ORIGINAL PAPER

Assessing aquatic macrophyte community change through the integration of palaeolimnological and historical data at Loch Leven, Scotland

Jorge Salgado · Carl Sayer · Laurence Carvalho · Thomas Davidson · Iain Gunn

Abstract Submerged macrophytes have a critical role in lake ecosystems affecting nutrient cycling, sediment stability, and community composition across multiple trophic levels. Consequently temporal changes in the composition of submerged plant populations can have profound ecological implications and key significance from the perspective of lake conservation. By focusing on macro-remains of aquatic macrophytes and extensive historical plant records spanning the last approximately 180 years, this study seeks to evaluate a combined historical-palaeolimnological approach for establishing pre-disturbance macrophytes communities in Loch Leven, Kinross, Scotland and to provide new information regarding temporal trends in its macrophyte vegetation as well as potential drivers of change. Some 81% of the species historically recorded for the core site (east side of St. Serf's Island) were found as macro-remains. *Potamogeton* taxa were underrepresented, whereas remains of *Elatine hexandra*, a small species never recorded historically were found. The core sequence showed good agreement with known floristic changes including an early (pre- ca. 1850) loss of *Isoetes lacustris* and *Lobelia dortmanna* and a more recent (post-1910) shift to dominance by *Potamogeton* and *Chara* taxa associated with eutrophic conditions. A clear pattern in the relationship between macrofossil principal component analysis (PCA) and loss on ignition suggested a key control of sediment conditions on macrophyte community structure. In particular the major macrophyte community change of the mid-nineteenth century was concurrent with a substantial increase in organic matter, likely linked to a historic lake lowering (early 1830s) which would have beached the former gravel-sand shoreline leading to a much siltier lake littoral. Although recent monitoring data show signs of ecological recovery our study illustrates that Loch Leven remains a long way from its reference state as a lake with characteristic soft-water macrophytes. To achieve a full recovery, sediment properties would need to change in addition to nutrient reduction. Consequently restoration strategies will need to compromise between the desirability of achieving the pre-disturbance state and what is feasible and practicable. Our study shows the clear potential role of a combined palaeolimnological-historical approach for informing lake management decisions.

J. Salgado (✉) · C. Sayer · T. Davidson
Environmental Change Research Centre, Department of Geography, University College London, Gower Street, London WC1E 6BT, UK
e-mail: jorge.salgado@ucl.ac.uk

L. Carvalho · I. Gunn
Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 OQB, UK

Introduction

Macrophytes play a critical role in lake ecosystems by affecting nutrient cycling, sediment stability, community composition, and food web interactions (Scheffer 1998). As a consequence, changes in the coverage and composition of plant populations in a lake can have profound ecological implications. As well as impacting upon the structure and functioning of lakes, such changes are also of key significance from the perspective of nature conservation. Macrophyte communities are central to conservation-based classifications of lakes (Palmer et al. 1992; Stelzer et al. 2005; Duigan et al. 2006) and to measures of ecological quality and 'reference condition' as defined by the EU Habitats Directive (European Commission 1999) and the Water Framework Directive (WFD) (European Parliament 2000), respectively. Given the conservation and ecological significance of submerged macrophytes much importance is placed, therefore, upon establishing historical community shifts in lakes and in understanding the key drivers of change. In terms of the WFD, ecological quality must be measured in relation to a reference condition, or baseline. For this reason, there is a clear need to validate methods for establishing pre-disturbance macrophyte communities, particularly in lowland regions where existing references sites are rare or absent.

Currently two approaches can be used to establish pre-disturbance communities and longer-term changes to macrophyte communities; historical plant records and palaeolimnological methods, both of which have their own intrinsic advantages and disadvantages (Sayer et al. 1999; Davidson et al. 2005). Historical records, which rarely extend beyond the mid-1800s and may post-date early changes, are often biased towards rare species and may also be influenced by variability in collecting and recording effort. Palaeolimnological reconstructions of past vegetation dynamics are derived from a range of plant macro-remains (seeds, leaves, spines and spores etc.) and micro-remains (pollen) in dated sediment cores (Birks 2001; Rasmussen and Anderson 2005; Davidson et al. 2005; Ayres et al. 2008; Sayer et al. in press). They have the advantage over historical records in providing a continuous record of change over a potentially much longer timescale (e.g. 10,000 years), but suffer from bias due to the differential production, transport and preservation of different types of remains from different species (Birks 1980; Zhao et al. 2006). Ideally, therefore, reconstructions of past plant communities should be based on both methods together. Comparisons of approaches have so far only been attempted for small lake basins (Davidson et al. 2005) where spatial variability of vegetation and their remains is less of an issue and good agreement between historical and palaeolimnological data has been demonstrated. Larger lakes, however, present a greater challenge as historical surveys have often focused on restricted areas within the basin (e.g. accessible bays), or surveys of particular species (e.g. dominant or easily identifiable taxa only). Similarly, in large lakes, there are greater uncertainties over the value of palaeo-records from a single core to represent whole-basin changes.

One such site where the value of combining approaches can be assessed is Loch Leven. This is a large, yet predominantly shallow lake in the Scottish lowlands, known to have undergone major nutrient enrichment over at least the last century (Bailey-Watts and Kirika 1999; Carvalho and Kirika 2003) with associated changes in macrophyte communities (Morgan 1970; Jupp et al. 1974; Carvalho et al. 2004). Despite considerable interest in its restoration, pre-disturbance plant communities are not well known in Loch Leven. Hence, by integrating historical plant records and macrofossil data, this study aims to (1) evaluate a combined approach for establishing pre-disturbance macrophyte communities in large lakes; (2) provide new information regarding temporal change in the submerged vegetation of the Loch; and (3) examine macrophyte responses to enrichment and other potential drivers of change.

Study site

Loch Leven (56°10′N, 3°30′W) is a lowland lake (107 m above sea level) close to the town of Kinross in Scotland (Fig. 1). The loch has a mean depth of 3.9 m, a maximum depth of 25.5 m, and a surface area of 13.3 km^2 (Smith 1974). It has two deep depressions (both having a depth of about 25 m), one to the southwest of St. Serf's Island, and the other to the north, but large areas of the loch are shallow with potential for submerged macrophyte colonisation (Fig. 1). The loch

