

# Ecological sensitivity of marl lakes to nutrient enrichment: evidence from Hawes Water, UK

EMMA WIIK<sup>\*†</sup>, HELEN BENNION<sup>\*</sup>, CARL D. SAYER<sup>\*</sup>, THOMAS A. DAVIDSON<sup>‡§</sup>,  
SUZANNE MCGOWAN<sup>¶\*\*</sup>, IAN R. PATMORE<sup>\*</sup> AND STEWART J. CLARKE<sup>††</sup>

<sup>\*</sup>Environmental Change Research Centre, Department of Geography, University College London, London, U.K.

<sup>†</sup>Institute of Environmental Change and Society, Research and Innovation Centre, University of Regina, Regina, SK Canada

<sup>‡</sup>Lake Group, Department of Bioscience, Aarhus University, Silkeborg, Denmark

<sup>§</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus, Denmark

<sup>¶</sup>School of Geography, University of Nottingham, Nottingham, U.K.

<sup>\*\*</sup>School of Geography, University of Nottingham Malaysia Campus Jalan Broga, Selangor Darul Ehsan, Malaysia

<sup>††</sup>The National Trust, Bury St Edmunds, Suffolk, U.K.

## SUMMARY

1. Highly calcareous (marl) lakes are infrequent but important freshwater ecosystems, protected under the EU Habitats and Species Directive. *Chara* lakes have been considered resistant to eutrophication owing to the self-stabilising properties of charophyte meadows. However, the opposite is suggested by the large-scale biodiversity declines in marl lake taxa in Europe, and evidence of charophyte sensitivity to eutrophication. We combined contemporary, palaeolimnological and archival methods to investigate the eutrophication of Hawes Water, a shallow marl lake in north-west England (U.K.).

2. Changes in aquatic macrophyte and invertebrate communities were reconstructed through the analysis of historical macrophyte surveys and sedimentary plant and animal macrofossils in two dated sediment cores from the littoral and deep zones of the lake. In addition, chlorophyll and carotenoid pigments were analysed to track changes in primary production from benthic and pelagic areas. Substantial changes in macrophyte communities were detected over centennial timescales, suggesting high ecosystem sensitivity considering the presently moderate phosphorus concentrations in Hawes Water (mean annual total phosphorus 20  $\mu\text{g L}^{-1}$ ).

3. Two apparent periods of threshold-like change were identified from the sediment record: (i) changes in cyanobacteria (aphanizophyll + myxoxanthophyll to canthaxanthin + zeaxanthin) and potentially in nutrient stoichiometry, reductions in the maximum macrophyte colonisation depth and water clarity, reduced charophyte and *Potamogeton* diversity, and increases in Nymphaeaceae; and (ii) severe reductions in light availability inferred from subdecadal doubling in phytoplankton abundance, substantial increases in *Daphnia* abundance and the extinction of charophytes from higher water depths.

4. Further, change in both the littoral and deeper water has confined key marl lake taxa to smaller niches. In the littoral, increasing siltation and reed and Nymphaeaceae densities caused extinction of *Littorella uniflora* in the early 1900s and have reduced the evenness of Characeae with suspected imminent extinction of two highly localised *Chara* spp. In the deeper water, upslope creep of maximum colonisation depth has reduced habitat for intermediate-depth marl lake taxa leading to the loss of four *Potamogeton* and one *Chara* species, and replacement of these taxa by *Nuphar lutea*.

5. The large changes in macrophyte community composition and increased incidences of turbid water have reduced the distinctive and valued marl lake features of Hawes Water, indicating that marl lakes can, as a habitat type, be highly sensitive to eutrophication. The persistence of abundant generalist macrophyte species at considerable water depth may be a feature of high-alkalinity lakes in clearwater, macrophyte-dominated states, but is a distinct eutrophication response in marl lakes rather than an indication of resistance to eutrophication.

Correspondence: Emma Wiik, Laboratory Building, Department of Biology, University of Regina, 3737 Wascana Parkway, Regina, Saskatchewan, S4S0A2 Canada. E-mail: emma.wiik@uregina.ca

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## Introduction

Marl lakes are calcite-depositing, high-alkalinity lakes, globally distributed in areas of carbonate geology. They are distinct from other lake types owing to their particularly clear, blue-green water, white calcareous sediments, and remarkably high macrophyte colonisation depths (>10 m). Further, the macrophyte community composition of marl lakes, consisting of a diversity of charophyte and *Potamogeton* species (Palmer, Bell & Butterfield, 1992; Duigan, Kovach & Palmer, 2007), is recognised in the European Union Habitats and Species Directive (EC-DG ENV, 2007), awarding marl lakes special protection as a habitat. However, wherever marl lakes are found, their characteristic macrophyte species are declining, while taxa tolerant of human impact, especially eutrophication, are becoming more abundant (Sand-Jensen *et al.*, 2000; Kłosowski, Tomaszewicz & Tomaszewicz, 2006; Bastrup-Spohr *et al.*, 2013). Consequently, concerns over the ecological quality of marl lakes have been raised (Blaženčić *et al.*, 2006; Pentecost, 2009; Azzella *et al.*, 2013). Eutrophication effects, such as increased phytoplankton production, associated reduced water transparency, as well as low sediment cohesion (Egerton, Kopaska & Downing, 2004; Schutten, Dainty & Davy, 2005) can be particularly damaging to marl lakes because they restrict macrophyte colonisation depth and induce an upslope retreat of charophytes and Potamogetonaceae. The retreat in turn compresses plant communities into a much narrower depth range and thereby reduces species diversity (Middelboe & Markager, 1997; Penning *et al.*, 2008).

Traditionally, marl lakes have been considered resilient to eutrophication owing to the precipitation of phosphorus with calcite (coprecipitation) (Otsuki & Wetzel, 1972; House, 1990; Robertson *et al.*, 2007). Calcite deposition occurs predominantly in summer when photosynthesis increases pH and when water temperatures are relatively high, both of which induce carbonate oversaturation (Brunskill, 1969; Murphy, Hall & Yesaki, 1983). Therefore, macrophytes (especially charophytes) can prevent phytoplankton dominance and maintain clearwater conditions via recycling of sediment-bound nutrients, and inducing coprecipitation in the water column. The strong negative feedback exerted by charophytes on external nutrient loading may lead to threshold responses once the latter exceeds their buffering

capacity, following the predictions of regime shift and alternative stable state hypotheses (Scheffer *et al.*, 1993; Scheffer & van Nes, 2007; Blindow, Hargeby & Hilt, 2014). Despite prevailing theory suggesting resistance of *Chara* lakes to eutrophication, empirical evidence suggests that the macrophyte communities of marl lakes may actually be highly sensitive to nutrient enrichment (Wiik *et al.*, 2013). For example, substantial declines in charophyte stands have been associated with total phosphorus (TP) exceeding only 7 µg L<sup>-1</sup> (Free *et al.*, 2007) and nitrate-N (NO<sub>3</sub>-N) exceeding 2 mg L<sup>-1</sup> (Lambert & Davy, 2011). Further, shifts between clear and turbid conditions have occurred at relatively low TP concentrations (from c. 20 to 70 µg L<sup>-1</sup>, respectively) (Hargeby, Blindow & Andersson, 2007). However, owing to the high biomass attained by charophytes, substantial amounts of nutrients can be locked into the benthos (Pełechaty *et al.*, 2013; Pukacz, Pełechaty & Frankowski, 2014), detracting from the relevance of pelagic measures of eutrophication (e.g. TP, chlorophyll *a*). Substantial ecological degradation in the benthos may occur prior to any increases in planktonic production.

It seems likely that the overwhelming majority of marl lakes have been impacted by human activity (Jeppesen, Jensen & Søndergaard, 2002; James *et al.*, 2005; Bennion *et al.*, 2011), while minimally impacted sites tend to lie in inaccessible, less researched areas (Blaženčić *et al.*, 2006), leaving knowledge gaps at the early stages of eutrophication where more subtle, yet significant, community responses may occur. Palaeolimnological analyses can provide a means to estimate pristine conditions, and also detect changes in marl lakes over the decadal-centennial timescales relevant to long-term eutrophication impacts, providing potentially more ecologically meaningful information than extrapolation from extant analogue sites (Osborne & Moss, 1977; Moss, 1979; Sayer *et al.*, 2010a).

Our study aimed to establish the early ecological changes that occur in marl lakes as a response to minor nutrient enrichment. We applied a combination of historical investigations, limnological monitoring (2009–2010) and palaeolimnology to Hawes Water (Lancashire, U.K.) which currently has moderate limnetic phosphorus and chlorophyll *a* concentrations. Hawes Water has previously been described as the 'best example of a lowland marl lake in England' (Bennion *et al.*, 2009) and is classed as oligotrophic (Skelcher, 2014). We hypothesised

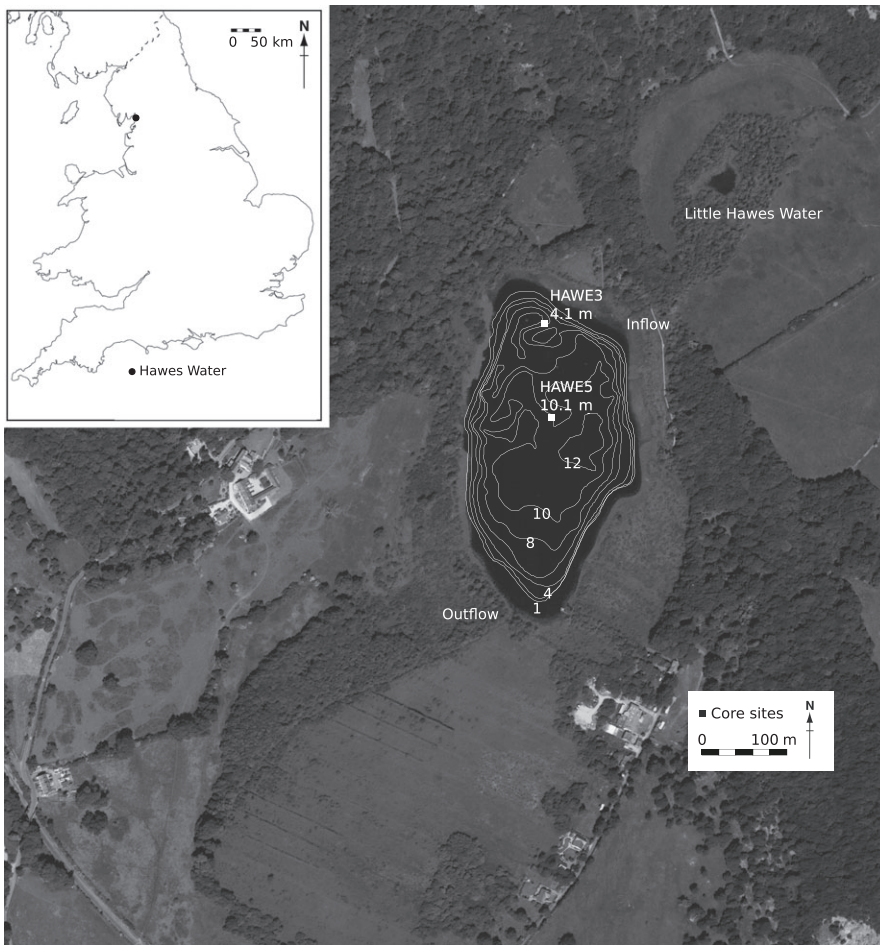


Fig. 1 The location, bathymetric profile and coring sites of Hawes Water.

that intensification of agricultural practices and nitrogen deposition since the 1800s (McGowan *et al.*, 2012; Moorhouse *et al.*, 2014) and especially since the mid-1900s (Vickery *et al.*, 2001; Robinson & Sutherland, 2002) in north-west England (Baddeley, Thompson & Lee, 1994; Pitcairn, Fowler & Grace, 1995) have resulted in major ecological shifts in Hawes Water, associated with upslope macrophyte movement and changing biological community composition.

