.

It is difficult to compare different taxonomic groups in a single ordination because of the range in units of measure used and variation in the number of taxa between groups. PCA of a correlation matrix of all the data combined would solve the units-of-measure problem (by giving each taxon equal weighting in the analysis), but not the richness issue. Instead, we use the concept of fused dissimilarities that has been employed with supervised self-organising maps to allow the analysis of

disparate data sets on a common footing (Melssen, Wehrens & Buydens, 2006). A fused dissimilarity matrix is created by first computing a separate dissimilarity matrix for each taxonomic group; here, we used Hellinger distances. These dissimilarities are then normalised to the unit interval so that the maximal pairwise dissimilarity for each group takes the value 1. Finally, a weighted sum of the dissimilarity matrices over the taxonomic groups is computed. Here, we used equal weights, thus giving to each group equal weighting to their contribution to total between-sample dissimilarity [see Simpson (2012) for a palaeolimnological account of fused dissimilarities]. Having obtained a single between-sample dissimilarity matrix, we proceeded by fitting a PCoA to this matrix. PCoA is similar to PCA in extracting important, orthogonal directions of variation from a multivariate data set, but is not restricted to using Euclidean distances. Alternatively, PCoA can be thought of as embedding the fused dissimilarity matrix in a Euclidean space which we visualise via the extracted principal coordinates. PCoA therefore provides a visualisation of the main patterns in the core samples over time, based upon contribution from all taxonomic groups in a principled manner.

One problem with applying PCoA directly to a dissimilarity matrix, as here, is that we lose information about the taxa and thus have little basis for placing so-called species scores into a PCoA biplot. Instead, for each species, we fitted a vector in PCoA axes 1 and 2 space, which points in the direction of maximal correlation with species 'abundance' using a standard linear regression of the PCoA axes one and two scores of the species abundance

$$E(z_j) = \beta_0 + \beta_1 x_1 + \beta_2 x_2,$$

where $E(z_j)$ is the expectation of the transformed abundance of the jth species z, β_0 is the constant term, x_1 and x_2 are the scores, and β_1 and β_2 are the estimates of the coordinates of the end point of the vector, drawn from (0, 0), on the first and second PCoA axes, respectively. The angle θ between the vector and the first PCoA axis is given by $\theta = \arctan(\beta_2/\beta_1)$ and the maximal correlation is given by r, the multiple correlation coefficient of the regression (the square root of the R^2 for the model). The statistical significance of the observed correlation r for each species was assessed via permutation tests, although we used this only as a rough guide to select species for plotting on the ordination figure to reduce clutter rather than for formal hypothesis testing, and no correction for multiple comparisons was therefore made.

Principal curves and fused dissimilarities were computed using the *analogue* package (version 0.16-0; Simpson, 2007; Simpson & Oksanen, 2014). The *vegan* package (version 2.2-0; Oksanen *et al.*, 2014) was used for PCA, PCoA and vector fitting. These analyses were performed in R (version 3.1.1; R Core Team, 2014). The R code used for these analyses is available from https://github.com/gavinsimpson/groby-pool.

Results

Core chronologies

All cores (GROB2, GROB4, GROB5, GR95B and C31) exhibit a characteristic boundary between an upper organic gyttja layer and a lower inorganic silt/clay section at *c.* 60 cm. This change in sediment type has been previously assigned to the period of the Parliamentary Enclosure Act of 1789 when arable agricultural activity moved from outside the Groby Pool catchment area to within (David *et al.*, 1998). After the Act, the focus of cultivation shifted to fields within the Groby Pool catchment, while the previously cultivated land outside was converted to pasture (David & Roberts, 1990). Thus, a date of *c.* 1790 was assigned to this level in each core.

GROB4 had a poor ^{210}Pb record with low concentrations, even in the upper sediments, and an inventory <25% of the estimated atmospheric flux. Therefore, it was not possible to produce a chronology based on the ^{210}Pb data. However, the ^{137}Cs record was good with a well-defined peak at 20.5 cm probably corresponding with 1963 fallout maximum from the testing of nuclear weapons. Such a well-resolved ^{137}Cs peak adds confidence in the recent sediment record and suggests negligible post-depositional movement. The mean post-1963 sedimentation rate for GROB4 is therefore calculated as 0.14 g cm^{-2} year^{-1} (0.55 cm year^{-1}).

The SCP depth-date profiles for the three cores are shown in Fig. 2 together with the depths allocated to 1963 from the ^{137}Cs peak and the 1790 clay–gyttja boundary. The SCP-derived chronologies for GROB2, GROB4 and GROB5 were in good agreement, with all three cores displaying a reasonably steady sediment accumulation rate from 1850 to *c.* 1960, followed by a slight acceleration in post-1960 decades typical of lakes of this type (Rose *et al.*, 2011). The SCP chronologies are in very good agreement with the ^{137}Cs 1963 peak. Extrapolation of the SCP-derived mean accumulation rate for 1850–1960 to lower sediment depths shows a good agreement with the *c.* 1790 clay layer supporting the suggestion that this accumulation rate was reasonably consistent over this

c. 170-year period (Fig. 2). While extrapolated dates should be treated with great caution, this accumulation rate is also used to provide chronological estimates for sediment depths below 60 cm (1790). Errors on SCP dates are typically ±5 years for recent decades, ±10 years for the mid-20th century and ±25 years for the mid-19th century (Rose & Appleby, 2005). Uncertainties on pre-1850 and extrapolated dates are greater still. The good correlation between SCP chronologies for the three cores and also between the loss-on-ignition profiles for sediment cores across the lake basin (David *et al.*, 1998) allows confidence in cross-correlation of the derived chronologies using these determinants and indicates that dating errors on the combined core data sets are probably similar to those of the individual cores themselves.

Plant macrofossils

The plant macrofossil record included 17 submerged and two floating species, and three major zones were identified (Fig. 3). Characeae (including *Chara*, *Nitella*, particularly *Nitella opaca* and *Tolypella* spp.) were characteristic of the base of the sequence corresponding to the period prior to the early 1800s (Zone 1). The lower zone also contained macrofossils of *Gloeotrichia* spp. (cyanobacteria), *Eleocharis acicularis*, *Ranunculus* sect. *Batrachium*, *Myriophyllum spicatum*, *Myriophyllum alterniflorum*, *Potamogeton* spp., *Utricularia vulgaris* agg, *Zannichellia palustris* and trichosclereids of Nymphaeaceae (*Nuphar* and *Nymphaea*) (Fig. 3). The pollen record of core C31 provided additional information, indicating that *Littorella uniflora* was present in the early 1700s. Total species richness in Zone 1 was high with 13 taxa recorded.

There was a post-*c.* 1800–20 shift in the macrofossil record with the disappearance of *M. spicatum*, *Gloeotrichia* spp., *Nitella* spp. and *Tolypella* spp., a decline of Characeae and Nymphaeaceae and the continued representation of *R.* sect. *Batrachium* and *U. vulgaris* agg. (Fig. 3). Species richness declined to eight or nine taxa in Zone 2. In the mid-1900s (Zone 3), the plant remains displayed a further change, with the loss of many species (Characeae, *U. vulgaris* agg.), an increase in the representation of remains of fine-leaved *Potamogeton* type (most likely *P. pusillus* or *P. berchtoldii*) and *C. truncata* seeds, and the (re)appearance of *Z. palustris* (Fig. 3). Consequently, species richness declined further to only four (possibly five) species. The palaeoecological data agreed well with the historical botanical record of the site which revealed a clear succession in the aquatic plant community over the last 200–300 years (Davidson *et al.*, 2005).