Fig. 1 Bathymetry of Loch Leven showing location of the site for core LEVE 14
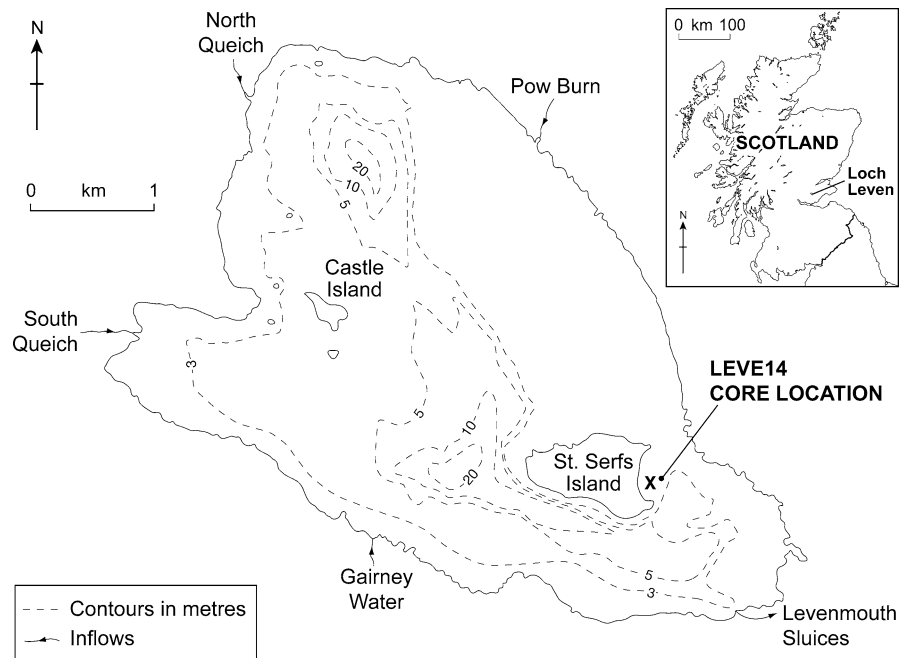
is alkaline (alkalinity 1.2 m equiv l^{-1}) and currently eutrophic with mean (2001–2005) annual average total phosphorus (TP) and chlorophyll *a* concentrations of 62 and 37 μg l^{-1}, respectively.

Loch history

Over the course of the Holocene water levels in Loch Leven have undergone a progressive decline of several metres due to natural erosion of its outflow channels (Haworth 1972). A more abrupt lowering occurred between 1830 and 1832 when, in order to reclaim more land for agriculture, water levels were reduced by about 1.4 m by cutting a new channel for the out-flowing River Leven. As a consequence of this event, about 5 km^2 or 30% of the lake area was lost from its previous area of about 18.3 km^2 (Kirby 1974). Although the outflow has not been modified since this date, regulation of the water level by sluice gates at the outflow does result in significant intra-annual water level fluctuations. Highest water levels are generally observed in winter and spring and lowest levels in late summer and autumn with a range of around 1 m over a single year (Smith 1974; unpublished data).

In addition to historical morphological changes, studies of diatom profiles in dated sediment cores

(Haworth 1972) suggest nutrient enrichment both prior to and following the lowering of lake level in the 1830s which allowed considerable agricultural expansion in close proximity to the Loch. Evidence for more severe eutrophication since the 1950s, linked to inputs of phosphorus-rich effluent from a nearby woollen mill and several sewage treatment works, comes from further studies of diatom micro-fossils (Haworth 1972; Bennion et al., unpublished data) and from water quality monitoring since the 1960s (Carvalho and Kirika 2003). Following catchment management measures in the 1970s, 1980s and 1990s, there has, however, been a significant declining trend observed in phosphorus concentrations (Ferguson et al. 2008). There have been recorded shifts in macrophyte communities over the past 100 years and more recently some signs of recovery with an increase in plant coloni-sation depth (Ferguson et al. 2008). Due to these relatively good historical records and its well established history of environmental changes, Loch Leven was chosen as a suitable site for comparing palaeolimnological and historical data for aquatic plants, for identifying reference macrophyte com-munities and for examining community response to enrichment and recovery.

Materials and methods

Coring

A sediment core (LEVE 14) was retrieved in May 2006 from the bay off the east of St. Serf's Island in Loch Leven (Fig. 1) using a wide-diameter (7.4 cm) Livingstone piston corer. The core was collected from a water depth of 220 cm. The core was 141 cm in length and was extruded in the field at 1-cm intervals.

Core chronology

Thirteen sediment samples from the top 60 cm of the core length were analysed for ^{210}Pb, ^{226}Ra, and ^{137}Cs isotopes using standard methods (Appleby and Old-field 1978; Appleby et al. 1986, 1992) at Liverpool University Environmental Radioactivity Laboratory (Fig. 2).

Lithostratigraphic and macrofossil analysis

Fifty-one samples from the core (2-cm intervals above 58 cm and 4-cm intervals below 58 cm) were utilised to estimate the percentage organic matter and gravi-metric $CaCO_3$ content of the sediment using standard loss-on-ignition (LOI) procedures (Dean 1974).

A total of 31 core samples (2-cm intervals above 40 cm and 5-cm intervals below 40 cm) of between 25 and 30 cm^3 were analysed for macrofossils with the volume of sediment used determined by water displacement (Birks 2001). Samples were washed

through sieves of 355 and 125 μm and analysed after Davidson et al. (2005). All macrofossil counts were standardised as numbers of fossils per 100 cm^3. For some fossils poor preservation and taxonomic limi-tations necessitated the use of aggregate categories. For example, *Potamogeton berchtoldii* Fieb., and *Potamogeton pusillus* L., are impossible to separate by leaf remains alone so were combined as *P. pusillus/P. berchtoldii*. Furthermore, *Potamogeton* seed fragments had to be combined as *Potamogeton* spp., while leaf remains of *Myriophyllum* spp. (probably including *Myriophyllum spicatum* L., and *Myriophyllum alterniflorum* DC.) and trichoschlereid cells from water-lilies (probably *Nymphea alba* L., the only historically recorded species) were grouped as *Myriophyllum* spp., and Nymphaeaceae respec-tively. *Chara* oospore identification also proved difficult and consequently different morphologies were classified as *Chara* 1, 2 and 3. These morpho-types were tentatively associated with *Chara globu-laris* Thuill., *Chara aspera* Dethard ex. Wild and *Chara vulgaris/contraria* respectively. The macro-fossil data was plotted stratigraphically (Fig. 3) using C2 version 1.5 (Juggins 2007).

Historical aquatic macrophyte data

Historical aquatic macrophyte records were collected from a range of literature sources. Pre-1910 records were derived mostly from Hooker (1821) and Balfour and Sadler (1863). Data from 1905 to 1910 were obtained from West (1910), the first comprehensive macrophyte survey of the Loch giving species