## Methods

### Study site

Hawes Water is a small (5.7 ha) and shallow ( $Z_{\max} = 12.2$  m,  $Z_{\text{mean}} = 4.2$  m) mesotrophic (mean annual TP  $20 \mu\text{g L}^{-1}$  and chlorophyll *a* (chl *a*)  $12 \mu\text{g L}^{-1}$ ) kettlehole lake in Silverdale, Lancashire, U.K. (54.11N 2.49W; Fig. 1). It lies in a shallow basin of Carboniferous limestone in Gait Barrows National Nature Reserve. The lake is within a Special Area of Conservation and is designated as an example of habitat 3140 'hard oligo-

mesotrophic waters with benthic vegetation of *Chara* spp.' under the European Union Habitats and Species Directive (EC-DG ENV, 2007). The catchment encompasses  $1.7 \text{ km}^2$  and consists, in addition to the nature reserve, of holiday lets with private sewage management, and pasture. Annual P loads are estimated at  $51.27 \text{ kg}$ , and the retention time is *c.* 0.32 years (Goldsmith *et al.*, 2003).

Hawes Water has a long history of autochthonous carbonate precipitation extending through the Late Glacial to the present day (Marshall *et al.*, 2002). During the early Holocene, the maximum extent of the lake encompassed *c.* 1 km in length and 400 m in width; however, changes in sea level and therefore water table depth gradually lowered water levels of the lake (Jones *et al.*, 2011). Marginal *Chara* marl deposits were incised following late-Holocene reductions in water levels, exposing a terrestrialised marl bench (Jones *et al.*, 2011).

Hawes Water is naturally spring and groundwater fed; however, an artificial inflow and outflow were created in the 1800s, which lowered lake water levels and connected Hawes Water to Little Hawes Water within a



pasture to the north. The land surrounding the lake was subsequently improved from fen to arable. Water levels increased and fen development recommenced following discontinued maintenance of drainage ditches in the early 1900s (Oldfield, 1960) until clearance again in the 1960s. Reed swamp is currently developing in the margins as a result of renaturalisation. Given the steeply shelving bathymetric profile of the lake, areas of shallow water are restricted to the lake margins (Fig. 1).

The limnology of Hawes Water is more thoroughly reported in Wiik *et al.* (2014). Briefly, peaks in pH occur during the summer months when marl precipitates on macrophytes (*Nuphar lutea*, *Potamogeton coloratus*, *Potamogeton lucens*, *Chara* spp.) leading to a decline in alkalinity and very low or undetectable concentrations of soluble nutrients. Maximum Secchi depth (>5 m) occurs during the winter, and minima of ~1 m coincide with peaks in chl *a* concentrations (28 µg L<sup>-1</sup>). TP peaks occur in winter (max 40 µg L<sup>-1</sup>), and soluble reactive P (SRP) is constantly low (<5 µg L<sup>-1</sup>). Thermal and chemical stratification begins in May/June and ends in September, with a thermocline at *c.* 5–6 m. Subsurface oxygen maxima develop in late spring/early summer.

#### Contemporary macrophyte surveys

The macrophyte community and sediment type were monitored semi-quantitatively by standard shore and boat surveys (JNCC, 2005) using a bathyscope and a rake to determine submerged taxa. Shore surveys were 80 m long and extended to water depths ranging from 25 to >75 cm. Boat surveys departed from the centre of the shore section, and multiple points were recorded up to the maximum depth of macrophyte colonisation. The maximum depth of colonisation was assessed with several rake throws. Four sections were selected in total, and additional littoral areas were thoroughly surveyed in 2010 in an attempt to find rare charophyte species. Macrophytes were identified to genus or species level in the field excepting charophytes which were sent for identification to Nick Stewart (recorder of charophytes for the Botanical Society of Britain and Ireland). Charophyte nomenclature followed Bryant & Stewart (2002).

#### Core collection

Two sediment cores were taken from Hawes Water to capture ecological changes in the littoral and pelagic zone (Fig. 1). A littoral core (HAWE3, 71 cm) was taken in October 2009 at a depth of 4.1 m at the northern end of the lake using a wide-bore (internal diameter

140 mm) 'Big Ben' piston corer (Patmore *et al.*, 2014). The site is a vegetated subsurface mound (known as the 'Chara mound') separated from the lake margins by deeper open water habitat. A deep-water core HAWE5 (31 cm) was taken in January 2011 from the central-northern end of the lake at a water depth of 10 m using a Glew corer (internal diameter 40 mm) (Glew, 1991). Both cores were extruded at 1-cm intervals.

#### Core chronology and lithostratigraphy

Freeze-dried sediments from cores HAWE3 and HAWE5 were dated through analysis of <sup>210</sup>Pb, <sup>226</sup>Ra, <sup>137</sup>Cs and <sup>241</sup>Am by direct gamma assay in the Bloomsbury Environmental Isotope Facility (BEIF) at University College London. The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low-energy gamma rays within the sample (Appleby, Richardson & Nolan, 1992). <sup>210</sup>Pb dates were calculated using the constant rate of supply (CRS) model (Appleby, 2001). Carbonate and organic carbon contents of HAWE3 and HAWE5 were quantified by loss on ignition (LOI) following Dean (1974).

#### Pigments

Chlorophyll and carotenoid pigments were analysed at all levels of the HAWE3 core following McGowan *et al.* (2012). Freeze-dried samples were extracted overnight at -4 °C in a mixture of acetone, methanol and water (80 : 15 : 5). Extracts were filtered with a 0.22-µm PTFE filter, dried under N<sub>2</sub> gas and redissolved in a 70 : 25 : 5 mixture of acetone, ion pairing reagent (IPR 0.75 g tetrabutyl ammonium acetate and 7.7 g ammonium acetate in 100 mL water) and methanol for injection into an Agilent 1200 series high-performance liquid chromatography (HPLC) unit with separation conditions modified from Chen *et al.* (2001).

#### Macrofossils

On a whole-lake scale, macrofossils of single sediment cores have been shown to reflect changes in the dominant component of biological communities (Leví *et al.*, 2014; Davidson *et al.*, 2005; Zhao *et al.*, 2006). Macrofossils, representing macrophyte, cladoceran, trichopteran, algal, bryozoan and molluscan communities were enumerated every 4 cm for HAWE3 and every 6 cm for HAWE5. Approximately 30 cm<sup>3</sup> of sediment per sample

was used for analysis of both cores. Samples were soaked in 5% KOH overnight and sieved through meshes of 125 and 355  $\mu\text{m}$  (HAW3) and 250  $\mu\text{m}$  (HAW5). All material of the larger size fractions, and a subsample of c. 15% of the 125  $\mu\text{m}$  size fraction, was analysed. Macrofossil counts were expressed as numbers per 100  $\text{cm}^3$ . Abundance scores between 0 and 3 (high numbers indicate high abundance) were used for *Chara* spp. stem encrustations (HAW3), and for bryophyte, mollusc and Nymphaeaceae trichosclereid (leaf cell) remains (HAW5).

Where species-level detail was not attainable, remains were aggregated to genus or higher level. This includes *Daphnia hyalina* agg. ephippia (HAW3) (U.K. species other than *D. magna* and *D. pulex*), *Daphnia* spp. ephippia (HAW5) (U.K. species other than *D. magna*), *Potamogeton pusillus* agg. leaf tips (*P. pusillus* and *P. bertholdii*) and Nymphaeaceae trichosclereids (*Nymphaea alba* and *Nuphar lutea*). Molluscs were mostly identified to family or genus level. Oospores are morphologically highly plastic and were therefore aggregated as *Chara* spp. for numerical purposes. However, oospore morphotypes were also tentatively identified using reference collection material and an oospore key (Haas, 1994). Uncalcified and calcified oospores were counted separately.

Trichoptera frontoclypea were identified by Malcolm Greenwood and Paul Wood at the Department of Geography, Loughborough University, and moss remains, by Graeme Swindles at the Department of Geography, University of Leeds and Pauline Lang at the Scottish Environment Protection Agency.

#### Historical survey records

Historical macrophyte records were assembled from Natural England archives, survey data held at UCL, old scientific publications and reports, and through personal communication with scientists and field naturalists familiar with the site. Unpublished limnological monitoring data were provided by J. Marshall.

#### Data analysis

Numerical analysis was performed on HAW3 using the statistical software R version 2.1.2 (R Development Core Team, 2010) with the packages analogue (Simpson, 2007; Simpson & Oksanen, 2011) and vegan (Oksanen *et al.*, 2011).

The uppermost two core levels of the pigment data set were omitted from analysis given their large diage-

netic changes, indicated by profiles of fucoxanthin and chlorophylls + chlorophyll derivatives. Lutein (chlorophyte and higher plant biomarker) coeluted with zeaxanthin (cyanobacterial biomarker), and so the two are reported together.