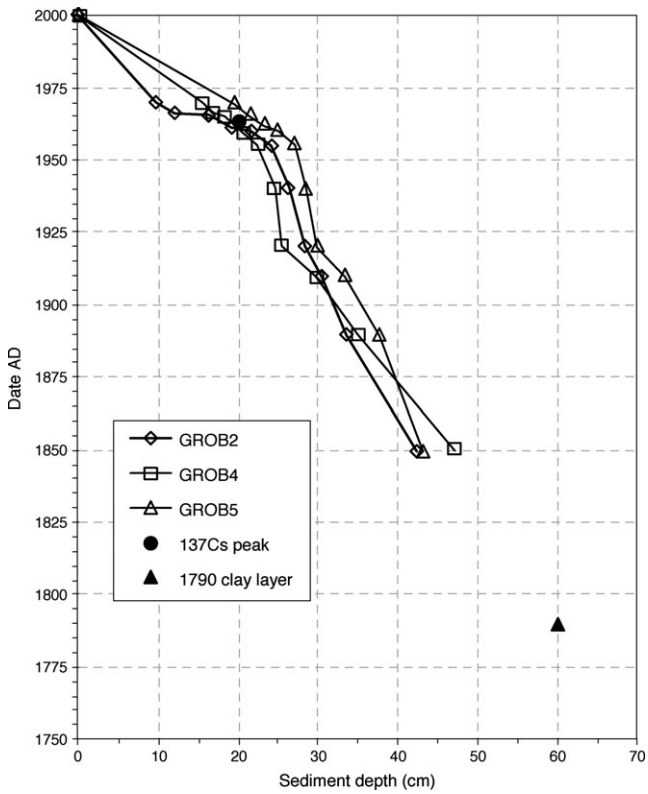

Fig. 2 The spheroidal carbonaceous particle (SCP) depth–date profiles for cores GROB2, GROB4 and GROB5. The ^{137}Cs peak in GROB4 (filled circle) and the clay layer (filled triangle) are indicated.

Animal macrofossils and ephippia

Three zones were identified for the cladoceran subfossils in GROB5 (including both chitinous and ephippial remains) with two main periods of change (Fig. 4a). Zone 1a comprised a diverse, mixed assemblage of benthic (e.g. *Alona costata*, *Graptoleberis testudinaria*), semi-planktonic (e.g. *Chydorus sphaericus*) and pelagic (e.g. *Bosmina longirostris*) taxa. A change occurred post-1850 (Zone 1b) with a decline in benthic taxa, most clearly with a fall in the number of Chydoridae ephippia, and the start of a slow rise in more pelagic taxa, such as *B. longirostris*, *Ceriodaphnia* spp. ephippia and *Daphnia hyalina* agg. ephippia (Fig. 4a). The second period of major change occurred from the mid-1900s (Zone 2) and was characterised by a marked increase in the abundance of ephippia of all the pelagic *Daphnia* aggregates (*D. hyalina* agg., *Daphnia magna* agg. and *Daphnia pulex* agg.). Furthermore, the benthic taxa *Eurycercus lamellatus* and *Pleuroxus aduncus* all increased in abundance at this

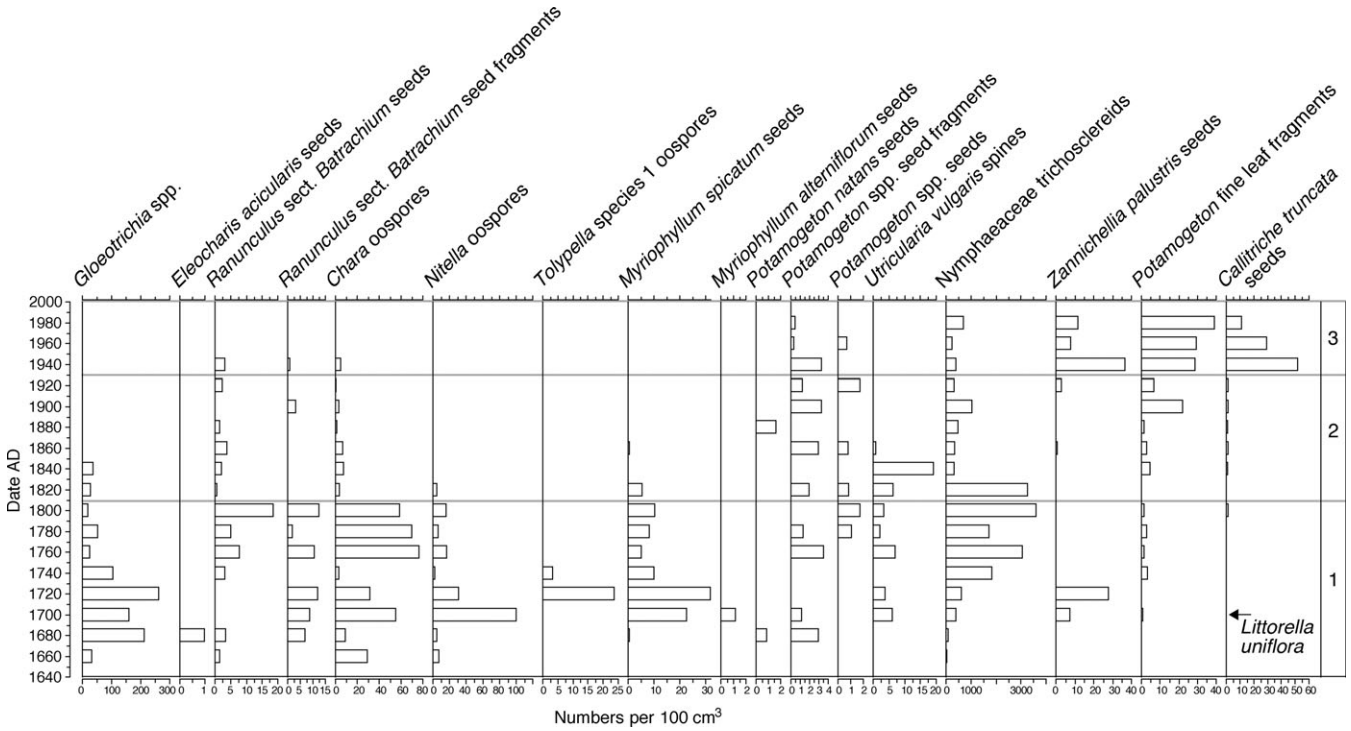

Fig. 3 Summary aquatic plant macrofossil stratigraphy for cores GROB2, GROB4 and GROB5 combined. Note the different scaling of the *x*-axes.

time, as did the benthic, but also at times, semi-planktonic *C. sphaericus* (Fig. 4a).

The Cladocera ephippia data from the aggregate of GROB2, GROB4 and GROB5 provide a greater number of samples, particularly for the lower core section, than GROB5 alone enabling shifts in the early part of the record to be more readily discerned (Fig. 4b). Three zones are evident: Zone 1 (pre-1810) dominated by chydorid spp. with *Ceriodaphnia* spp., *Leydigia* spp. and *D. hyalina* agg. also abundant; Zone 2 (1810–1930) with a notable decline in *Leydigia* spp. and a marked increase in *Bosmina* spp.; and Zone 3 (post-1930) with a decline in chydorid spp., *Ceriodaphnia* spp. and an increase in all of the *Daphnia* aggregate groups, namely *D. hyalina*, *D. magna* and *D. pulex* (Fig. 4b). The overall shift from a predominantly benthic to a planktonic dominated fauna, seen in the chitinous remains, is therefore also seen in the ephippia data.