Fig. 2 Radiometric chronology of Loch Leven core LEVE 14 showing the CRS model ^{210}Pb dates together with 1986 and 1963 depths suggested by the ^{137}Cs stratigraphy
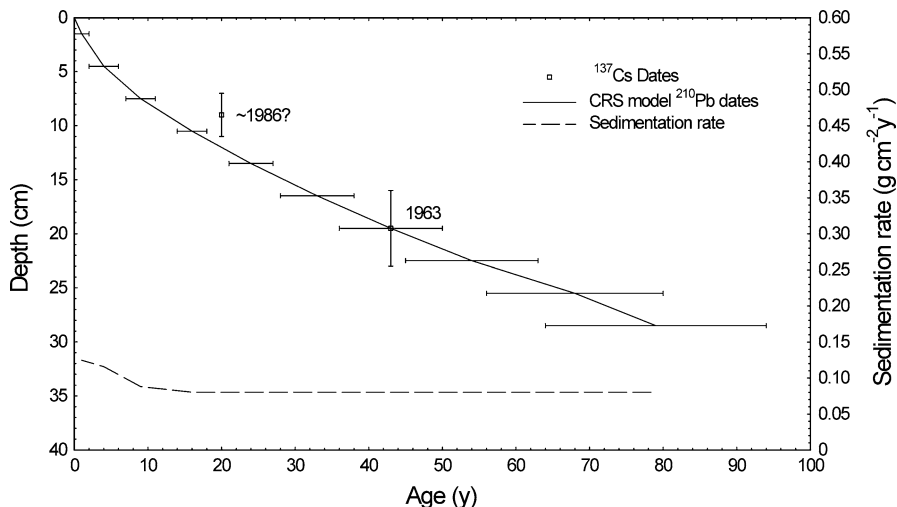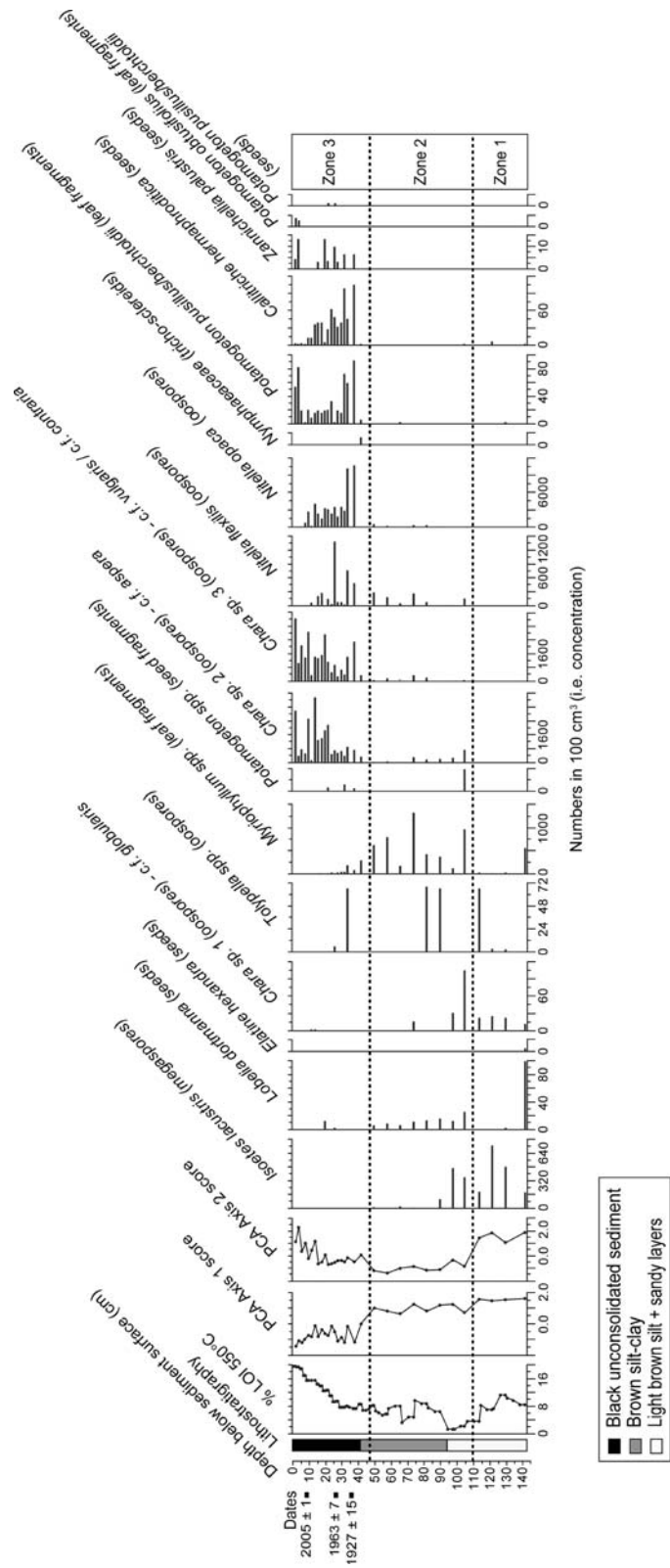
Fig. 3 Summary of the plant macrofossil concentration stratigraphy for LEVE 14. The 2006–1927 dates were ascribed by radiometric analysis. Zones 1, 2 and 3 correspond with major changes in macrophyte community composition as inferred by principal component analysis (PCA)

abundances and localities. Mid-century records were obtained from Young (1936), Spence (1964, 1967), Pollard (1966, unpublished) and more recent (post-1970) data were obtained from Jupp et al. (1974), Jupp and Spence (1977a, b), Bailey-Watts (1979), Robson (1986, 1990), Murphy and Milligan (1993), Griffin and Milligan (1999), Carvalho et al. (2004) and Carvalho (unpublished data). All macrophyte data were reduced to presence/absence to permit a comparison with the earliest surveys.

Data manipulation and analysis

Principal components analysis (PCA) was preformed using CANOCO 4.5 and CanoDraw for Windows version 4.1 (ter Braak and Šmilauer 2003) to explore temporal patterns in the macrofossil data and to establish zone boundaries representing points of major vegetation change, defined according to major changes in sample scores on PCA axes 1 and 2. To explore relationships between macrofossil shifts and changes in sediment composition, LOI data was used as a supplementary species variable in the macrofossil PCA. To facilitate comparisons between the macrofossil data and more sporadic local (St. Serf's Island region) historical macrophyte records, both were amalgamated into 5-year time periods, an interval likely appropriate to the temporal resolution of the core samples.

Results

Core chronology

^{210}Pb dates place 1963 (atomic weapons testing peak) at 19.5 cm, in good agreement with the ^{137}Cs record (Fig. 2). There was a small discrepancy between the ^{137}Cs inferred depth (7–11 cm) of 1986 (Chernobyl explosion peak) and its position inferred from the ^{210}Pb inventory (12 cm). However, since the ^{137}Cs peak was poorly defined between 7 and 11 cm a correction to the ^{210}Pb results using this ^{137}Cs date as a reference point was not thought appropriate. The ^{210}Pb chronology suggests relatively constant sedimentation from the late 1920s through to the late 1990s, with a mean accumulation rate during this period of 0.080 ± 0.018 g cm^{-2} yr^{-1} (0.29 cm yr^{-1}). During the past few years this appears to have significantly increased to a contemporary value of

0.12 g cm^{-2} yr^{-1} (1.1 cm yr^{-1}). If sediment accumulation rates in the late 1920s were extrapolated to the base of the sediment core, the base of the core would represent ca. 1492, but dates prior to ^{210}Pb dating are not known with certainty at the present time.

Lithostratigraphy

The core exhibited three relatively distinct lithostratigraphic layers (Fig. 3). The uppermost layer (0–39 cm) consisted of a black, unconsolidated sediment; the middle layer (40–95 cm) was composed of a brown silt–clay; the lowermost layer (96–141 cm) was a mixture of light brown silts with some sandy layers. LOI values were highest in the upper section with a steady increase evident from 30 to 0 cm (8–20%). Below this section LOI was more variable with very low values (<2%) associated with sandy layers, particularly between 86 and 104 cm.