The absolute abundances of individual pigments (Leavitt, 1993) and macrofossil remains (Levine & Schindler, 1988) in a core profile may not accurately portray their relative abundance as part of a composition owing to differential preservation and/or production. In order to dampen the effect of non-comparable abundances, and to stabilise variance, both data sets were log-transformed and standardised prior to analysis. Ecological distances were measured using Bray–Curtis dissimilarities given the suitability of this metric for data sets with numerous zero values (Beals, 1984). Bray–Curtis dissimilarities cannot be mapped using PCA owing to the data structure requirements of the latter (Legendre & Gallagher, 2001), and therefore, ordination was performed using non-metric multidimensional scaling (nMDS). Core zonation was determined by clustering using Ward linkage.

The similarity between community changes in data sets, as indicated by ecological distance matrices, can be assessed by graphical comparison of their ordinations. In Procrustes analysis, two ordinations are rotated and scaled in order to maximise their fit onto each other, which has been shown to be robust for the analysis of ecological data sets (Peres-Neto & Jackson, 2001). The similarity between community change in the pigment and macrofossil data was assessed with symmetric nMDS-based Procrustes analysis for matching stratigraphic levels ( $n = 17$ ), using the R PROTEST function to test significance and correlation (Peres-Neto & Jackson, 2001).

Diagrammatic reconstructions of macrophyte communities and colonisation depths in Hawes Water for the present, the mid-1900s and the late 1800s/early 1900s were informed by a combination of the following sources of information: (i) palaeolimnological analyses in this study; (ii) historical survey data on macrophyte presence and distribution encompassing the early 1900s to the present; (iii) macrophyte surveys conducted in this study in 2009 and 2010; (iv) data for macrophyte community composition, depth zonation and maximum colonisation depth in comparable marl lakes (Jupp, Spence & Britton, 1974; Spence, Barclay & Allen, 1984; Pentecost, 2009; Hilt *et al.*, 2010) or lakes with similar species assemblages (Spence, 1967, 1982); and (v) ecological literature (morphology, habitat, distribution) on British charophytes (Stewart & Church, 1992; Moore, 2005) and Potamogetonaceae (Preston, 1995).

## Results

### Macrophyte communities in 2009 and 2010

Similar macrophyte communities were observed in the 2009 and 2010 surveys in Hawes Water. The margins (<75 cm water depth) were densely vegetated with *Phragmites australis*, *Typha angustifolia*, *Schoenoplectus lacustris* and *Cladium mariscus* (85–90% of total marginal habitat (TM)). *Salix* spp. were occasional in the shallowest areas (<5% TM). In open water patches within the emergent vegetation to the north, east and south, *Utricularia* sp., *Nuphar lutea* and *Potamogeton coloratus* were locally abundant (c. 5% TM). *Chara virgata*, *Chara aspera* and *Chara contraria* were very scarce (<5% TM). In 2010, filamentous algal growth was abundant in the reedswamp, and sediment in the margins was unconsolidated. *Fontinalis antipyretica* was locally frequent (<5% TM) in the shallower water, and *Lemna minor* as well as *Lemna trisulca* occurred in the north-east margins close to the inflow.

Emergent vegetation became less dense with increasing water depth. Below c. 75 cm, *P. coloratus* remained locally abundant, and *N. lutea* became dominant, with submerged mats of *Chara aculeolata* covering marl shelves mainly to depths of c. 2 m (but up to 3.9 m in an area off the regular transects in 2010). In deeper water, communities were dominated by *N. lutea* which was the deepest coloniser. Open water habitat covered most of the lake, as vegetation was restricted to depths <5.5 m.

Several species existed as occasional patches including *Elodea canadensis* (found only once in 2009), *Potamogeton lucens* (recorded <4 m depth along the southern margins), *Nymphaea alba*, *Hippuris vulgaris* (in the west and north) and an unidentified ornamental *Nymphaea* cultivar. The distribution of *Myriophyllum spicatum* was restricted to a subsurface mound (4 m depth; the coring site) off the north shore where *N. lutea* was dominant.

### Historical macrophyte communities

Seven historical macrophyte survey data points were obtained, two from the beginning of the 20th century (1911, 1915), one from the mid-1900s (1969) and four from the end of the century (1982, 1993, 1995, 1999). These survey data are not floristically complete (i.e. all species present not recorded) and therefore provide species presence data only. Changes in *Chara* nomenclature and taxonomy (Bryant, Stewart & Stace, 2002) challenge historical interpretations. For example, *C. curta* and *C. aspera* were recorded separately in 1999, but these can also be synonymous depending on naming authorities, which were unfortunately not always available for these data. *C. globularis* (last recorded 1915) may also refer to *C. virgata* (recorded in 2009/2010), and therefore, the former may still be present in the lake.

Historical records suggest that several species have disappeared from the lake throughout the 1900s (last record in parentheses) including *Littorella uniflora* (1911); *Chara vulgaris* var. *papillata* (1915); *Chara globularis*, *Chara*

**Table 1** Historical records of macrophytes in Hawes Water, and all species recorded in 2009/2010

Date	Flora	Source
2009 & -10	<i>Chara aculeolata</i> , <i>Chara aspera</i> , <i>Chara contraria</i> , <i>Chara virgata</i> , <i>Fontinalis antipyretica</i> , <i>Cladium mariscus</i> , <i>Elodea canadensis</i> , <i>Hippuris vulgaris</i> , <i>Lemna minor</i> , <i>Lemna trisulca</i> , <i>Myriophyllum spicatum</i> , <i>Nuphar lutea</i> , <i>Nymphaea alba</i> , <i>Phragmites australis</i> , <i>Potamogeton coloratus</i> , <i>Potamogeton lucens</i> , <i>Schoenoplectus lacustris</i> , <i>Typha angustifolia</i> , <i>Utricularia vulgaris</i> agg.	Surveys by author
1999	<i>C. hispida</i> var. <i>hispida</i> (syn. <i>C. aculeolata</i> ), <i>C. hispida</i> var. <i>major</i> ; <i>Chara rudis</i> to 4 m depth; <i>P. lucens</i>	Survey by C. Newbold
1995	<i>C. aculeolata</i> , <i>C. aspera</i> , <i>Chara curta</i> , <i>C. hispida</i> , <i>C. rudis</i> , <i>P. lucens</i> , <i>Potamogeton natans</i>	1996 Natural England report for Cumbria County Council and ARC
1993	<i>Chara</i> sp. recorded at HAWE3 coring site at depths around 4 m	Field notes by J. Marshall
1982	Encrusted <i>C. aspera</i> abundant, <i>C. rudis</i> to 7 m depth; <i>E. canadensis</i> , <i>P. lucens</i> ; 'Water was very brown in colour and visibility was poor.' – M. Wade	Diver survey by C. Newbold <i>et al.</i>
1969	<i>C. aculeolata</i> , <i>C. aspera</i> , <i>C. mariscus</i> , <i>N. lutea</i> , <i>N. alba</i> , <i>P. australis</i> , <i>Potamogeton crispus</i> , <i>Potamogeton friesii</i> , <i>P. lucens</i> , <i>Potamogeton obtusifolius</i>	School trip; J. Birks
1915	<i>C. aculeolata</i> , <i>Chara fragilis</i> subsp. <i>delicatula</i> (possibly syn. <i>C. globularis</i> ), <i>C. rudis</i> , <i>C. vulgaris</i> var. <i>papillata</i> , <i>P. friesii</i> , <i>P. lucens</i> , <i>P. obtusifolius</i> , <i>H. vulgaris</i> , <i>N. lutea</i> , <i>N. alba</i> ; 'The Characeae are in considerable quantity and much encrusted'	W. H. Pearsall, in Druce, (1916)
1911	A record of <i>Littorella uniflora</i>	Druce (1911)
1850	The water is very clear	Davis (1850); Dean & Jackson (1905)

*hispida* var. *hispida*, *Chara rudis* (1999); *Potamogeton crispus* (1969); *Potamogeton friesii*, *Potamogeton obtusifolius* (1984); and *Potamogeton natans* (1995) (Table 1).

The data, including comprehensive plant cover maps, suggest that species evenness (similarity in % cover between species) has reduced in the lake over the 20th century. For example, *C. aculeolata* and *C. aspera* notwithstanding, charophyte species recorded in 2009 were not found in 2010 and it seems that any findings were chance occurrences of very scarce populations. *C. rudis*, previously recorded to depths of 7 m (1982), later 4 m (1999), is now absent, reflecting decreasing colonisation depths to the point of extinction. The northern mound currently hosting *N. lutea* and *M. spicatum* only was, during a coring trip in 1993, described as 'mostly *Chara*' and named the *Chara* mound (J. Marshall, field notes). In contrast, it was noted in 1915 that 'The Characeae are in considerable quantity and much encrusted' (Table 1).

*Hippuris vulgaris* was recorded, in addition to the west fringe, at the north and south ends of the lake in 1982 (noted as 'frequent' (F) on the DAFOR scale), and the north end in 1999, showing that the distribution of the species has diminished. This is also the case with *P. lucens*, and *E. canadensis*, also recorded as F in 1982. *Utricularia vulgaris* agg., on the other hand, has increased in abundance, recorded as 'rare' in 1982 and currently abundant throughout the lake margins.

#### Core chronologies and geochemical characteristics

**HAWE3.** Core HAWE3 comprised a mixture of marl-coated macrophyte stem encrustations and organic material, with considerable fluctuation in composition throughout (Fig. 2a). Overall, carbonate content was high (48 to 57%), low values coinciding with darker brown sediment between 43 and 10 cm. Organic matter fluctuated inversely to carbonate and was relatively low (4 to 13%). The dating profile of HAWE3 extended from 0 cm (2009) to 16.5 cm (1947), with sediment accumulation rates fluctuating around  $0.077 \text{ g cm}^{-2} \text{ yr}^{-1}$  for the last sixty years (Fig. 2a).

**HAWE5.** HAWE5 was characterised by much finer sediment than HAWE3 and lacked encrusted stem remains. Relatively high organic content at the core base (Fig. 2b) was reflected by a dark brown/black sediment colour. Carbonate content increased upcore to 24.5 cm, ranging from 13 to 44%. At 24.5 cm, carbonate content stabilised and fluctuated only slightly between 39 and 50% around a mean value of 43%, with slightly lower concentrations above 11.5 cm. Organic matter was generally higher

than HAWE3 (11 to 66%). The dating profile of HAWE5 extended from 0 cm (2011) to 8.5 cm (1894) and reflected much lower sedimentation rates in the profundal than in the littoral (Fig. 2b). Sedimentation rates increased over time, from  $<0.01 \text{ g cm}^{-2} \text{ yr}^{-1}$  in the first half of the 20th century to  $>0.01 \text{ g cm}^{-2} \text{ yr}^{-1}$  in the latter half. Sedimentation rate roughly doubled between the late 1990s and the 21st century (c.  $0.015$  to  $>0.03 \text{ g cm}^{-2} \text{ yr}^{-1}$ ).