The lowermost part of the animal macrofossil record (Zone 1) was characterised by high abundance of the testate amoeba *Centropyxis* spp. along with *Orthotricia* spp. (caddisfly), Oribatida (mites) and Prosobranch opercula (snails) (Fig. 5). Statoblasts of the bryozoans *Cristatella mucedo* and *Plumatella* spp. were both present. There was a shift at *c.* 1810 with a decline in *Orthotricia*, Oribatida and *C. mucedo* (Zone 2), followed by a further change at *c.* 1890 characterised by an increase in remains of Mollusca, namely *Pisidium* spp. and Planorbidae, and a marked decline in *C. mucedo* (Zone 3) (Fig. 5). Fish scales and fragments of *Perca fluviatilis* (perch) were present throughout the record but were most abundant in the mid- to late 1800s, and during the period *c.* 1800–1910, remains of Cyprinidae and *Esox lucius* (pike) were also found (Figs 1 & 5). Egg cocoons of the fish leech, *Piscicola geometra*, were present from *c.* 1830 to 1960 (Figs 1 & 5).

Chironomids

Three zones were identified in the chironomid record (Fig. 6b). Prior to the mid-1800s, the chironomid assemblages comprised a wide variety of species associated with aquatic plants typically found in meso- to eutrophic waters (e.g. *Corynoneura scutellata*, *Cricotopus* spp.) and a small percentage of mud-dwelling, benthic forms (Zone 1) (Fig. 6b). From the mid-1800s, the plant-associated taxa began to decline and the benthic taxa (e.g. *Procladius holotanypus* sp., *Chironomus plumosus* grp., *Polypedium nubeculosum* grp.) increased in importance (Zone 2). By *c.* 1930, the diversity of the assemblage had been reduced with the mud-dwelling, benthic form *P. holotanypus* codominant with the littoral *Tanytarsini*. Post-1930 (Zone 3), the benthic, mud-dwelling taxa were more abundant relative to the plant-associated taxa and

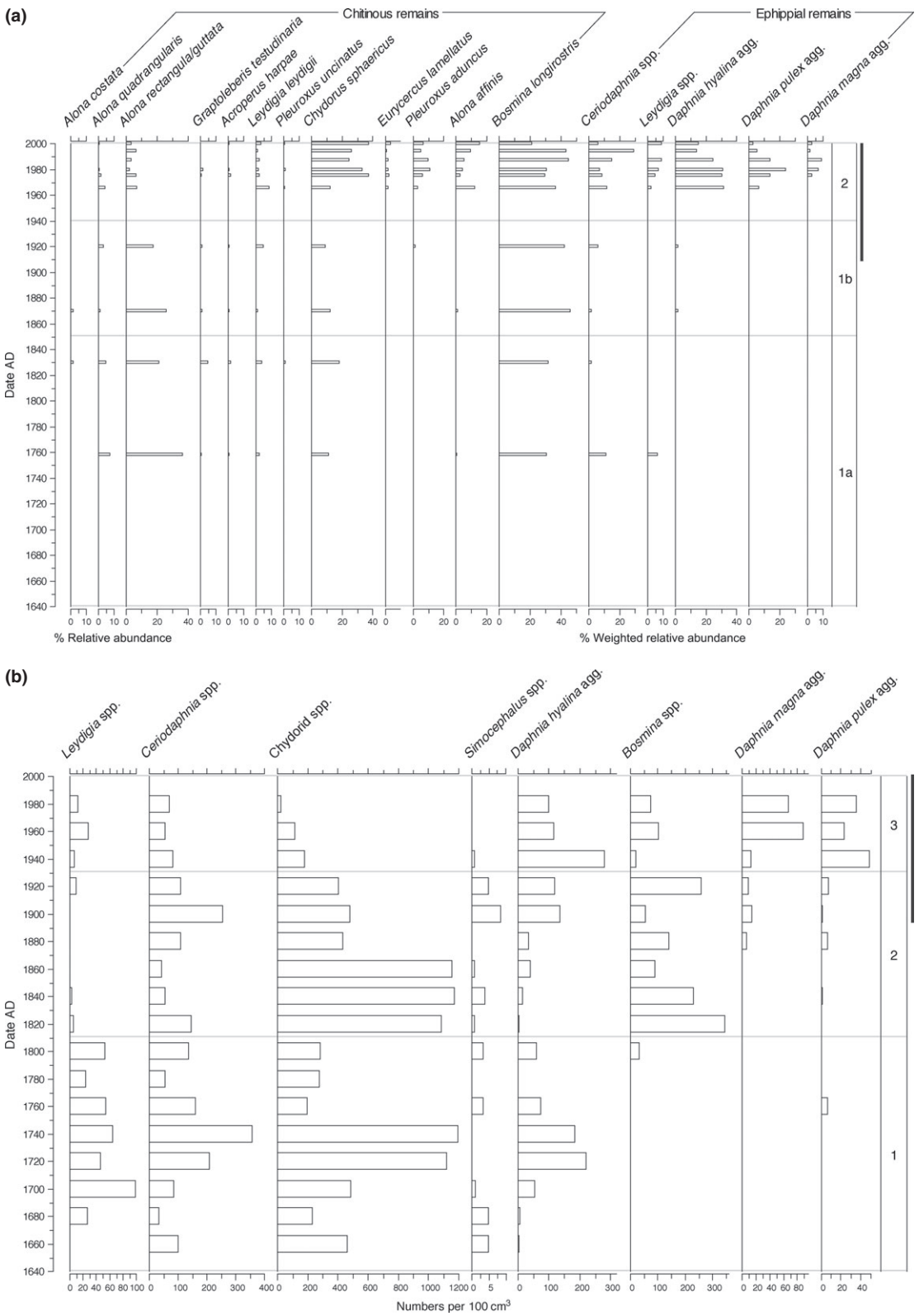

Fig. 4 (a) Summary zooplankton stratigraphy for core GROB5 including chitinous and selected ephippial remains, (b) Cladocera ephippia stratigraphy for aggregated data from cores GROB2, GROB4 and GROB5. Note the different scaling of the *x*-axes. The black bar indicates the increase in *Daphnia* spp. (see text).