Macrofossil data

Seventeen macrophyte species were represented by macro-remains in the core (Fig. 3). A PCA of the core data is given in Fig. 4 and plots of scores for PCA axes 1 and 2 are given in Fig. 3. Some 47.7% of the total variance in the species data is explained by λ_1 and λ_2 with eigenvalues of 0.320 and 0.157 respectively. Two major compositional changes were evident within the macrofossil data as indicated by shifts on both PCA axis 1 (at approximately 50 cm) and in PCA axis 2 (at approximately 110 cm), giving three zones. The first group (top right of Fig. 4a) corresponds closely to the deepest light brown silt/sand section and contains predominantly *Isoetes lacustris* L., *Chara* 1 (= *C. globularis*), *Tolypella* spp., and *Elatine hexandra* (Lapierre) DC (from 104 to 141 cm—Zone 1). The second zone (bottom right of Fig. 4a) is roughly equivalent to the brown silt/clay section and is characterised by *Lobelia dortmanna* L., *Chara* 2 (= *C. aspera*), *Chara* 3 (= *C. vulgaris/contraria*), *N. flexilis*, *N. opaca* and *Myriophyllum* spp. (from 49 to 104 cm—Zone 2). Finally, the third zone (left hand side of Fig. 4a) corresponds with the increasingly organic, less consolidated black sediments and includes the species *Zannichellia palustris* L., *Potamogeton* spp., *Callitriche hermaphroditica* L., and different charophyte species (from 41 to 0 cm—Zone 3). The PCA plot with LOI data used as a supplementary

Fig. 4 PCA of presence-
absence macrophyte
macrofossil data (**a**)
showing relationship
between macrophyte
species and LOI data (**b**).
Numbers given next to the
points are sediment sample
depths. Proportional circles
in **b** indicate the organic
matter content of the
sediment (*see scale*)
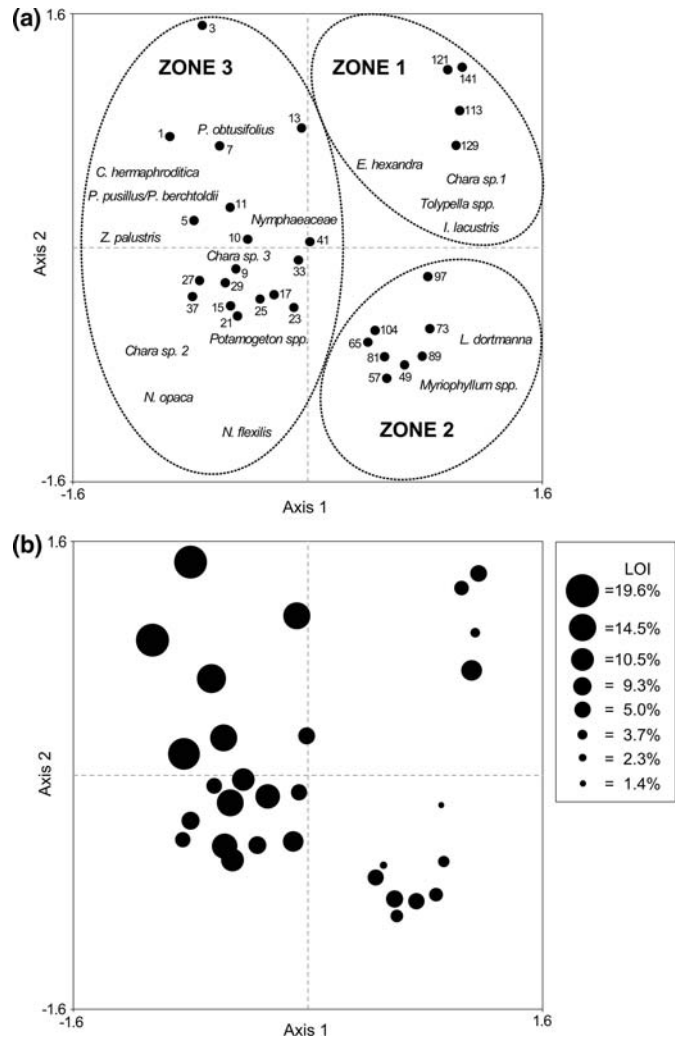
species variable, suggests a strong relationship between these major macrophyte compositional changes and the organic matter content of the sediment. When plotted graphically, there is the suggestion of a step change on PCA axis 1 with higher and lower scores above and below around 9% LOI respectively (Fig. 5).

Historical macrophyte data

A total of 35 submerged and 2 floating macrophyte species have been historically recorded for Loch Leven (Table 1). Pre-1900 records are scattered with only a few species described including *I. lacustris*, *Eleocharis acicularis* (L.) Roemer and Schultes, *Pilularia globulifera* L., *M. alterniflorum*, *M. spicatum*, *Subularia aquatica* L., *Utricularia vulgaris* L.,

L. dortmanna and *Nitella flexilis* L. Overall this community suggests an oligotrophic-mesotrophic lake. West (1910) recorded a total of 21 species of macrophyte including: *Littorella uniflora* (L.) Ashers, *E. acicularis*, *M. spicatum*, *M. alterniflorum*, and *C. hermaphroditica* with a species-rich (*n* = 7) *Potamogeton* assemblage and several species of charophyte including *C. aspera*, *C. globularis*, *Chara vulgaris/contraria* agg., *Nitella opaca* Agardh., and *Tolypella glomerata/nidifica* agg. None of the typical oligotrophic, soft water taxa *P. globulifera*, *S. aquatica* and *L. dortmanna* were recorded in this or any subsequent survey suggesting a profound influence of eutrophication upon the macrophyte community from at least this time onwards. Between 1910 and 1966 historical records
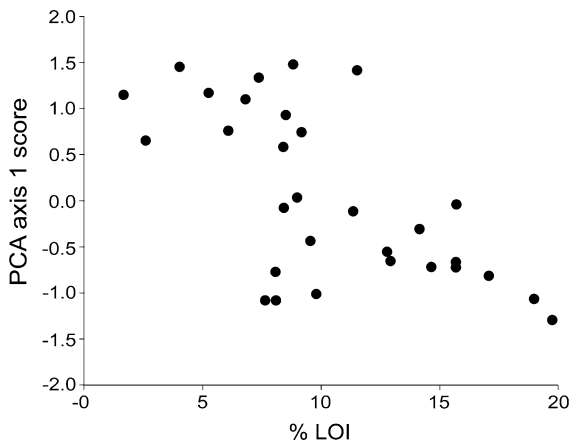
Fig. 5 Relationship between macrophyte macrofossil PCA axis 1 scores and organic matter content of the sediment. A marked shift on PCA axis 1 is observed at approximately 9% LOI. This step change in sediment-plant relations could correspond with the dramatic water lowering of the 1830s

are scant with a general absence of good surveys. However, by the mid-1960s, very detailed surveys of the macrophyte community resumed (Pollard unpublished data; Jupp et al. 1974), with the data suggesting a shift to a more eutrophic community with absence of many formerly recorded species including a number of broad-leaved *Potamogeton* taxa (*Potamogeton gramineus* L., *Potamogeton lucens* L., *Potamogeton praelongus* Wulfen, *Potamogeton x angustifolius* W. D. J. Koch ex. Roth), *Nymphaea alba* L., *M. spicatum,* and *T. glomerata/nidifica*. Four new species were recorded for the

Loch during this period: *Potamogeton pectinatus* L., *Potamogeton crispus* L., *Z. palustris* and *Ceratophyllum demersum* L., all of which are typical of highly eutrophic waters (Duigan et al. 2006). Additionally the nuisance algae *Cladophora* spp., and *Enteromorpha intestinalis* L. were recorded, with the former abundant in the 1970s (Jupp et al. 1974). The dominant taxa had also shifted to *P. filiformis*, *P. pectinatus* and *Z. palustris*, although *C. aspera* remained a co-dominant, whereas *Elodea canadensis* Michx., had declined. More recent surveys (Robson 1986, 1990; Murphy and Milligan 1993; Griffin and Milligan 1999; Carvalho et al. 2004; Carvalho unpublished data) show some signs of macrophyte recovery with an increase in plant colonisation depth (from 1.5 m in 1974 to 4.5 m in 2006) and a decline in the abundance of nuisance algae (Carvalho unpublished data). The dominant plant taxa have altered since the 1980s with a decline in *C. aspera* and *P. filiformis* and (re)appearance or increases of *C. vulgaris/contraria*, *T. glomerata/T. nidifica* and *P. pectinatus*.