**Cross-comparison of core depth ages.** The dating profile of HAWE5 (1894–2011) extended further back in time than that of HAWE3 (1947–2009), which hindered comprehensive cross-comparison (Fig. 2a,b). Owing to the fluctuation of sedimentation rates where the dating record of HAWE3 terminated (16.5 cm), extrapolation of sediment age further downcore was not possible. Instead, approximate aging was undertaken using the similarities between the macrofossil record of both cores, namely abrupt changes in the amount of terrestrial wetland material, and of *Juncus* seed and *Chara* oospore abundance, aged around the early 1800s in HAWE5. These changes occurred at 48.5 cm in HAWE3.

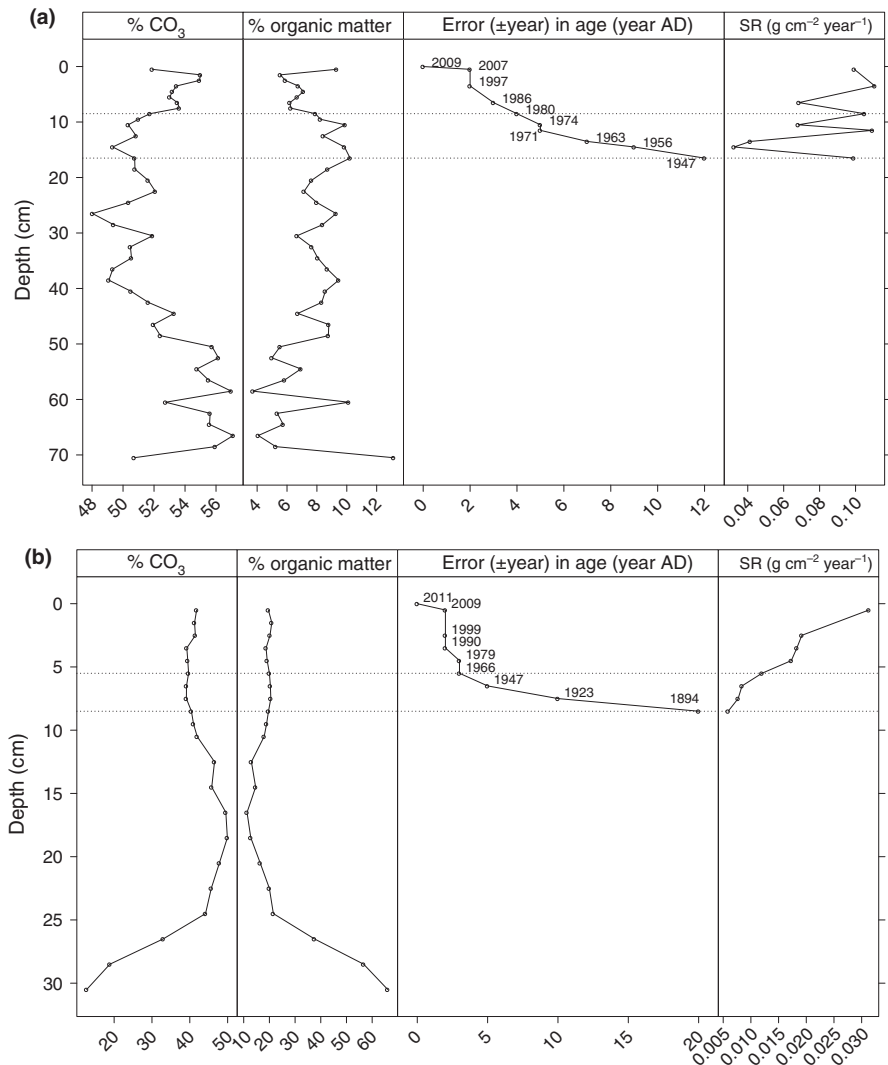
#### Stratigraphic clusters and community change

Four major stratigraphic zones were identified in the HAWE3 pigment and macrofossil data through cluster analysis (Fig. 3a,b). Although comparison of the clusters between the proxies was restricted by the lower resolution of the macrofossil data, similar groupings were evident particularly for the core base and top (Fig. 3a,b). The lowermost clusters consisted of base to 50.5 cm for pigments, and base to 48.5 cm for macrofossils (pre-1800s), and the top clusters of 12.5 (1960s) to the core top for both data sets. Discrepancies in clusters for the middle section of the core (pigments: 49.5–37.5 cm; 36.5–13.5 cm; macrofossils: 44.5–28.5 cm, 24.5–16.5 cm) indicated an earlier change in pigments (phytoplankton, epiphytes, macrophytes) compared with macrofossils (macrophytes, molluscs, cladocerans, bryozoans).

Further, cluster analysis showed pigment samples 49.5–37.5 cm to be more similar to the upper core (from 12.5 to 2.5 cm) than to levels between 36.5 and 13.5 cm. This was reflected by a relatively large ecological distance between 36.5 and 13.5 cm and all other clusters in ordination space (Fig. 3b). For macrofossils, ecological change was more monotonic in time, with 44.5–28.5 cm in one cluster and 24.5–16.5 cm and 12.5–0.5 cm in another (Fig. 3a).

There was a very high degree of concordance in the patterns of temporal change between the pigment and





**Fig. 2** Loss-on-ignition and sedimentation rate (SR) for cores HAW3 (a) and HAW5 (b), with <sup>210</sup>Pb-derived dates with errors.

macrofossil data, reflected by the high PROTEST correlation of 0.77 ( $P < 0.002$ ). There was no strong pattern between stratigraphic position and residuals; however, slightly less agreement was apparent within the lowermost 30 cm (Fig. 3c). Particularly strong concordance was evident for samples at 68.5, 36.5 and 0.5 and poor for samples at 64.5, 52.5 and 44.5.

#### Zone 1: pre-1800s

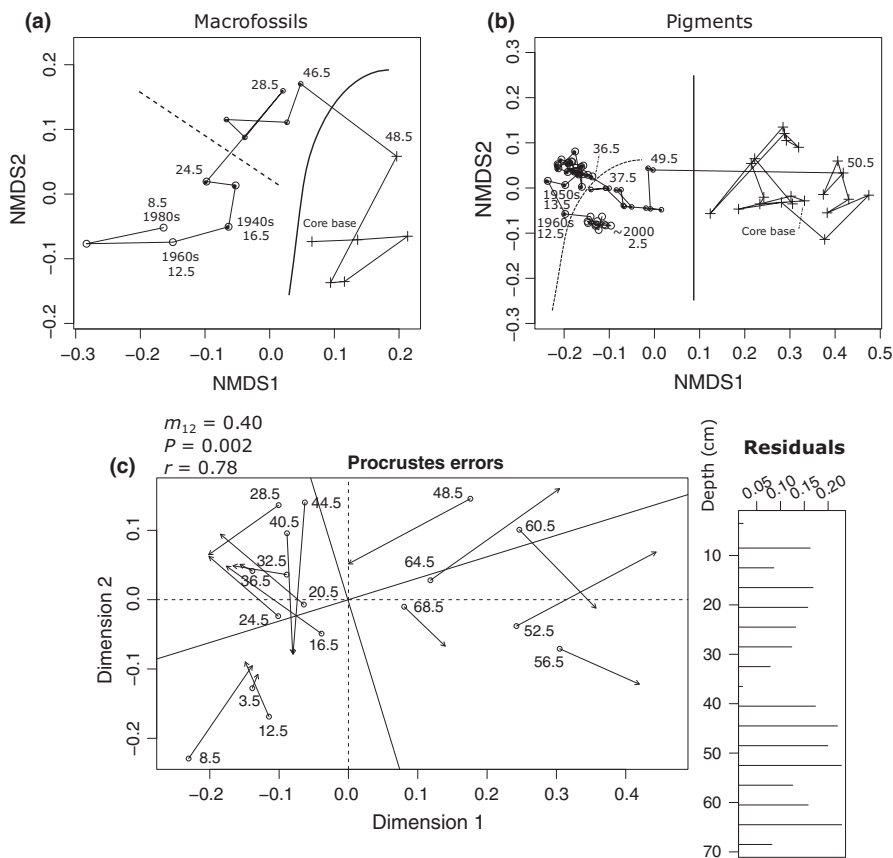
The concentration of pigments, including ubiquitous pigments (chl *a*, pheophytin *a* and  $\beta$ -carotene), was very low in zone 1 (Fig. 4). Pigment profiles of chlorophylls and their degradation products (not shown) indicated stable preservation conditions over time.

Abundant remains of terrestrial wetland taxa occurred in zone 1, including *Juncus* spp. seeds, and leaves of *Sphagnum* subsection *acutifolia* (those of the ombro-

trophic *Sphagnum austinii* in particular). DOC influx to the lake was also indicated by a strong amber and black colour dissolved from the sediment during processing. Pockmarked mollusc shells, rounded marl agglomerations and the absence of well-preserved encrusted *Chara* stem remains indicated diagenetic dissolution of carbonate structures.

Aquatic remains included numerous calcified and uncalcified *Chara* oospores and leaves of hypnoid mosses cf. *Platyhypnidium riparioides* (Figs 5 & 6). Further, a small number of *Potamogeton coloratus* seeds (56.5 cm, 52.5 cm) and one seed of *Potamogeton* cf. *perfoliatus* (56.5 cm) were found (Fig. 5). Leaf cells of Nymphaeaceae were relatively low in abundance (Figs 5 & 6); a small number of *Nymphaea alba* seed fragments (23.5 cm), *P. berchtoldii/pusillus* leaf tips (11.5 cm) and a marl-encrusted *M. spicatum* turion (23.5 cm) were found in HAW5.





**Fig. 3** nMDS (a, b) and Procrustes analysis (c) of HAWE3 macrofossil and pigment data. Core levels (c), and where available, dates as years (a, b), are shown between the core base and top where larger community shifts take place. nMDS symbols represent different clusters; solid lines, a major cluster division; and dashed lines, subordinate cluster divisions.