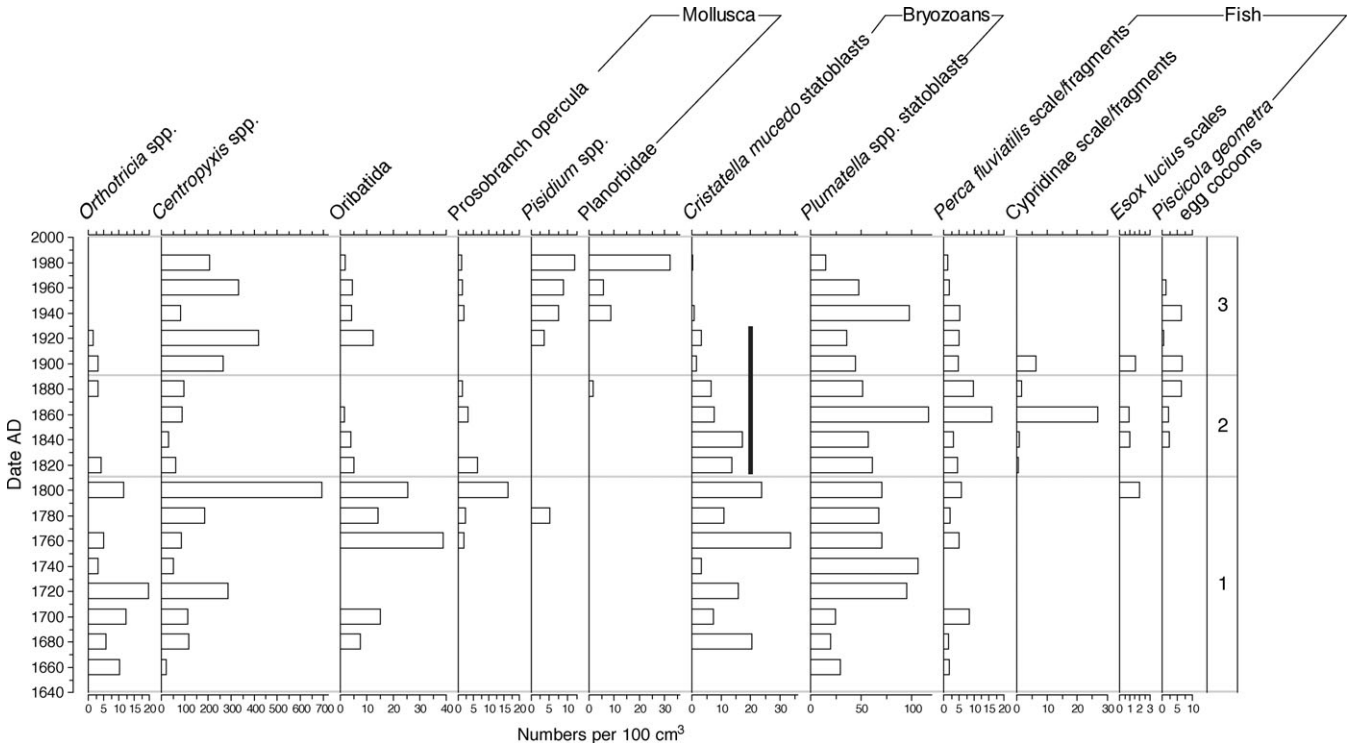

Fig. 5 Summary macrofossil stratigraphy for invertebrates and fish remains (aggregated data from cores GROB2, GROB4 and GROB5). Note the different scaling of the *x*-axes. The black bar indicates the decline in *Cristatella mucedo* statoblasts (see text).

the relative abundance of eutrophic taxa increased markedly (Fig. 6b).

Diatoms

Three zones were identified in the diatom record (Fig. 6a). The pre-1880 diatom flora (Zone 1) was dominated by small benthic species of *Staurosira*, *Staurosirella* and *Pseudostaurosira* (formerly *Fragilaria* spp. and hereafter termed *Fragilaria* spp.) (Fig. 6a). The period *c.* 1880–1940 (Zone 2) was characterised by a decline in *Fragilaria* spp. and a sharp increase in *Cyclostephanos dubius*, a small centric planktonic diatom which first began to expand earlier in the record at *c.* 1820. *Stephanodiscus parvus*, another planktonic form, also started to increase from *c.* 1880 (Fig. 6a). The period 1940–95 (Zone 3) saw the continued expansion of *S. parvus*, replacing *C. dubius* as the dominant planktonic form. The epiphyte *Cocconeis placentula* increased from 1940, while the relative abundance of *Fragilaria* spp. declined still further (Fig. 6a).

Whole-ecosystem shifts

The variance explained by the PrC compared with principal component axis 1 (PC1) shows that for macrophytes, diatoms and chironomids, the former improves on the latter by combining a substantial amount of the variance on principal component axis 2 (PC2) into a single combined measure of compositional change in time (Table 1). However, the sparsity of data for chitinous remains of Cladocera in GROB5 makes it difficult to model the arch, and hence, the PrC provides a poor reflection of community change. For the Cladocera ephippia data (GROB2, GROB4 and GROB5 combined), PrC fails to improve on PCA as the data appear to be genuinely two-dimensional rather than one-dimensional bent into an arch. Hence, both PC1 and PC2 are shown (Fig. 7). The stratigraphic plots for plants, Cladocera ephippia (PC2) and chironomids, exhibit a marked, unidirectional change in the record in the early 1800s, and for diatoms, a major shift a few decades later in the late 1800s, suggesting a common response to 19th century eutrophication at all levels of the food web (Fig. 7). The plots for all four organism groups (here Cladocera ephippia PC1) show a gradual and progressive shift since 1900 reflecting continual turnover in the assemblages as eutrophication has advanced at the site during the 20th century (Fig. 7).

The PCoA biplot shows community-level change across all groups for the three main periods in the lake