Discussion

Comparing macrofossil and historical macrophyte data

Despite the inevitable errors associated with dating the sediments, when comparing the historical and

Table 1 Historically-recorded submerged and floating-leaved macrophytes in Loch Leven at various dates since 1821

* Species historically recorded close to St. Serf's Island (LEVE 14 core site)
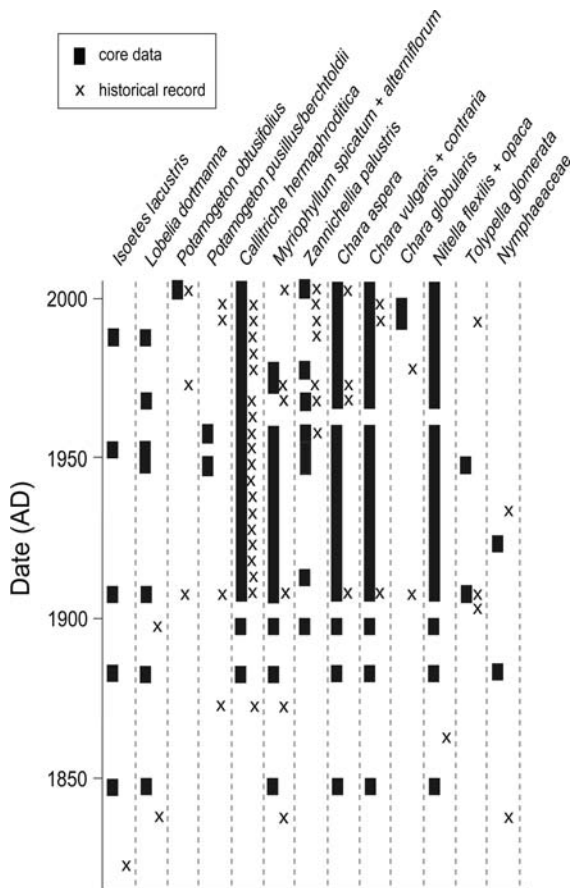
Fig. 6 Comparison of historical and macrofossil records on the basis of their presence absence. To facilitate comparisons between records, the data were amalgamated into 5 year time periods. The macrofossil record is based on LEVE 14; Comparisons before 1900s are tentative as dates prior to ^{210}Pb dating are not known with certainty at the present time. X historical records; *black box* macrofossil record

spp., could be the result of low seed production along with a poor preservation and/or difficulties associated with the identification of vegetative material (Davidson et al. 2005; Zhao et al. 2006). Furthermore, an additional important factor at Loch Leven may be selective feeding on *Potamogeton* and its seeds by waterfowl. Both tufted duck (*Aythya fuligula* L.) and pochard (*Aythya farina* L.) are present in very large numbers (>1,000) at Loch Leven and are known to feed on *Potamogeton* fruits (Alison and Newton 1974) and even actively select pondweed seeds (Martin and Uhler 1939; Martin 1951; Cramp and Simmons 1980). Additionally, mute swans (*Cygnus olor* L.), which also consume submerged vegetation, are abundant at the loch (average 150) and frequently congregate off St. Serf's Island to feed. Further, as indicated by Martin (1951), *Potamogeton* fruits germinate preferentially with passage through the guts of wildfowl. It is possible therefore, that this selective herbivory may have reduced the sedimentary representation of *Potamogeton* by enhancing seed germination and/or dispersing the fruits to terrestrial habitats (e.g. duck roosting areas). The absence of *E. canadensis* sediment remains is more simply due to a lack of production of seeds in the UK and an apparent lack of preservation of their leaves (Davis 1985), while only terrestrial plants of *L. uniflora* flower and set seed, such that seeds may rarely reach deeper water (Nielsen et al. 1991).

The comparison also highlighted two taxa, *I. lacustris* and *L. dortmanna*, that showed sporadic occurrences throughout the core, but were only recorded historically prior to 1900 (Fig. 6). Whether the sediment remains fill in a more complete picture of the actual history of these two taxa at the site is debatable. Given the very comprehensive surveys of the loch in 1910 and from 1966 onwards, it is unlikely that they were present during these periods, particularly *L. dortmanna*, which has a very visible and characteristic flowering stalk that emerges above the water surface. Notwithstanding the possibility that they were genuinely missed in surveys of a large lake, it seems likely, as discussed below, that post-1900 occurrences represent some degree of re-working of older sediments by water level fluctuations and/or storm events.

In general terms, the two approaches (historical records and macrofossils) combine effectively to give a more complete picture of macrophyte community change over time than either method in isolation. The

macrofossil data there was a very close agreement between the two records, especially post-1900 (Fig. 6). Of the 35 submerged macrophyte species described in the historical record for the entire loch (Table 1) a total of 17 (49%) were present in the plant macrofossil record from core LEVE 14 (Table 1). However, of the 16 submerged taxa historically-recorded for the St. Serf's area, a total of 13 (81%) species left macro-remains suggesting a much better reflection of the local community. As observed in previous studies (Davis 1985; Davidson et al. 2005), despite a rich historical record, most *Potamogeton* spp., *E. canadensis* and *L. uniflora* left no remains. This poor species representation of *Potamogeton*

palaeolimnological records from a single core (Fig. 3) highlighted many of the key taxa abundant locally around St. Serf's at least since 1910 (*C. hermaphroditica*, *Myriophyllum* spp., *Chara* and *Nitella* spp.) and also represent known compositional changes in the loch. For example, key features of change shown in both the historical and macrofossil records include; a post-1970s decline of *Myriophyllum* (probably *M. alterniflorum*), the appearance of *C. hermaphroditica* around the 1920s and an increased prevalence of *Z. palustris* in the twentieth century (Fig. 3). Further, the macrofossils provide data on plant communities for historical periods when surveys were not undertaken, for instance zone 1 and between 1927 and 1965 in Loch Leven, thus giving a much more continuous record of aquatic vegetation change. Historical surveys added more species records (e.g. *E. canadensis* and *Potamogeton* spp.) and generally (although not always) provided higher taxonomic resolution (e.g. charophyte and *Myriophyllum* species), although the palaeolimnological record also afforded unique species information as *E. hexandra* was only recorded by macrofossils.