Molluscs (Sphaeriidae, *Radix* cf. *peregra* and *Bithynia* spp.) were present in this section, with a slight decrease in abundance at 52.5–48.5 cm (Fig. 7). In contrast, round and oblong morphotypes of *Plumatella* statoblasts increased *c.* fourfold between these two core levels. No ephippia of pelagic cladocerans were recorded in HAWE3, but very scarce remains were found in HAWE5. Carapaces of the macrophyte-associated *Pseudochydorus globosus* were relatively low in number.

Trichopteran frontoclypea were recorded infrequently in this zone with the following species appearing in both cores: *Limnephilus marmoratus*, *Ecnomus tenellus* and *Mystacides longicornis* (data not shown). Further, HAWE3 included *Mesophylax impunctatus*, *Mystacides azurea* and *Sericostoma personatum*. HAWE5 included *Oecetis lacustris*, *Athripsodes aterrimus*, *Holocentropus piscicornis* and *Polycentropus irroratus*. It is noteworthy that eight of the ten species recorded from HAWE5 occurred at 23.5 cm, six exclusively in this level. *M. impunctatus*, *S. personatum* and *Polycentropus flavomaculatus* are species associated with stony, exposed surfaces. The other species are not exclusively found in one habitat, although all aforementioned species are generally associated with still or

slow-flowing water (Wallace, Wallace & Philipson, 2003; Edgington & Hildrew, 2005).

#### Zone 2: pre-1800s/1800s

Most pigments increased markedly in zone 2, especially those from siliceous algae (diatoxanthin, fucoxanthin), chlorophytes (chl *b*, phaeophytin *b*) and cryptophytes (alloxanthin) (Fig. 4). Cyanobacterial pigments did not follow the same pattern; increases in myxoxanthophyll, canthaxanthin and lutein–zeaxanthin in this core section were very modest, and aphanizophyll was only occasionally above detectable levels.

Influx of terrestrial matter was reduced compared with zone 1 as indicated by only a slight yellow tint in the sample water, and lower abundances of terrestrial remains (*Juncus*, *Sphagnum*). There was no evidence of calcite dissolution in the macrofossil material, and well-preserved *Chara* stems were abundant throughout this core section. In contrast, the abundance of oospores was markedly lower (100s) compared with zone 1 (1000s) (Fig. 5) and no seeds of Potamogetonaceae or *Juncus* were recorded. The abundance of Nymphaeaceae remains was similar to the earlier core section.

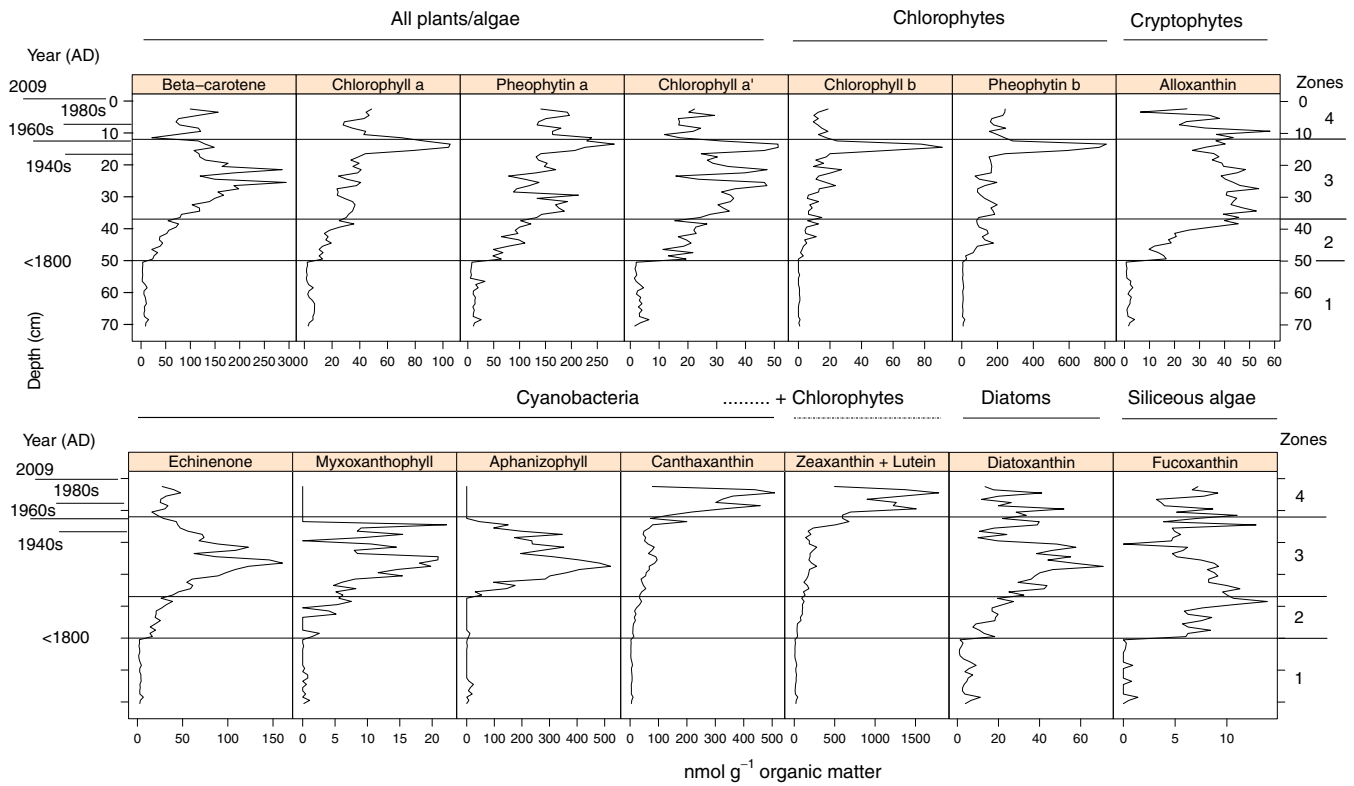


Fig. 4 HAWE3 pigment data ordered by group. Solid lines demarcate stratigraphic clusters.

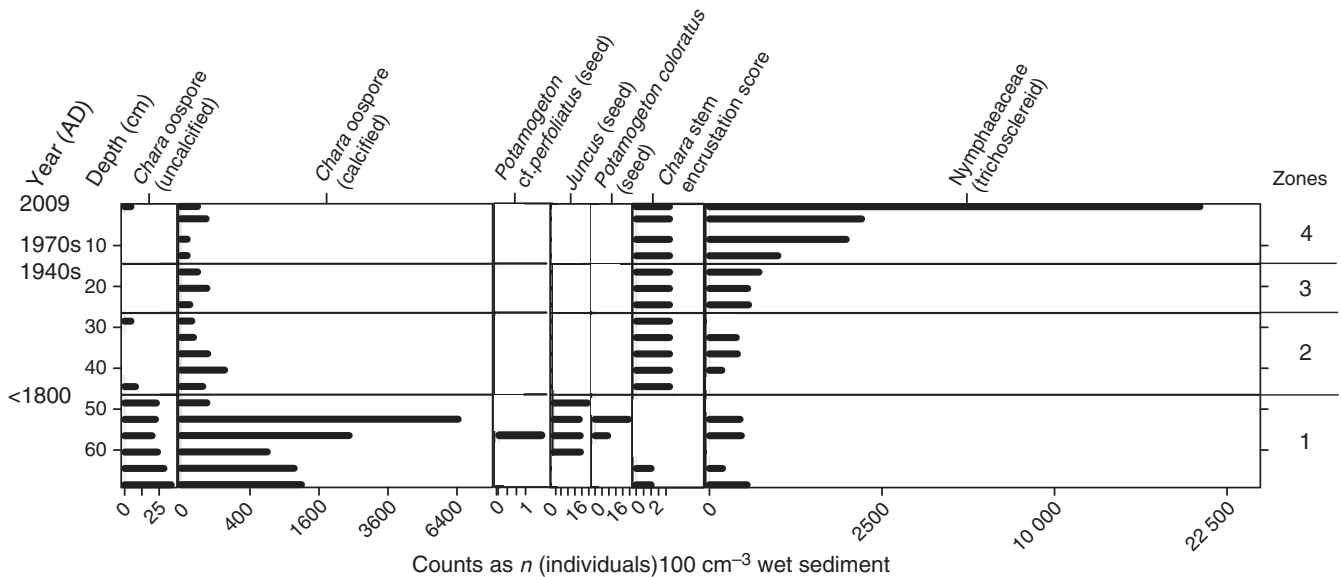


Fig. 5 Plant macrofossil data from HAWE3. Solid lines demarcate stratigraphic clusters.

Among the mollusc remains, those of *Bithynia* spp. and the Sphaeriidae were found in lower abundances than in zone 1, and the remaining taxa did not display changes (Fig. 7). Between 48.5 and 40.5 cm, there was a fourfold increase in the abundance of oblong

*Plumatella* statoblasts, followed upcore to 28.5 cm by an equally dramatic decrease. Remains of *P. globosus* were more abundant than in zone 1, and no pelagic cladoceran taxa were recorded. Trichopteran head shields in this core section were largely absent ( $n = 3$ ) and those