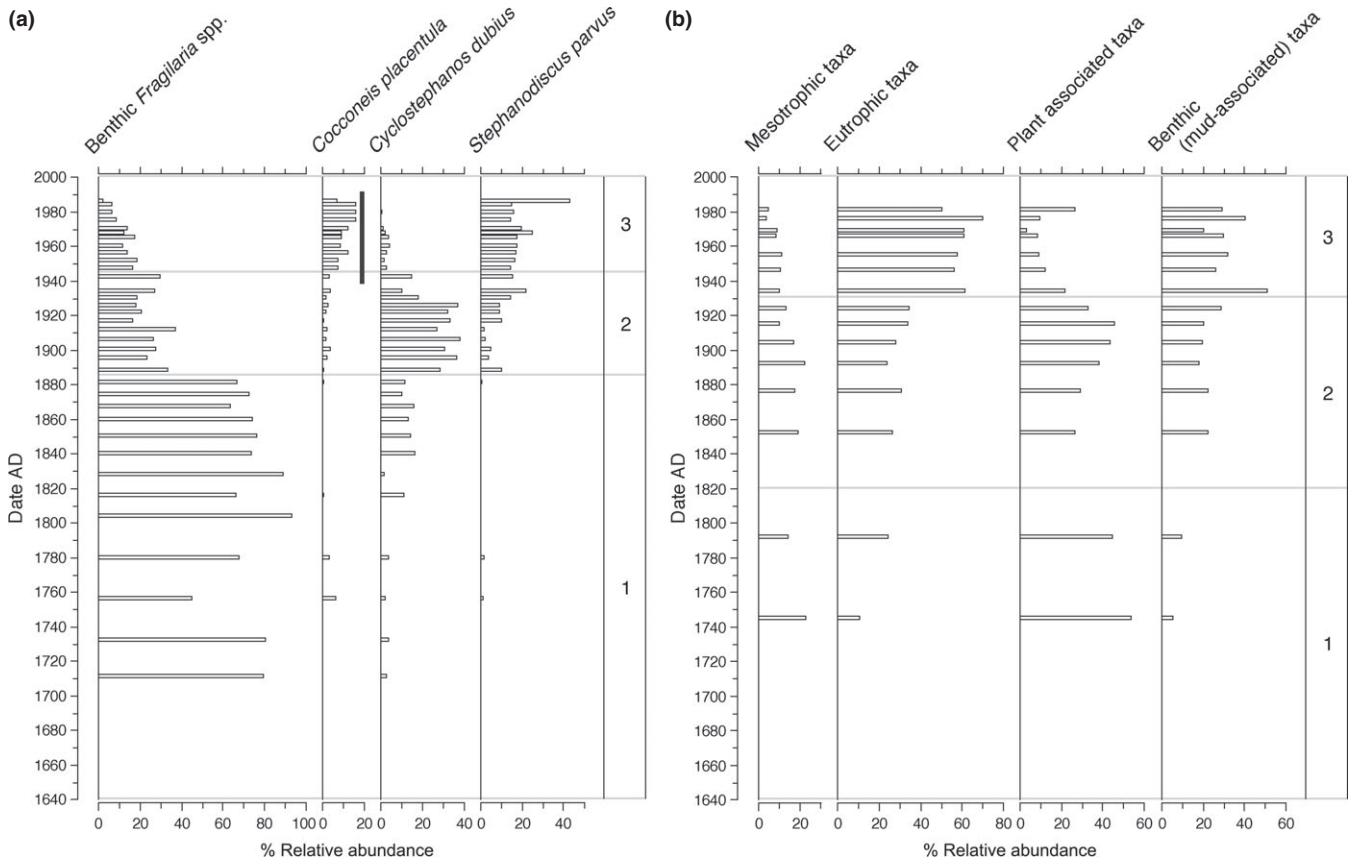

Fig. 6 Summary (a) diatom and (b) chironomid stratigraphy for core GR95B. The black bar indicates the increase in *Cocconeis placentula* (see text).

history (Fig. 8). The samples from the earliest period (pre-1800) are located in the upper right quadrant and the taxa most strongly correlated with these are the Charophytes (NITEL, TOLY1), *M. spicatum* (MSPIC), the benthic Cladocera *Leydigia* (LEYD), the bryozoans *C. mucedo* (CRIST) and *Plumatella* spp. (PLUM), the benthic diatoms *Fragilaria* spp. (FRAGB), *Navicula* spp. (e.g. NAVSUB) and *Amphora veneta* (AMVEN), and mesotrophic chironomids (CHM) including *Psectrocladius sordidellus* (PSEC2) (Fig. 8). The samples spanning the middle period in the lake's history from *c.* 1850 to 1940 are positioned towards the bottom of the plot. Taxa most strongly correlated with these samples include the planktonic diatom *C. dubius* (CSDUB), both benthic (chydorid spp.: CHYD) and pelagic (*Bosmina* spp.: BOSM) Cladocera, and a mesotrophic (CHM) and planktonic (CHP) chironomid fauna (Fig. 8). The samples representing the most recent period in the lake's history from *c.* 1940 are positioned to the left of the plot. Taxa strongly correlated with these samples include fine-leaved *Potamogeton* spp. (POTFL), *Z. palustris* (ZPLA) and *C. truncata* (CTRUN), pelagic *Daphnia* taxa (DHAL, DMAG, DPUL), Mollusca (PISID, PLANO), testate amoebae (CENTRO), the planktonic diatoms *S. parvus* (SPARV) and *Cyclostephanos tholiformis* (CSTHOL), the plant-associated diatom *C. placentula* (COPLAC), and benthic (CHB) and nutrient-tolerant (CHE) chironomid species (Fig. 8). The time track shows a clear trajectory from right to left of the plot reflecting the progressive species turnover in all components of the food web over the last 200 years (Fig. 8).

Table 1 Variance explained by the principal curves (PrC) compared with principal component axis 1 (PC1) for each biological group and also principal components analysis axis 2 (PC2) for ephippia

	Plants	Cladocera	Ephippia	Diatoms	Chironomids
PrC	0.723	0.714	0.552	0.642	0.413
PC1	0.603	0.672	0.543	0.494	0.331
PC2			0.830		

Discussion

Long-term ecosystem response to eutrophication

Eutrophication of Groby Pool since the mid- to late nineteenth century has been attributed to the conversion of

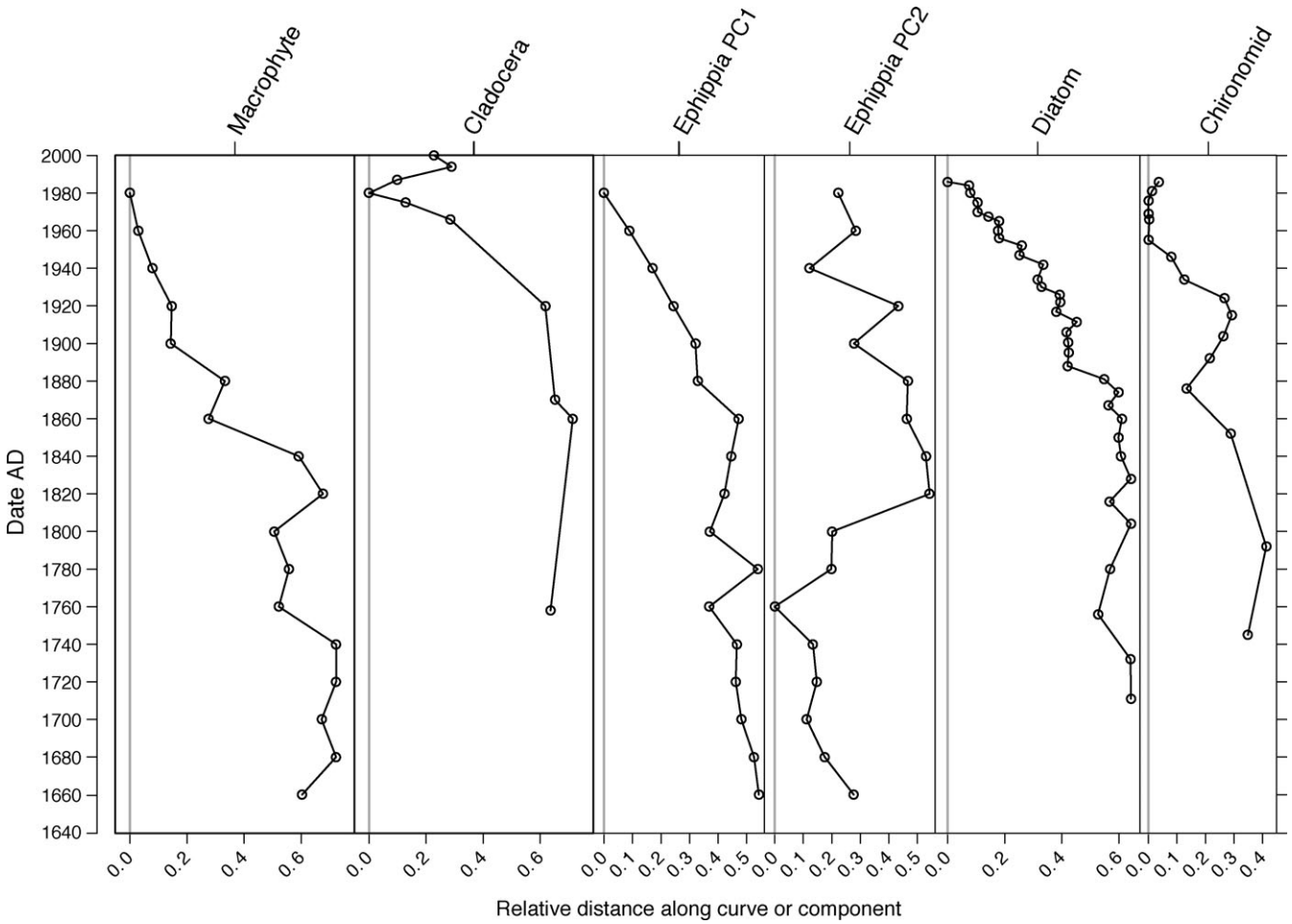

Fig. 7 Principal curve and principal component (PC) 1 and 2 scores (Cladocera ephippia only). Scores are normalised to the interval (0, 1) then scaled by the relative proportion variance explained by each curve or component.

pasture to arable land (Sayer *et al.*, 1999), with a more recent phase of enrichment following the influx of treated sewage effluent into the lake inflow in 1935 (Sayer, 2001). The most marked changes in the biological indicators coincided with these two major events, resulting in broadly synchronous stratigraphic shifts across all biological groups in the early 1800s and remarkable synchronicity in the mid-1900s.