Loch Leven macrophyte history: a successional model

During the last century there has been a widespread and dramatic decline in the ecological integrity of European soft-water lakes with communities of submerged macrophytes severely affected (Roelofs 2002). This has been attributed to combinations of hydro-chemical changes (acidification, eutrophication and alkalinisation), hydrological disturbances and habitat destruction (Arts 2002; Sand-Jensen et al. 2008). Although the successional changes caused by acidification are quite well documented (Vöge 1988; Arts 1990, 2002), the compositional changes that result due to eutrophication are less well known. Arts (2002) and recently Sand-Jensen et al. (2008) have described the key changes in macrophyte species composition that occur as a soft water lake becomes more eutrophic. First, an increased supply of nutrients causes a temporary increase in soft water species richness. Second, a decline of isoetid species is accompanied by the appearance and/or expansion of more rapid growing elodeid species (e.g. *Myriophyllum* spp.). Finally, all soft water species disappear and faster growing elodeid species (e.g. *Potamogeton*

spp. and *Elodea* spp.), and nymphaeids become dominant. At Loch Leven our results indicate a similar successional trend, and clear patterns in the relationship between sediment colour, LOI and key macrofossil shifts suggest that, in addition to eutrophication, substrate was a key driver of change. In turn, sediment changes at the core site were likely partly the result of historic water-level changes, particularly the lake lowering of the early 1830s. It is possible then, to generate a 3-phase model of macrophyte development for Loch Leven (phases correspond to the 3 zones given in Fig. 3) with the novelty of including potential controlling factors such as basin morphology, water chemistry and hydrology (Fig. 7).

An oligotrophic-mesotrophic macrophyte assemblage (phase a)

This phase, as represented by zone 1 in the macrofossil record (Fig. 3), undoubtedly covers a period prior to the 1830s water level lowering and consequently Loch Leven would have been a larger and deeper water body than that of today (Morgan 1970; Haworth 1972). The macrofossils indicate a macrophyte community dominated by *I. lacustris*, and *L. dortmanna,* with the additional presence of *E. hexandra*, *Myriophyllum* spp., and *Chara* 1 (= *C. globularis*), an assemblage generally indicative of oligotrophic-mesotrophic conditions (Palmer et al. 1992; Murphy 2002). Undoubtedly other species were present including *L. uniflora*, which was recorded from 1910 to present (Table 1) and is almost always associated with *I. lacustris* in particular in Scottish Lochs (Spence 1967). During this period the sediment had a lower organic matter and a higher sand content as is typical of marginal areas in nutrient poor lakes in Northern Europe (Smolders et al. 2002). In these kinds of lakes erosion of lakeshore sediment results in a flush of finer sediments (i.e. silts, clays and organic matter) into the open water, whilst sands, gravels and bigger rocks tend to stay near the shoreline (Spence 1967). As a consequence, sediment texture becomes finer and richer in organic matter as water depth and distance from the shore increases. This process of elutriation is proportional to lake depth and area, being more pronounced in larger, deeper lakes (Mortimer 1941). It is likely that this process similarly affected the

Fig. 7 Inferred three-phase macrophyte community changes in Loch Leven with consideration of potential controlling factors including sediment characteristics and hydrological changes. *Bold* lettering highlights inferred dominant sediment types. **a** an oligotrophic–mesotrophic macrophyte assemblage, **b** a mesotrophic macrophyte assemblage, **c** a eutrophic macrophyte assemblage in a shallower lake
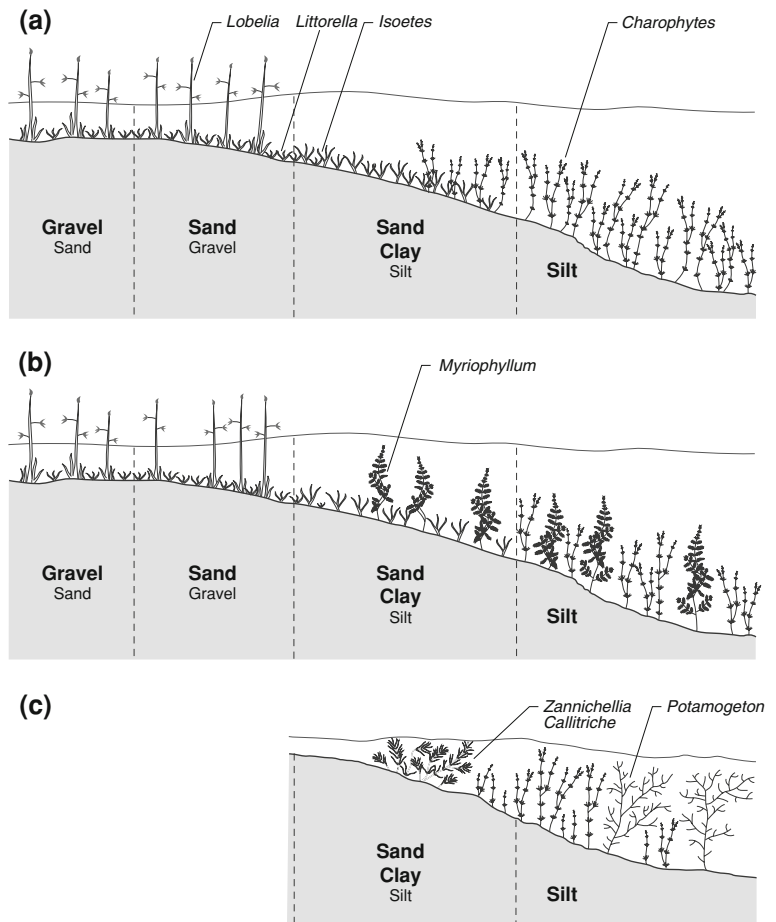
shorelines of Loch Leven, with terraces and different sediment textures forming around the edges of the lake basin. Fluctuating LOI (Fig. 3) during this phase is probably due to this process and to natural lake level fluctuations. Following this idea, we can hypothesise on a macrophyte distribution along the shore with *L. dortmanna* and *L. uniflora* abundant on the shallow sandy sediments of the terrace near the shore, followed by *I. lacustris* and subsequently charophyte species growing on the finer sediments in deeper water (Fig. 7a). Such a zonation has been described for other undisturbed large lakes with natural water level fluctuations (Spence 1964, 1982).

A mesotrophic macrophyte assemblage (phase b)

This phase (zone 2 in Fig. 3) sees the first appearance of several charophyte species (i.e. *Chara* 2 (= *C. aspera*),

Chara 3 (= *C. vulgaris/contraria*), *N. flexilis* and *N. opaca*) and a significant expansion of *Myriophyllum* (probably *M. alterniflorum*). Between 95 and 85 cm core depth, coincident with the transition to a browner sediment colour, there is also evidence for reduced abundances of *I. lacustris* and *Chara* 1 (= *C. globularis*). In combination, these community shifts suggest an early influence of nutrient-enrichment and promotion of a taller growing elodeid community as described by Arts (2002) and Sand-Jensen et al. (2008). This is consistent with previous diatom-based palaeolimnological studies at Loch Leven, which suggest increasing phosphorous inputs from around the early 1800s onwards (Haworth 1972; Bennion unpublished data). In this phase the macrophyte distribution along the shore would probably have been similar to phase a, but with a significant expansion of *Myriophyllum* spp., growing on the finer deeper sediments (Fig. 7b).