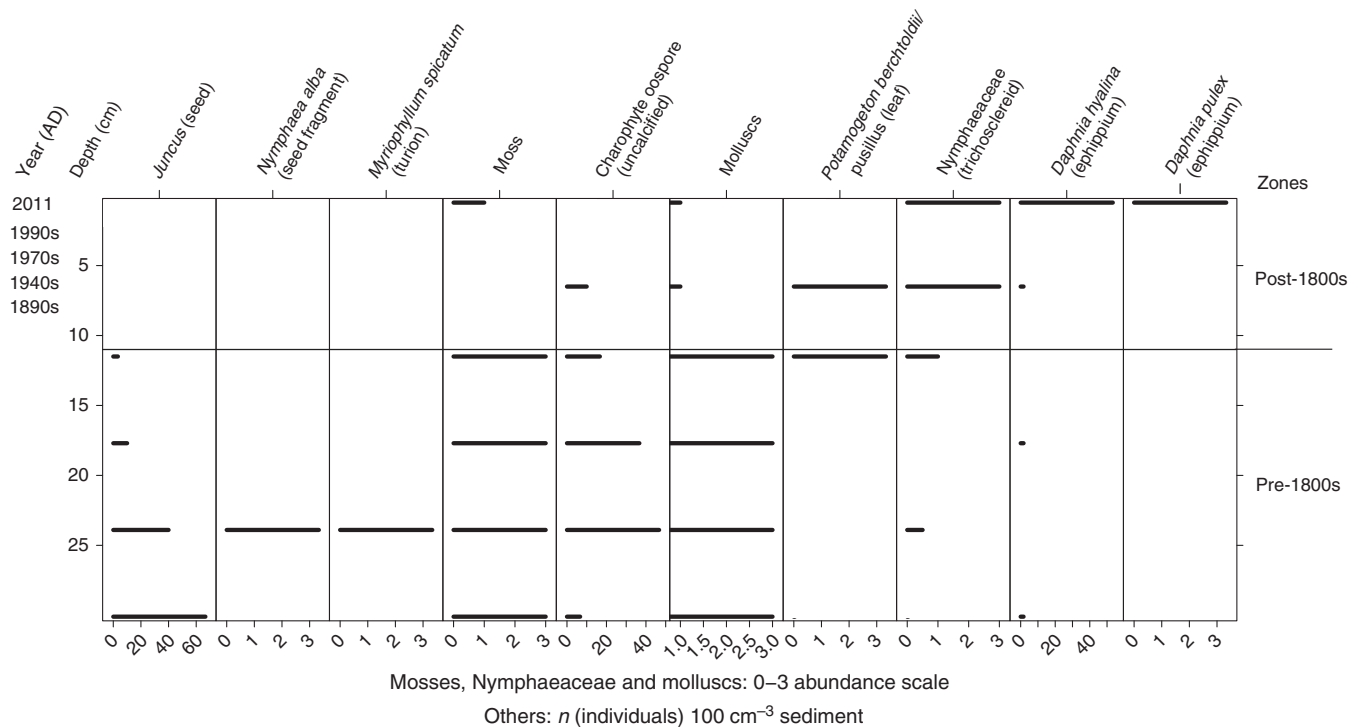


Fig. 6 Macrofossil data from HAWE5. Owing to differences in the dating profiles and data resolution between HAWE5 and HAWE3, the core zonation of HAWE3 was not applied to HAWE5. The solid line shows the change in macrofossil composition matched with HAWE3 and identified as the period of hydrological alteration.

found were towards the base of the section, identified as *M. longicornis*, *A. aterrimus* and *P. irroratus* (data not shown). These taxa show broad habitat preferences including sand, mud and vegetation (Wallace *et al.*, 2003; Edington & Hildrew, 2005).

#### Zone 3: 1800s/1900s to the late 1960s

Pigments from cyanobacteria (echinenone, aphanizopyll and myxoxanthophyll), including potentially nitrogen-fixing taxa (Hertzberg & Liaaen-Jensen, 1971), siliceous algae (diatoxanthin) and all algae ( $\beta$ -carotene), increased steeply to 25.5 cm and displayed a variable, but decreasing trend, upcore. Concentrations of alloxanthin were relatively stable in this core section, and fucoxanthin varied with no trend. Ubiquitous pigments (chl *a*, phaeophytin *a*,  $\beta$ -carotene) increased between 36.5 and 25.5 cm, levelling off thereafter and increasing in variability. In the upper end of the zone (16.5–13.5 cm; 1940s–1960s), there was a distinct peak in the chlorophylls. No changes in pigment preservation were indicated by chl *a*: degradation product values (not shown).

The transition from zone 2 to zone 3 (28.5–24.5 cm) in HAWE3 marked a small increase in Nymphaeaceae remains, mirrored in HAWE5 (Figs 5 & 7). *Chara* stem

encrustations remained abundant in HAWE3, and *P. pusillus/berchtoldii* leaf tips were numerous in HAWE5 (Fig. 6). Based on fossil evidence, historical photographs and macrophyte survey data (Table 1), macrophyte colonisation depth decreased, macrophyte abundance increased, and community composition became more mesotrophic towards the latter period of zone 3 (Fig. 8).

Within the invertebrate community, the beginning of zone 3 was marked by a relatively large increase in *Bithynia* spp., and a fourfold decrease in the abundance of oblong *Plumatella* statoblasts (Figs 5 & 7). Further upcore, the abundances of the aforementioned taxa were relatively stable. Two Trichoptera species were recorded, *P. flavomaculatus* (16.5 cm; 1940s) and *Cyrrnus flavidus* (20.5, 16.5 cm; c. 1930s–1940s), the latter appearing in the core record for the first time. *C. flavidus* is a species found in a variety of habitats, especially among macrophytes, in still water.

#### Zone 4: late 1960s–early 2000s

The transition to zone 4 marks a succession in cyanobacterial pigments (Fig. 4). Aphanizopyll and myxoxanthophyll declined to undetectable concentrations, and echinenone to relatively low concentrations, coincident

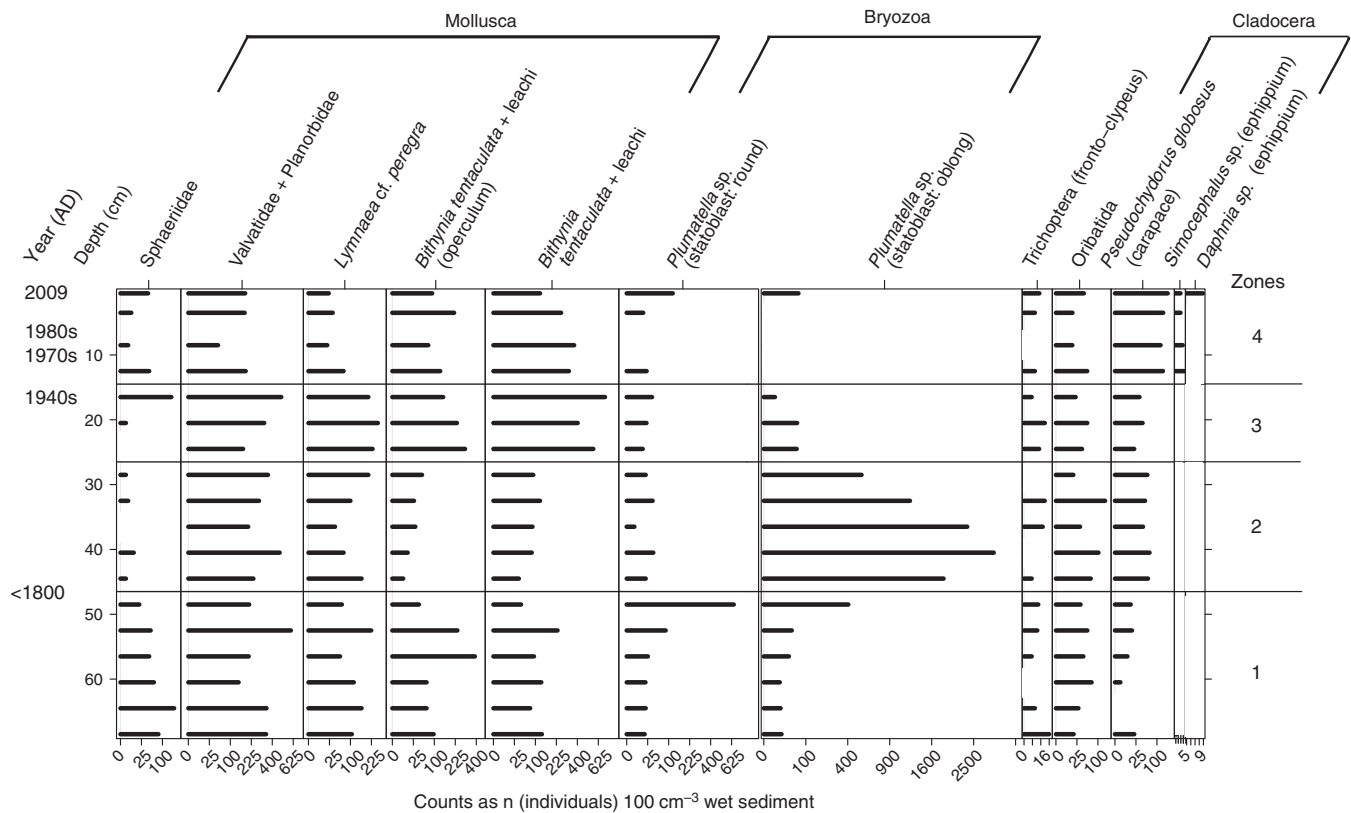


Fig. 7 Animal and bryozoan macrofossil data from HAWE3. Solid lines demarcate stratigraphic clusters.

with sharp increases in canthaxanthin and lutein–zeaxanthin, which occur primarily in cyanobacteria that do not fix nitrogen (Hertzberg & Liaaen-Jensen, 1971; Steenbergen, Korthals & Dobrynin, 1994). Chlorophylls *a* and *b* decreased to concentrations similar to those preceding the distinct peak around 14.5 cm (1950s).  $\beta$ -carotene, fucoxanthin, diatoxanthin and alloxanthin did not change noticeably in the uppermost 12.5 cm (post-1970s).

Macrofossils in zone 4 showed little change. *Chara* stems remained abundant, oospores remained low in abundance, and no seeds of Potamogetonaceae were recorded (Fig. 5). However, there was a large and steady increase in Nymphaeaceae trichosclereids towards the core top of HAWE3, the uppermost sample (2000s) containing 10 times more trichosclereids than the previous level (3.5 cm; late 1990s). A similar increase occurred in HAWE5. Compared with macrophyte community composition in the earlier 1900s (Fig. 8, Table 1), reduced diversity of intermediate-depth macrophyte species, reduced macrophyte colonisation depth, and dominance of Nymphaeaceae, characterised the latter stages of zone 4 (Fig. 8).

Molluscs showed a slight decrease in abundance towards the core top, *Lymnaea peregra* and the Valvatidae

and Planorbidae in particular (Fig. 7). The *Plumatella* statoblast morphotypes were recorded only occasionally. Cladocerans (*Simocephalus* sp., *P. globosus*) increased in abundance between 16.5 and 12.5 cm (1940s–1960s) and then displayed little variability to the core top. The first records of *Daphnia* spp. occurred in the uppermost samples of both cores (Figs 5 & 6). The only trichopteran species recorded in this zone was *C. flavidus*.