Pre-c. 1800. The flora and fauna in the lowermost part of the Groby Pool sediment record indicate a low nutrient, clear water lake prior to the early 1800s. Macrophytes and benthic algae probably dominated primary production during the 1700s and early 1800s as indicated by prevalence of *Fragilaria* spp., typically bottom-dwelling diatoms found loosely attached to stable sediment surfaces and the bases of emergent macrophytes (Sayer, 2001), and benthic cladocerans (e.g. *A. costata*, *G. testudinaria*). The general structure of the Cladocera assemblage, large numbers of benthic taxa (each with small relative abundance) and the high proportion of chydorid spp., suggests that macrophyte cover was high (Ogden, 2000). In agreement with the diatoms and cladocerans, the pre-1800 chironomid assemblages were relatively diverse, comprising numerous taxa typically associated with aquatic macrophytes (e.g. *C. scutellata*, *Cricotopus* spp., *P. sordidellus*). Submerged plants can provide protection and a food source for phytophagous chironomids and act as a stabiliser for sediment dwelling taxa (Pinder, 1986; Whitehouse *et al.*, 2008).

The plant macrofossil data suggest that a diverse (*c.* 13 taxa) community of submerged aquatic vegetation was present with *L. uniflora*, *U. vulgaris*, *M. alterniflorum*, *M. spicatum*, *Potamogeton* spp. and several species of Characeae (including *Chara*, *Nitella* and *Tolypella* spp.), as well as floating-leaved Nymphaeaceae. A similar macrophyte assemblage has been recorded in the pre-enrichment period of other northern European shallow

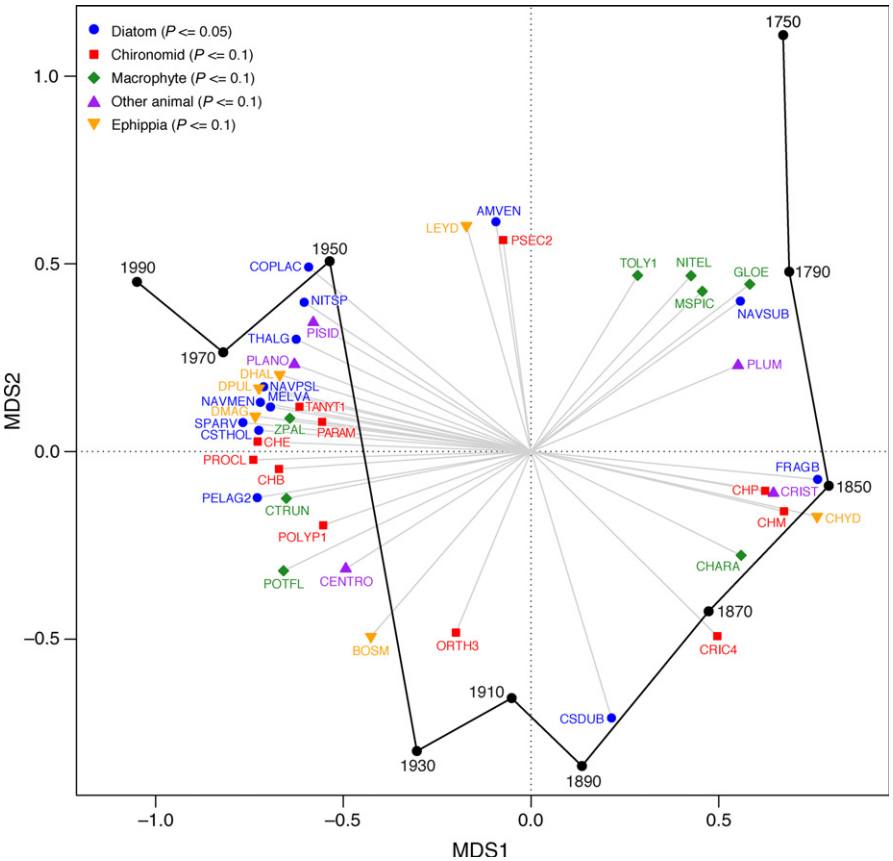

Fig. 8 Principal coordinates analysis biplot of the fused dissimilarity matrix showing the first two principal coordinates. The solid, black lines connect amalgamated sediment core samples in time order and are labelled with the assigned 20-year interval. Light grey vectors and symbols represent the magnitude and strength of vectors fitted into the space spanned by the first two principal coordinates. Symbol shape and colour (online version) depict the five taxonomic groups considered. Only those taxa with a significant correlation, *r*, with the first two principal coordinates, as assessed by permutation tests, are shown. The *P*-value threshold for each taxonomic group used to indicate a significant *r* is shown in the figure legend. No accounting for multiple comparisons was made as we use the *P*-value only as a guide to select species to be retained for plotting as a means of reducing clutter. Explanation of codes and full names for taxa are listed in Appendix S1.

lakes (Odgaard, Rasmussen & Anderson, 1997; Sayer *et al.*, 2010a). Furthermore, in an analysis of macrophyte survey data from *c.* 3500 waterbodies across the U.K., Willby, Pitt & Phillips (2009) noted that high alkalinity, shallow lakes in high ecological status had a characteristic flora 'typified by *L. uniflora*, *M. alterniflorum* and *Potamogeton gramineus*, growing alongside a range of more widely distributed floating-leaved and submerged open water species, such as *Nuphar lutea*, *Nymphaea alba* and *Potamogeton natans*, various stoneworts (especially *Chara virgata*), *M. spicatum* and *Potamogeton perfoliatus*'. This description seems to capture Groby Pool prior to the mid-1800s, suggesting minimal disturbance and low nutrient concentrations. Reasonably high numbers of charophyte oospores in the lower core indicate that charophytes were prevalent in the past (Zhao *et al.*, 2006). The occurrence of several overwintering species (e.g. *Chara* spp. and *M. spicatum*) suggests year-round plant dominance (Sayer, Davidson & Jones, 2010c), possibly limiting the nutrients available to phytoplankton and resulting in high water clarity and predominance of benthic production (van den Berg *et al.*, 1998). In summary, the pre-1800 condition of Groby Pool can be described as mesotrophic with clear water, a diverse submerged macrophyte community and dominance by benthic diatoms and plant-associated Cladocera and chironomids.