A eutrophic macrophyte assemblage in a shallower lake (phase c)

In this phase the macrofossil data (Fig. 3) and historical records (Table 1) suggest substantial shift (i.e. reduction of *I. lacustris, L. dortmanna* and *Myriophyllum* and increases in *Z. palustris* and *Potamogeton* spp.) to a macrophyte community more typical of highly eutrophic conditions. Concurrently, sediment colour shifts from brown to black and in contrast to phases (a) and (b) where LOI fluctuates due to the occurrence of sandy sections, there is a steady increase in LOI towards the sediment surface (Fig. 3). Allowing for some error in the dating model it seems likely that this change corresponds to the major loch lowering of the 1830s. This would have dropped loch levels below the former gravel-sandy shoreline thus eliminating the near-shore isoetid zone (Fig. 7c). In addition the transition to more unconsolidated and organic sediments could have affected community structure by influencing plant rooting (Schutten et al. 2005). For example, previous studies have concluded that *Isoetes* and *Myriophyllum* spp. need firm sediments to grow on (Smolders et al. 2002; Barko et al. 1986) with *I. lacustris* and *L. dortmanna* both preferring coarse-grained substrates (Spence 1967; Sand-Jensen et al. 2005). Additionally, in eutrophic systems, the isoetid shoot to root ratio tends to increase along with a decrease in shoot density (Smolders et al. 2002). Thus, the potential for uprooting is increased when sediments become more fluid and unconsolidated as may have occurred after ca. 1830.

The lake lowering would also have enhanced nutrient inputs to the loch due to agricultural cultivation close to the lake shore and evidence suggests that nutrient inputs increased further still during the twentieth century with symptoms of eutrophication (i.e. algal blooms) becoming well established from the 1960s onwards due to inputs of phosphorus-rich effluent (Morgan 1970; Bailey-Watts and Kirika 1999). These eutrophic conditions undoubtedly favoured colonization by the previously unrecorded species *E. canadensis* (historically-recorded post-1910) and increased dominance of *Z. palustris, C. hermaphroditica, Chara* spp., *Potamogeton* spp. and *Nitella* spp. (Misra 1938; Barko and Smart 1983; Barko et al. 1986). Such plants will have been favoured due to enhanced growths of phytoplankton which tends to favour elodeid species capable of elongating their growing parts towards the water surface (Sand-Jensen et al. 2008). Thus, it is likely that both eutrophication and changes in sediment structure contributed to a very different macrophyte distribution in the Loch (Fig. 7c).

Recovery and management implications

Considerable reductions in point sources of phosphorus from industrial and sewage effluents have been achieved at Loch Leven during the last 25 years. There have been signs of positive ecological change in the loch since this time, including lower algal abundances, increased water clarity, and a measured increase in macrophyte colonisation depth (Carvalho and Kirika 2003; Ferguson et al. 2008). This study, however, demonstrates that Loch Leven remains a long way from its pre-disturbance state as an oligotrophic-mesotrophic lake with characteristic soft-water macrophytes. Here, we illustrate, as elsewhere (Sand-Jensen et al. 2008), that multiple causes are responsible for macrophyte community changes over time. The long-term development of macrophyte vegetation at Loch Leven reflects the interaction of different environmental variables such as water level changes, sediment structure and water chemistry.

Catchment management focused on reducing phosphorus loadings appears to be having some success at Loch Leven in terms of ecological recovery. It is, however, unlikely to regains its pre-disturbance macrophyte community if only one aspect of environmental change (phosphorus loading) is tackled and other aspects remain unaltered (lake morphology, sediment structure, nitrate loadings, etc.). Sediment removal as a possible measure to re-establish soft water macrophyte communities is economically out of the question in large lakes and management targets will need some compromise between pre-disturbance (ca. pre-1850s) conditions and what is economically feasible. In the case of Loch Leven, a suitable macrophyte target may be the diverse community dominated by pondweeds and charophytes recorded at the start of the twentieth century (West 1910), rather than isoetids which would require significant in-lake and catchment management to achieve and sustain. Nevertheless, given recent improvements in light penetration, it might be interesting to attempt the restoration of extinct isoetid species (e.g. *I. lacustris, L. dortmanna* and *S. aquatica*) through transplantation trials in

limited areas where suitable substrates still exist. This detailed understanding of environmental change in Loch Leven, specifically the dynamics in macrophyte communities over the long-term, was only provided through the considerable combined power of historical and palaeo-macrophyte records.

References

Alison A, Newton I (1974) Waterfowl at Loch Leven, Kinross. Proc R Soc Edinb B 74:365–381

Anon (1836) New statistical account of Scotland. 9, Fife and Kinross, 1845. Blackwood, Edinburgh

Anon (1971) Loch Leven I.B.P. Project. A Rep Nat Conserv Edinb

Anon (1972) Loch Leven I.B.P. Project. A Rep Nat Conserv Edinb

Appleby PG, Oldfield F (1978) The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. Catena 5:1–8

Appleby PG, Nolan PJ, Gifford DW, Godfrey MJ, Oldfield F, Anderson NJ, Battarbee RW (1986) ^{210}Pb dating by low background gamma counting. Hydrobiologia 141:21–27

Appleby PG, Richardson N, Nolan PJ (1992) Self-absorption corrections for well-type germanium detectors. Nucl Instr Meth B 71:228–233

Arts GHP (1990) Deterioration of Atlantic soft water systems and their flora, a historical account. Thesis, Catholic University Nijmegen, 197 pp

Arts GHP (2002) Deterioration of Atlantic soft water macrophyte communities by acidification, eutrophication and alkalinisation. Aquat Bot 73:373–393

Ayres KR, Sayer CD, Skeate ER, Perrow MR (2008) Palaeolimnology as a tool to inform shallow lake management: an example from Upton Great Broad, Norfolk, UK. Biodivers Conserv 17:2153–2168

Bailey-Watts AE (1979) The monitoring of Loch Leven macrophytes. Plankton Ecology Project Group, Edinburgh

Bailey-Watts AE, Kirika A (1999) Poor water quality in Loch Leven (Scotland) in 1995, in spite of reduced phosphorus loadings since 1985: the influences of catchment

management and inter-annual weather variation. Hydrobiologia 403:135–151

Balfour IB (1894) An old list of stations of rarer plants, ascertained to grow around Inverkeithing and north of the Forth by A. Robertson. Trans Proc Bot Soc Edinb 20:84–90

Balfour JH, Sadler J (1863) Flora of Edinburgh. Black, Edinburgh

Barko JW, Smart RM (1983) Effects of organic matter additions to sediment on the growth of aquatic plants. J Ecol 71:161–175

Barko JW, Adams MS, Clesceri NL (1986) Environmental-factors and their consideration in the management of submersed aquatic vegetation—a review. J Aquat Plant Manag 24:1–10

Birks HH (1980) Plant macrofossils in quaternary lake sediments. Arch Hydrobiol 15:1–60

Birks HH (2001) Plant macrofossils. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments, vol 3: terrestrial, algal and siliceous indicators. Kluwer, Dordecht, pp 49–74