## Discussion

### Hydrological change versus eutrophication

Understanding ecological responses to eutrophication requires that the effects of other impacts such as hydrological alteration are differentiated because they can have similar effects on the structure of benthic and pelagic habitats (Hannon & Gaillard, 1997; Luoto *et al.*, 2011). However, land improvement in catchments prone to water logging such as around Hawes Water often superimposes change in drainage on the top of increased nutrient export (Skaggs, Brevé & Gilliam, 1994; Snyder & Morace, 1997; Dils & Heathwaite, 1999), creating



### Hawes Water

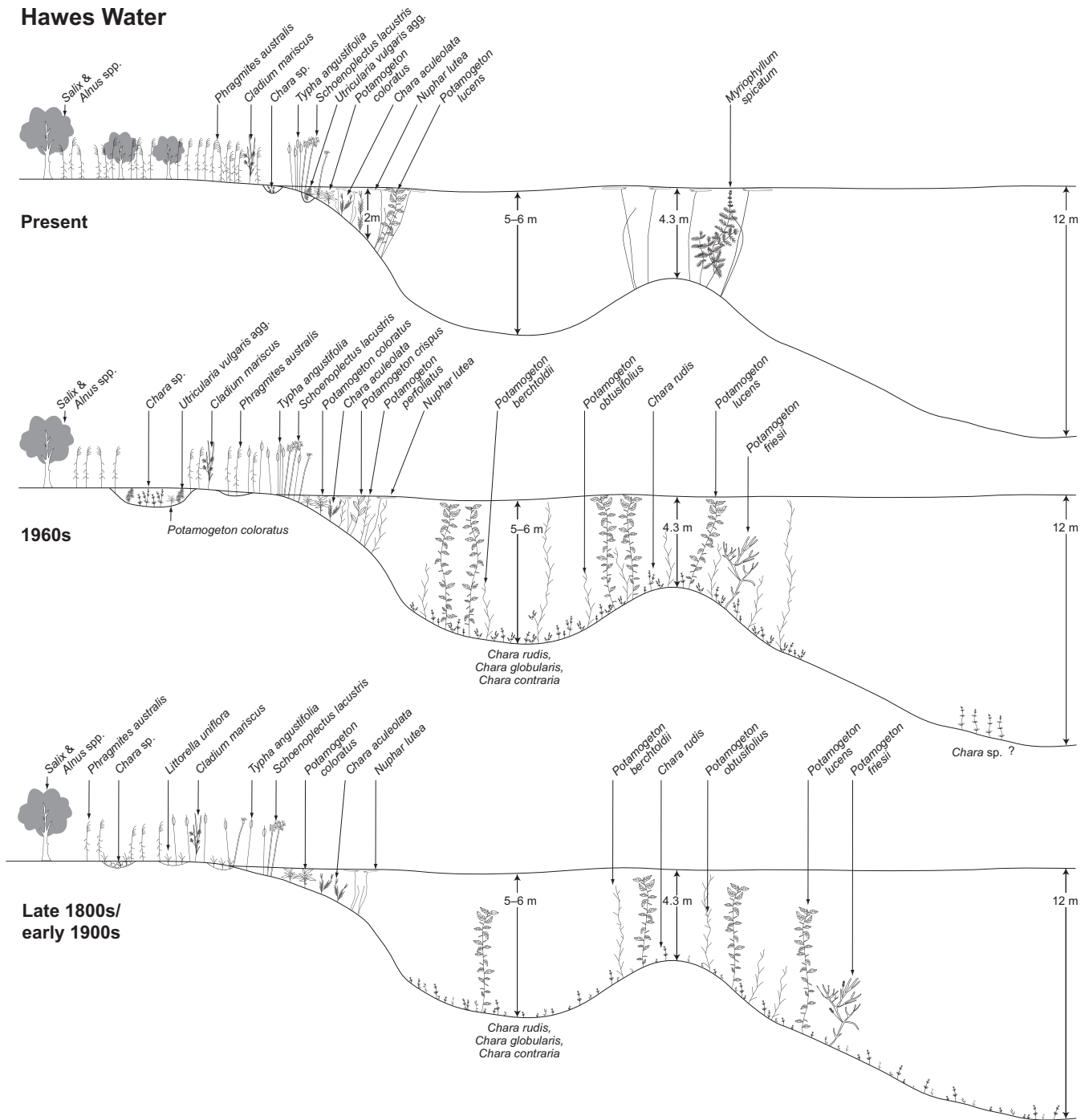


Fig. 8 Cross-sections of macrophyte community composition, showing the currently dominant community and historical communities based on available macrofossil and archival data.

concurrency between the two and making it difficult to disentangle individual effects. Further, a change in water source from exclusively ground water to ground and surface water, as in Hawes Water, changes the relative and absolute lake P and N loads, given the predominance of N in ground water and P in surface waters.

In Hawes Water, the clearest evidence in the palaeolimnological record for point change (as opposed to gradual and continuous) driven by water-level reduction was in the shift from zone 1 to zone 2 when inlets and outlets were created, characterised by large ecological distances between samples. This change resulted in

reduced influx of wetland soil and-macrofossils to the lake (in the macrofossil record) with the expansion of littoral habitat and reduction of pigment degradation in the water column (in the pigment record) (Leavitt, 1993; Cuddington & Leavitt, 1999).

Following the creation of inlets and outlets, the pattern of change in the core record suggests a predominance of long-term change in the biological compositions driven by eutrophication despite a second event of water level lowering around the 1960s (R. Petley-Jones, pers. comm.). There are three factors that indicate this dominance of nutrient enrichment above zone 2. Firstly, the fossil assemblages did not return to the compositions coincident with the first occurrence of water-level change, suggestive of a changing baseline. Secondly, no change was evident in pigment preservation conditions such as might have indicated a discrete water-level change. Thirdly, independent evidence of increasing nutrient loads to the lake following this period included increasing (allochthonous) organic sedimentation following the 1970s (core HW1; J. Holmes, pers. comm.), high nutrient concentrations in the inflow, expansion of private sewage works and occasional slurry applications in the catchment (Goldsmith *et al.*, 2003). Renaturalisation combined with reed bed management at the downstream Leighton Moss nature reserve has also introduced large numbers of both migratory and non-migratory birds to the area, which may have contributed to nutrient loads at Hawes Water. However, their potential nutrient impact could not be evaluated with available data.

#### Biological evidence of eutrophication in Hawes Water

The 'baseline' conditions in the pre-1800s, prior to hydrological alteration, indicated high water clarity and low total production with littoral marl-precipitating *Chara hispida/Chara contraria* agg. meadows consistent with the descriptions of marl lake habitats (Duigan *et al.*, 2007; EC-DG ENV 2007). A mixture of shallow- and deep-water species included *Potamogeton perfoliatus*, *Potamogeton coloratus*, *Myriophyllum spicatum* and Nymphaeaceae (including *Nymphaea alba*). High dependence on littoral primary production was further indicated by abundant macrophyte-associated molluscs (Gregg & Rose, 1985; Lodge & Kelly, 1985), and the absence of planktonic taxa.

The most recent biological condition of Hawes Water reflects substantial eutrophication compared with the early core record, following established trajectories of progressing eutrophication, namely (i) replacement of charophytes with angiosperms (Blindow, 1992; van den

Berg *et al.*, 1998), seen as a decline in charophyte diversity and coverage; (ii) increases in primary production in the water column (Schindler, 1978; Vadeboncoeur *et al.*, 2003), seen as increases in limnetic chl *a* (E. H. Fisher, R. T. Jones, S. Barnes, S. F. Crowley & J. D. Marshall, unpubl. data; this study) and in fossil *Daphnia* spp. ephippia (Davidson *et al.*, 2011); (iii) increases in the proportion of eutrophic indicator taxa in the plankton (Reynolds *et al.*, 2002), seen as recent increases in the relative abundance of the diatoms *Fragilaria crotonensis*, *Asterionella formosa* and *Stephanodiscus medius* in sediment cores (Bennion, 2004) consistent with abundances of *Stephanodiscus* sp. in algal blooms (E. H. Fisher, R. T. Jones, S. Barnes, S. F. Crowley & J. D. Marshall, unpubl. data); and (iv) reduced water transparency accompanied by reductions in macrophyte colonisation depth (Middelboe & Markager, 1997), seen as the decrease in *Chara rudis* from 7 m (1982) to 4 m (1999) followed by its extinction from the lake.

#### Timescales of change in biological community structure and indications of state change

Scheffer & van Nes (2007) suggested that transitions from macrophyte-dominated clearwater states to turbid phytoplankton-dominated states may occur as a gradual process punctuated by more major shifts in community composition. In marl lakes, where charophytes may maintain a particularly strong inertia to external nutrient loading owing to their high biomass potential and hence ability to sequester nutrients, critical thresholds and periods of rapid ecological change may be expected (Scheffer & van Nes, 2007; Blindow *et al.*, 2014). Two points of subdecadal ecosystem change, interrupting an otherwise largely gradual, century-scale biotic succession, were identified in the historical record of Hawes Water, lending support to ideas of threshold responses.

In the beginning of the core record following early land management, a gradual transition towards pelagic production occurred for *c.* 100 years. The increase in pigments of cyanobacteria, diatoms and cryptophytes was sustained, accompanied by a stagewise succession in the macrofossil record from the predominance of benthic taxa (charophytes and molluscs) to that of plankton-feeding *Plumatella* spp., and later floating-leaved Nymphaeaceae indicating increasing competition for light. Stagewise species successions are also evident in the palaeolimnological records of other (initially) *Chara*-dominated lakes (Davidson *et al.*, 2005; Ayres *et al.*, 2008; Sayer *et al.*, 2010a,b), suggesting that ecosystem

change under varying nutrient loadings is at least initially a gradual process.

The first state-like shift in the macrofossil and pigment record, with substantial subdecadal changes in the latter, occurred in the 1960s when large and sudden increases in pigments of non-nitrogen-fixing cyanobacteria followed previous declines in potentially N<sub>2</sub>-fixing cyanobacteria, suggesting increased nitrogen availability (Barica, Kling & Gibson, 1980; Levine & Schindler, 1988; Donald *et al.*, 2013). The change in cyanobacterial community composition coincided with increases in organic sedimentation rate, Nymphaeaceae trichosclereid remains, and decreases in mollusc and fossil oospore abundance. These changes suggest a reduction in benthic light availability and production, and a shift to taller-growing macrophytes. This period corresponds with historical records of a coexistence of a diverse angiosperm and charophyte community and therefore an intermediate eutrophication stage in the lake.

The second punctuation in the biological composition of Hawes Water occurred in the most recent history. Within a 10-year period between the end of the 1990s and 2010, summer chl *a* maxima increased more than twofold from <10 µg L<sup>-1</sup> (E. H. Fisher, R. T. Jones, S. Barnes, S. F. Crowley & J. D. Marshall, unpubl. data) to 28 µg L<sup>-1</sup> in 2009 (this study). Simultaneously, a marked increase in *Daphnia* spp. occurred in the core records, while *Chara rudis* became extinct in the lake and charophytes disappeared from the HAWE3 coring site. These changes indicate severe reductions in water clarity and increases in plankton production which are ongoing.