Early 1800s to mid-1900s. From the early 1800s, the macrophyte assemblage underwent considerable change, with increases of fine-leaved *Potamogeton* spp. and *R.* sect. *Batrachium* and marked declines of Characeae, *Myriophyllum* spp. and *Utricularia*. Species richness also declined to around eight species. Changes in the plant macrofossil stratigraphies are consistent with the early stages of eutrophication where tall angiosperms such as

Potamogeton spp. are favoured over *Chara* spp. (e.g. Blindow, 1992; Hargeby *et al.*, 1994; Brodersen *et al.*, 2001; Ayres *et al.*, 2008). Somewhat contrary to observations elsewhere, that floating-leaved vegetation typically increases with eutrophication (e.g. Ayres *et al.*, 2008; Wiik *et al.*, 2014), Nymphaeaceae abundance declined during the early enrichment phase, suggesting that water lilies retreated to the lake fringe. Competition between *N. alba* and the non-native *Nymphoides peltata* may have contributed to this pattern as botanical records for Groby Pool indicate that the former was present prior to around 1930 then subsequently disappeared while the latter appeared from this time (Davidson *et al.*, 2005). *Nymphaea alba* is known to decline with eutrophication and it is possible that *N. peltata* filled its niche. However, *N. peltata* does not produce trichosclereids and was therefore not represented in the sediment record.

From the early 1800s, a number of pelagic Cladocera taxa (*Ceriodaphnia* spp. and *D. hyalina* agg.) appeared and the proportion of *B. longirostris* increased, probably reflecting increases in pelagic primary production (Vadeboncoeur *et al.*, 2003; Davidson *et al.*, 2010; Hobbs *et al.*, 2012). Diatoms exhibited their first eutrophication-related shifts from the early 1800s with a rise in *C. dubius*, a spring and autumn bloomer in eutrophic lakes (Bradshaw & Anderson, 2003), followed by a more marked increase in this taxon along with *S. parvus*, another spring bloom former, after *c.* 1880. This suggests an intensification of planktonic diatom production during late winter–spring and declining light penetration (Sayer, 2001). Alterations in the chironomid community were also seen in the early to mid-1800s with a shift towards dominance by mud-associated forms and a relative decline in plant-associated taxa. Change in macrophyte habitat is a key driver of changing chironomid diversity in shallow lakes (Whitehouse *et al.*, 2008; Langdon *et al.*, 2010) and the shifts in the architecture and habitat structure of the submerged vegetation of Groby Pool are likely to have impacted on the chironomid species assembly.

After mid-1900s. The period from the mid-1900s represents a recent phase of accelerated eutrophication. The plant community shifted to dominance by fine-leaved *Potamogeton* spp., *C. truncata* and *Z. palustris* with a further reduction in species richness to just four or five species. According to studies of macrophyte seasonality in 39 Norfolk/Danish shallow lakes, dominance by fine-leaved *Potamogeton* species (e.g. *P. pusillus*, *P. berchtoldii* and *P. pectinatus*) and *Z. palustris* (a so-called PPZ community) is typical of highly eutrophic lakes in which macrophyte occupancy is high in early summer (June) but low to non-existent by late summer (August) (Sayer *et al.*, 2010a,c). Sayer *et al.* (2010a) also noted that the plant covered period was longer (covering both June and August) in lakes which supported abundant populations of Characeae and *C. demersum* – plants that are capable of overwintering (Fernández-Aláez, Fernández-Aláez & Rodríguez, 2002). Thus, in Groby Pool, it seems plausible that the transition from charophyte to fine-leaved *Potamogeton–Zannichellia* dominance might also indicate a decline in the seasonal duration of plant dominance.

The post-1930 plant community inferred from the macrofossils is very similar to the current aquatic vegetation of the lake, with the exception of *E. nuttallii* which is currently abundant in the pool but absent from the three cores. This submerged plant is capable of prolific growth and was recorded as abundant in site surveys from the 1940s. Nevertheless, *E. nuttallii* rarely leaves identifiable remains in sediments as the leaves do not appear to preserve and, as an evergreen perennial, it seldom produces seeds (Davidson *et al.*, 2005; Clarke *et al.*, 2014). The recent plant community of Groby Pool is typical of impacted alkaline, shallow lakes (Willby *et al.*, 2009) and the losses seen over time in the macrofossils are consistent with changes in aquatic macrophyte assemblages observed along modern nutrient gradients (Jeppesen *et al.*, 2000; Penning *et al.*, 2008).

Changes were seen across all of the other biological groups as plant diversity declined indicating that lake functioning was altered by changing plant architecture and a seasonal loss of aquatic plants. The abundance of planktonic Cladocera taxa markedly increased, especially *Daphnia* spp., suggesting a pronounced increase in pelagic primary production and/or low grazing pressure from zooplanktivorous fish (Davidson *et al.*, 2011), a matter we return to later. While a number of plant-associated Cladocera taxa were still present after the mid-1900s, *E. lamellatus* is a species which is more numerous as nutrient concentrations increase in the presence of plants (Davidson, 2006). Similarly, a strong shift was seen in the diatom assemblages at *c.* 1940 when *S. parvus*, a species widely associated with eutrophic shallow lakes (Bennion, 1994), began to dominate in the plankton and epiphytic taxa, especially *C. placentula*, became more abundant. In line with the Cladocera data, the diatoms also indicate a shift from benthic to phytoplankton-based primary production. Likewise, chironomid assemblages changed markedly from *c.* 1940, when an increase in benthic, mud-dwelling taxa rela-

tive to plant-associated taxa and a number of species known to tolerate moderately eutrophic conditions, low oxygen levels and high levels of organic pollution were observed (Moller-Pillot & Buskens, 1990). *Chironomus* spp. and *Procladius* spp., two of the most abundant taxa in the recent period, are associated with the soft, organic sediments characteristic of eutrophic, turbid lakes (Brodersen *et al.*, 2001; Langdon *et al.*, 2010). Macrophytes affect sediment stability, resuspension and oxygen conditions, and hence, changes in macrophyte habitat can have a profound influence on zoobenthic community composition (Brodersen *et al.*, 2001). Macrophytes also act as a food source and substratum for chironomids, and plant density and species richness have been shown to be primary controls on the distribution of chironomid communities in shallow lakes (Langdon *et al.*, 2010).

Exploring mechanisms of change using multi-indicator data

In addition to providing a more complete picture of ecological change at the study site than earlier palaeoecological studies focusing on only one or two biological groups, the multi-indicator data enable us to explore the potential causes of observed changes across individual fossil groups and species. While we cannot infer 'cause and effect' with complete certainty, adding indicators can help to isolate controlling influences and some hypotheses can be eliminated. To illustrate the power of the approach, we focus on three marked shifts in the palaeorecord and utilise the available data to evaluate possible explanations for these shifts. Key potential drivers considered are nutrients, macrophyte abundance (habitat) and fish density (zooplanktivory).