Carvalho L, Kirika A (2003) Changes in shallow lake functioning: response to climate change and nutrient reduction. Hydrobiologia 506:789–796

Carvalho L, Kirika A, Gunn I (2004) Long-term Patterns of change in physical, chemical and biological aspects of water quality at Loch Leven. Centre for Ecology and Hydrology, Edinburgh

Cramp S, Simmons KEL (1980) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Oxford University Press, Oxford

Davidson TA, Sayer CD, Bennion H, David C, Rose N, Wade MP (2005) A 250 year comparison of historical, macrofossil and pollen records of aquatic plants in a shallow lake. Freshw Biol 50:1671–1686

Davis FW (1985) Historical changes in submerged macrophyte communities of upper Chesapeake Bay. Ecology 66:981–993

Dean WE (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. J Sed Res 44:242–248

Duigan CA, Kovach WL, Palmer M (2006) Vegetation communities of British lakes: a revised classification scheme for conservation. Aquat Conserv 17:147–173

European Commission (1999) Interpretation manual of European Union Habitats. EUR 15, 2, Brussels

European Parliament (2000) Directive 2000/60/EC of the European Parliament, establishing a framework for community action in the field of water policy. Off J EU Comm 327:1–72

Ferguson CA, Carvalho L, Scott EM, Bowman AW, Kirika A (2008) Assessing ecological responses to environmental change using statistical models. J Appl Ecol 45:193–203

Griffin LR, Milligan AL (1999) Submerged macrophytes of Loch Leven, Kinross. Scottish Natural Heritage, Kinross

Haworth EY (1972) The recent diatom history of Loch Leven, Kinross. Freshw Biol 2:131–141

Hooker WJ (1821) Flora Scotica: or a description of Scottish plants. London

Juggins S (2007) C2 Version 1.5: Software for ecological and palaeoecological data analysis and visualisation [program]. University of Newcastle, Newcastle upon Tyne

Jupp BP, Spence DHN (1977a) Limitation on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. J Ecol 65:175–186

Jupp BP, Spence DHN (1977b) Limitation on macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments and waterfowl grazing. J Ecol 65:431–446

Jupp BP, Spence DHN, Britton RH (1974) The distribution and production of submerged macrophytes in Loch Leven, Kinross. Proc R Soc Edinb B 74:195–208

Kirby RP (1974) The morphological history of Loch Leven, Kinross. Proc R Soc Edinb B 74:57–67

Martin AC (1951) Identifying pondweed seeds eaten by ducks. J Wildlife Manage 15:253–258

Martin AC, Uhler FM (1939) Food of game ducks in the United States and Canada. Tech Bull US Dept Agri 634

Misra RD (1938) Edaphic factors in the distribution of aquatic plants in the English lakes. J Ecol 26:411–451

Morgan NC (1970) Changes in the fauna and flora of a nutrient enriched lake. Hydrobiologia 35:545–553

Mortimer CH (1941) The exchange of dissolved substances between mud and water in lakes. I and II. J Ecol 29:289–329

Murphy KJ (2002) Plant communities and plant diversity in softwater lakes of northern Europe. Aquat Bot 73:287–324

Murphy KJ, Milligan A (1993) Submerged macrophytes of Loch Leven, Kinross. Scottish Natural Heritage, Kinross

Nielsen SL, Gacin E, Sand-Jensen K (1991) Land plants of amphibious *Littorella uniflora* (L.) Aschers maintain utilization of CO_2 from the sediment. Oecologia 88:258–262

Palmer MA, Bell SL, Butterfield I (1992) A botanical classification of standing waters in Britain: applications for conservation and monitoring. Aquat Conserv: Mar Freshw Ecosyst 2:125–143

Rasmussen P, Anderson NJ (2005) Natural and anthropogenic forcing of aquatic macrophyte development in a shallow Danish lake during the last 7000 years. J Biogeogr 32:1993–2005

Robson TO (1986) Final report on the survey of the submerged macrophyte population of Loch Leven, Kinross. Nature Conservancy Council

Robson TO (1990) Final report on the distribution, species diversity and abundance of macrophytes in Loch Leven, Kinross. Nature Conservancy Council

Roelofs JGM (2002) Soft-water macrophytes and ecosystems: why are they so vulnerable to environmental changes? Introduction. Aquat Bot 73:285–286

Sand-Jensen K, Borum J, Binzer T (2005) Oxygen stress and reduced growth of *Lobelia dortmanna* in sandy lake sediments subject to organic enrichment. Freshw Biol 50:1034–1048

Sand-Jensen K, Pedersen NL, Thorsgaard I, Moeslund B, Borum J, Brodersen KP (2008) 100 years of vegetation decline and recovery in Lake Fure, Denmark. J Ecol 96:260–271

Sayer CD, Roberts N, Sadler J, David C, Wade PM (1999) Biodiversity changes in a shallow lake ecosystem: a multiproxy palaeolimnological analysis. J Biogeogr 26:97–114

Sayer CD, Burges A, Kan K, Davidson TA, Peglar S, Yang H, Rose N (in press) Long-term dynamics of submerge macrophytes and algae in a small and shallow eutrophic lake: implications for the stability of macrophyte dominance. Freshw Biol

Scheffer M (1998) Ecology of shallow lakes. Chapman and Hall, London

Schutten J, Dainty J, Davy AJ (2005) Root anchorage and its significance for submerged plants in shallow lakes. J Ecol 93:556–571

Smith IR (1974) Structure and Physical Environment of Loch-Leven, Scotland. Proc R Soc Edinb B 74:81–100

Smolders AJP, Lucassen E, Roelofs JGM (2002) The isoetid environment: biogeochemistry and threats. Aquat Bot 73:325–350

Spence DHN (1959) Studies on the vegetation of Shetland. 11. Reasons for the restriction of the exclusive pioneers to serpentine debris. J Ecol 47:641–649

Spence DHN (1964) The macrophytic vegetation of freshwater lochs, swamps and associated fens. In: Burnett JH (ed) The vegetation of Scotland. Oliver & Boyd, Edinburgh

Spence DHN (1967) Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J Ecol 55:147–170

Spence DHN (1982) The zonation of plants in freshwater lakes. Adv Ecol Res 2:37–125

Stelzer D, Schneider S, Melzer A (2005) Macrophyte-based assessment of lakes—a contribution to the implementation of the European Water Framework Directive in Germany. Int Rev Hydrobiol 90:223–237

ter Braak CJF, Šmilauer P (2003) CANOCO reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca

Vöge M (1988) Tauchuntersuchungen der submersen vegetation in skandinavischen seen unter berücksichtigung der isoetiden-vegetation. Limnologica 19:89–107

West G (1910) A further contribution to a comparative study of the dominant Phanerogamic and higher cryptogamic flora of aquatic habitats in Scottish lakes. Proc R Soc Edinb 30: Flora of Scottish Lakes

Young W (1936) A list of the flowering plants and ferns recorded from Fife and Kinross. (v. -c.85). Trans Proc Bot Soc Edinb 32:3–173

Zhao Y, Sayer CD, Birks HH, Hughes M, Peglar SM (2006) Spatial representation of aquatic vegetation by macrofossils and pollen in a small and shallow lake. J Paleolimnol 35:335–350