The abrupt changes at the turn of the century may be seen as pre-empted in the long-term pigment record. Firstly, pigments of cyanobacteria, chlorophytes and cryptophytes in the HAWE3 record increased between the 1800s and early-mid-1900s, a pattern that has been identified with transitions from macrophyte to plankton dominance (McGowan *et al.*, 2005). Following the increase, a plateau and decrease in the total abundance of primary producer pigments occurred, a pattern linked with changes in the dominant photosynthetic habitat from the benthic to the pelagic zone (McGowan *et al.*, 2005). The changes in the pigment record (37 cm, mid-to late-1800s) predated those in the macrofossil record (c. 26 cm, early 1900s), suggesting that early primary producer changes pre-empted larger, and lagged, changes in ecosystem composition in Hawes Water. The differences in timing may be the result of the short lifespan, and high surface area-to-volume ratio of microphytes, which can respond to environmental conditions in very short time frames within a growing season. In

contrast, perennation, overwintering turion development, propagule banks and growth form plasticity, can introduce ecological lags on macrophyte community responses (May & Carvalho, 2010). Therefore, more subtle responses such as changes in seasonality (Sayer *et al.*, 2010a) and fertility (Stross, 1979; Bonis & Grillas, 2002) may provide evidence of impact prior to the much more conspicuous community shifts at higher levels of impact.

#### *Habitat marginalisation of key macrophyte taxa – reed encroachment and profundal light deterioration*

*Reed density and littoral habitat structure.* Early photos from Hawes Water in the latter 1800s–early 1900s reveal remarkably open lake margins and low reed density, with *Littorella uniflora* (Druce, 1911) in the shoreline and trichopterans indicative of coarse substrates. At this time, intermediate-depth charophytes such as *Chara rudis* and *C. globularis* occurred in ‘considerable quantity and much encrusted’, and the water was described as very clear (Davis, 1850). In contrast, increased sedimentation (this study), absence of coarse-substrate trichopterans and reed encroachment (Oldfield, 1960) symptomatic of eutrophication (Mäemets & Freiberg, 2004; Liira *et al.*, 2010) occurred in Hawes Water during the latter 1900s, when no further records of *L. uniflora* were made.

*Littorella uniflora* is a species frequently ascribed to softwater lake types and lakes where water levels frequently fluctuate (EC-DG ENV, 2007), but is importantly also characteristic of low-impact, oligotrophic marl lakes (Duigan *et al.*, 2007; Proctor, 2010), becoming absent with eutrophication (Sledge, 1936; Walker, 1955; Madgwick *et al.*, 2011). The occurrence of *L. uniflora* in marl lakes may specifically be conditional on coarse sediment, low siltation and low reed development (Pearsall, 1918; Jeffries, 2010; Proctor, 2010), indeed the species may persist in impacted sites that have retained coarse sediment in the littoral (Sayer *et al.*, 2012; see also Kowalewski *et al.*, 2013, for other isoetids). The sensitivity of *L. uniflora* to impact, particularly with regard to sediment characteristics, strongly suggests that siltation and reed development led to its extinction from Hawes Water.

Encroachment of Nymphaeaceae in the reedswamp has also occurred, with currently highly abundant *N. lutea* within the 1 m contour. In contrast, the Characeae in shallow water are becoming increasingly marginalised, with *C. contraria* and *C. virgata* only found in localised patches (<1% cover) in 2009 (extensive searches through the reedswamp were undertaken in 2010). It is therefore highly likely that further simplifications in the

marginal habitat will occur as eutrophication progresses, to the detriment of defining marl lake taxa whose niches are becoming increasingly small.

*Macrophyte community quality and sensitivity to eutrophication in intermediate-depth lakes.* Kettlehole lakes such as Hawes Water typically have a very low surface area-to-volume ratio and therefore a relatively low percentage of shallow littoral (<1–2 m) habitat. However, in oligotrophic marl lakes where light availability is high, the 'littoral' as defined by rooted macrophytes can extend to depths beyond 10 m (e.g. Spence *et al.*, 1984; Schwarz & Hawes, 1997; Pybus, Pybus & Ragneborn-Tough, 2003). Such marl lakes are sensitive to eutrophication-driven reductions in light availability owing to the disappearance of macrophyte beds from higher water depths (Genkai-Kato & Carpenter, 2005). For example, in Hawes Water, a 10-m colonisation depth would make 95% of the benthos littoral, compared with the current 60% (c. 5 m).

Unsurprisingly, it is particularly the macrophyte species of intermediate and high water depths (see, e.g., Spence, 1967, 1982) that have declined in Hawes Water, including the extinct *C. rudis*, *P. obtusifolius*, *P. perfoliatus* and *P. friesii* and the diminished *C. aculeolata*, *P. lucens* and *H. vulgaris*. The high macrophyte diversity ( $n = 15$  without emergent taxa) in Hawes Water is mostly due to species within the 2-m-depth contour, and the % cover of most species is low. Most charophytes in Hawes Water also occur within this contour despite a suggested 5-m-depth limit via light measurements (Middelboe & Markager, 1997), indicating that charophytes may be highly sensitive to ecological change following sustained decreases in light availability and Nymphaeaceae encroachment. Indeed, *N. lutea* covers a depth zone of c. 50 to 500 cm and has taken over the depth zones previously inhabited by Potamogetonaceae and Characeae.

The decline of charophyte populations in Hawes Water given its modest nutrient concentrations supports the idea of high sensitivity of charophytes to eutrophication. The very shallow Tåkern and Krankesjön (Sweden; Zmean < 1 m) undergo shifts between turbid *Potamogeton*-dominated states and clear *Chara*-dominated states at relatively low limnetic TP (c. 30  $\mu\text{g L}^{-1}$ ) (Hargeby *et al.*, 2007). Malham Tarn, U.K., currently with TP of 18  $\mu\text{g L}^{-1}$ , undergoes oscillations between charophyte and elodeid dominance and is occasionally turbid with phytoplankton (Wiik *et al.*, 2014). Also Hawes Water undergoes periods of low transparency during phytoplankton blooms (this study), with descriptions of the water 'very brown in colour and visibility was poor' during a diver survey in 1982 (M. Wade, pers. comm.).

However, idiosyncrasies also occur among marl lakes with respect to the persistence of charophyte-dominated states under varying limnetic nutrient concentrations. For example, lakes Lubinskie and Wigry in Poland both have poorly developed angiosperm communities and high biomasses of *Chara* spp. to depths of c. 4 m despite TP of 100  $\mu\text{g L}^{-1}$  and 40–220  $\mu\text{g L}^{-1}$ , respectively (Pełechaty, Pukacz & Pełechata, 2004; Pełechaty *et al.*, 2013).

However, it is important not to confuse high macrophyte biomass with high ecological quality despite the importance of the former in maintaining high water transparency (e.g. Siong & Asaeda, 2006; Rodrigo *et al.*, 2007). Indeed, high biomass of charophytes is an implicit response to eutrophication that follows from the theoretical framework of clear state stabilisation, owing to their efficient growth and nutrient uptake (Pełechaty *et al.*, 2013; Pukacz *et al.*, 2014) and also the capability of some species of tall elodeid-type elongation (Haycock & Hinton, 2010; Malham Tarn, pers. obs.). Seemingly high ecological quality in terms of charophyte density may be a distraction from change detected using a longer time perspective, such as changes in species composition and diversity (Krolikowska, 1997; this study) and maximum colonisation depth (Hilt *et al.*, 2010).

Oligotrophic marl lakes matching historical marl lake descriptions of 'white chalky bottom' (Fuller & Esq, 1741), 'pale pellucid green water', 'desperately encrusted', 'starved beds of *Chara*' and 'spindly stems of *Potamogeton perfoliatus*' (Praeger, 1906) are more likely to reflect the natural, more modest abundance of marl lake macrophytes in reference condition (Rich *et al.*, 1971).

In considering lake rehabilitation options, the return of charophytes to deeper water is likely to be a slow process unless light conditions are substantially improved. Sexual reproduction in charophytes is dependent on light availability (Stross, 1979; Bonis & Grillas, 2002), and high dependence on vegetative reproduction has been encountered in declining charophyte meadows in eutrophic waters (N. Stewart & J. Harris, pers. comm.). Without surviving vegetation, the low numbers of oospores in the recent sediment at the coring location in Hawes Water will deter the re-establishment of charophytes even if limnetic conditions were favourable (Schwarz, Hawes & Howard-Williams, 1999; van den Berg, Coops & Simons, 2001).

## Implications

Considering the relatively low surface water nutrient and chl *a* concentrations in Hawes Water currently, the magnitude of ecological change that has taken place



since the early 1800s and particularly over the last century has important consequences for previously held views on marl lake resistance to eutrophication pressure. Marl lakes are evidently biologically very sensitive to changes in nutrient loading, especially where water depth gives rise to large changes in macrophyte coverage with only small changes in light penetration. The combination of data sources provides evidence of a reduction in maximum colonisation depth in Hawes Water that has led to macrophytes effectively moving upslope, and decreased coverage of macrophyte beds. These changes have led to the loss of several important marl lake taxa such as *C. rudis*, and a change from the dominance of charophytes and Potamogetonaceae to floating-leaved macrophytes.

It is also important to note the considerable changes in the margins of the lake, shifting from open, light and diverse habitat in the beginning of the 1900s to the presently dense, silted and shaded reedswamp with limited occurrences of charophyte stands and extinction of *Littorella uniflora*. Therefore, the reduction in deep macrophyte habitat is not met with refugia in the shallows. If nutrient inputs are unmanaged, it is highly likely that Hawes Water will undergo further ecological degradation in the near future following the trajectory established over the latter half of the 20th century.

Prior to this study, Hawes Water was considered to be in good ecological status. However, historical and palaeolimnological investigations have shown an extent of degradation not immediately apparent from short-term, contemporary data, revealing the value of a long time perspective, and focus beyond limnetic nutrient concentrations, in assessing marl lake ecology. Similar ecological declines under relatively low nutrient concentrations have occurred in other marl lakes, while in others exceptionally high biomasses of charophytes have developed. If marl lakes as considered a habitat type of low macrophyte biomass, exceptionally clear water and white sediments, and open littoral habitats are to be preserved, it will become extremely important and urgent to prevent further degradation under increasing anthropogenic pressure.

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