The post-c. 1900 increase in Daphnia spp.. There is a striking increase in *Daphnia* spp. ephippia post-*c.* 1900 (Fig. 4a,b). Given the central position of Daphniidae in aquatic food webs, they can be influenced by both bottom-up (nutrients) and top-down (predation by zooplanktivorous fish) factors. One explanation for the rise in *Daphnia* is enhanced phytoplankton productivity and thus greater food supply (Vanni, 1987). This is strongly supported by the diatom data which exhibit a marked increase in planktonic taxa since the late 1800s suggesting an ample supply of phytoplankton for *Daphnia* to graze on. Thus, in the absence of additional data, a simple eutrophication signal is apparent. However, with additional proxies at our disposal, a second explanation of reduced fish abundance can be evaluated. Scales and scale fragments of percid and cyprinid fish, as well as cocoons of the fish leech *P. geometra*, were most abundant in the mid- to late 1800s after which they declined, coincident with the increase in *Daphnia*. The paucity of fish remains prior to 1800, and the abundance of *Daphnia* and *Ceriodaphnia* in very clear water conditions, suggests that Groby Pool had low fish abundance in the past. The pool is hydrologically isolated from other waterbodies and consequently the fish populations are susceptible to major changes, particularly species losses due to limited opportunities for natural dispersal.

Zooplanktivorous fish density is known to be an important structuring force on Cladocera assemblages (Davidson *et al.*, 2007), and the high abundance of the large-bodied Cladocera species *D. magna* in recent decades suggests that zooplanktivorous fish are either absent, or present in very low numbers (Cousyn & De Meester, 1998; Davidson, 2006). The observed increase in Mollusca since the early 1900s could also arise due to release from predation, lending further support to the theory of low fish abundance since *c.* 1900. Therefore, the multi-indicator analysis suggests that both top-down and bottom-up factors have promoted the recent rise in *Daphnia* spp.

The post-1840 decline in Cristatella mucedo. There is a marked decrease in the abundance of *C. mucedo* since *c.* 1840 as recorded by the animal macrofossils (Fig. 5). *Cristatella mucedo* is a freshwater bryozoan producing overwintering propagules called statoblasts, the chitinous valves of which are resistance to decay and are thereby preserved in the sediment record (Okamura *et al.*, 2013). This organism is characterised by a metapopulation ecology and hence is prone to population instability and periods of absence and of low abundance (Okamura *et al.*, 2013). It is possible, therefore, that the marked post-1840 decline in *C. mucedo* reflects its boom–bust ecology. However, a gradual and progressive decline in abundance of statoblasts since 1840 with continued presence is seen rather than the erratic changes and, in some cases, eventual extinction that have been observed in other lake cores displaying characteristics of population instability (Okamura *et al.*, 2013). We can, therefore, eliminate this explanation despite Groby Pool being an isolated site. Eutrophication is unlikely to explain the observed decrease in *C. mucedo* as studies have shown that bryozoan biomass responds positively to increasing nutrient concentrations (Hartikainen *et al.*, 2009). A more plausible explanation is competition for food with the increased *Daphnia* populations. While the diatom data suggest that planktonic algae were plentiful

after *c.* 1880, diatoms are just one of many food sources, and some degree of food loss is likely given the striking rise in *Daphnia*. Indeed, in lakes where grazing pressure on *Daphnia* is released due to fish kills, *Cristatella* remains in sediment cores decline dramatically (Sayer, C.D., Davidson, T.A., Rawcliffe, R., Langdon, P., Leavitt, P. & Rose, N., in prep.).

An additional explanation for the post-1840 decline in *C. mucedo* is loss of habitat and here the plant macrofossil data can shed some light. *Cristatella mucedo* occurs as gelatinous colonies loosely attached to surfaces such as macrophytes, roots, woody debris and rocks (Wood & Okamura, 2005); therefore, any decrease in macrophyte abundance would result in fewer plant substrates onto which the bryozoan could attach. The plant macrofossil data clearly indicate a decline in overwintering submerged vegetation, pointing to a shorter period of plant growth since the mid-1800s. A decline in the abundance of floating-leaved vegetation is also indicated by the plant macrofossil data with a substantial decrease in Nymphaeaceae trichosclereids from the mid-1800s, further supporting the suggestion that reduced habitat played a key role in the decline of *Cristatella*. Therefore, when evaluating the multi-indicator evidence for Groby Pool, increased competition for food and loss of habitat both provide probable explanations for the observed patterns in *C. mucedo*.

The post-1940 increase in Cocconeis placentula. *Cocconeis placentula* is an epiphytic diatom with a broad tolerance of environmental conditions (Burkholder, 1996). In the Groby sediment record, there is a notable increase in the relative abundance of this species from *c.* 1940 which Sayer *et al.* (1999) suggested may be due to eutrophication-driven increases in submerged plant biomass and abundance and thereby greater opportunities for colonisation by epiphyte communities. The animal macrofossil record is of value in offering an alternative explanation for the observed increase in *C. placentula* – increased grazing pressure from invertebrates. There is clear evidence of increased snail abundance in Groby Pool from the 1940s, most likely due to low fish predation as previously discussed, coincident with the rise in *C. placentula*. Experimental studies by Jones *et al.* (2000) showed that grazing exerted the largest influence on periphyton community composition. They provided evidence of an increase in *C. placentula* in the presence of snails, most likely because its adpressed form enables it to withstand high pressure grazing as well as reduce competition from taller growing algae. Further support for the grazing theory is provided by the small pulse of *C. placentula* in the diatom record from 1760 to 1780 which, in line with the post-1940 increase, is coincident with a rise in Mollusca remains and low numbers of fish scales, suggesting that high grazing pressure was being exerted on the algae at this time. On balance, therefore, resistance to increased grazing pressure from invertebrates is the most probable driver of the *C. placentula* increase.

The potential of the multi-indicator palaeoecological approach

The study illustrates how multi-indicator palaeoecological techniques can be used to infer long-term shifts in shallow lake biological structure in response to eutrophication and changing fish populations. The multi-indicator palaeoecological data suggest that eutrophication has had an effect through all trophic levels in Groby Pool with a major shift from benthic to pelagic pathways over the last 200 years (Vadeboncoeur *et al.*, 2003). Our approach shows how the different components of shallow lake food webs display apparently synchronous shifts in composition in response to increasing nutrient loads. An examination of ecological shifts over these longer timescales reveals that changes in response to enrichment were gradual rather than abrupt and were relatively slow with loss of plant diversity and associated alterations in other groups occurring progressively over several decades.

Over the last decade, there have been a number of elegant illustrations of the power of the multi-proxy approach (e.g. Birks & Birks, 2006; Davidson *et al.*, 2013; Michelutti & Smol, 2013). However, with few notable exceptions (Birks & Birks, 2001; Sayer *et al.*, 2010b; Guilizzoni *et al.*, 2012), rarely have such studies been conducted on as large a number of biological groups as here, most involving a mix of physical and chemical proxies with just one or two biological groups included to infer broader environmental change. Of course, handling data from several fossil groups and multiple cores is not straightforward, but the approach taken here, where plant and animal macrofossil data are amalgamated from three cores, has proved successful in revealing a strong sequence of events and coherent patterns which are consistent with botanical records from the site (Davidson *et al.*, 2005).

In conclusion, the case of Groby Pool demonstrates the potential of using the full array of fossil groups preserved in lake sediment cores to infer ecosystem dynamics and to contribute to our understanding of the mechanisms that may link biological assemblages to a range of forcing factors. By providing several potentially

independent lines of evidence that can help to evaluate alternative explanations for patterns in the data, well designed multi-indicator studies can make an important contribution to understanding biotic responses to environmental change and can move beyond inductive data-led studies to deductive, hypothesis-driven science. A more complete picture of changes in ecosystem structure and function can be painted by employing the full biological record, and the problems associated with the traditional single indicator approach can be overcome.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of codes and full names for taxa in Fig. 8.

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