Long term changes in aquatic plant communities in English lowland lakes.

by

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I declare that this thesis is composed by me and that the work it embodies has been done by me and has not been included in another thesis.

Signed, ………………..…………….
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Abstract

This thesis examines the use of historical macrophyte records to assess long term changes in macrophyte communities in lakes and potential reasons for these changes. In particular it uses historical records to assess changes in macrophyte communities in the Norfolk Broads and West Midland Meres, two sets of lowland, eutrophic lakes in England. It provides a critical examination of the use of historical records, highlighting some of the constraints common to such data such as variations in recording effort, and bias in species recording and site selection. Having acknowledged these issues a robust way to interpret such data is developed using a "change index" based on species persistence over the last 200 years within individual lakes. Species with high change index values represented species which had persisted or increased within the studied lake districts and were characteristic of eutrophic lakes. Conversely species with low index scores, which had declined in both the broads and meres over the last 200 years, included species associated with less fertile conditions but also a selection of typically eutrophic species. Averaging of change index scores in present day survey data served to identify the historically least changed lakes and to rank lakes in order of degree of botanical change over the last century.

In order to better understand the processes behind the decline of some species and survival of others in the Norfolk Broads and West Midland Meres an analysis of the ecological basis of the change index was then performed. Functional groups determined from morphological and regenerative traits displayed significant differences in change index values in both groups of lakes, but declining taxa occurred across a wide range of plant growth forms. Non-hierarchical clustering of species based on their ecological preferences, obtained from published literature, resulted in groups with distinct change index values, indicating that changes in the status of species could be partly explained by these preferences. Of these, trophic preference was consistently the most important factor, with species of less fertile habitats consistently experiencing the greatest declines. However, some characteristically eutrophic species have also declined significantly, particularly in the broads. In these cases increasing loss of shallow water, low energy habitats in the broads, or loss of fluctuating water levels and less alkaline marginal habitat in the meres, appear to have been contributory factors.

In addition to the change index approach, historical records were also used at a site level to complement palaeolimnological analysis and investigate the change in macrophyte community composition and structure at Barton Broad, Norfolk. Sediment samples were extracted from the bottom of the broad and analysed for sub-fossil remains and pollen of macrophytes. The historical records and palaeolimnological analysis combined showed that early communities did not consist entirely of low growing, oligotrophic and mesotrophic species as previously thought, but in fact comprised a mixture of these and other more characteristically high nutrient species typified by a taller, or free-floating growth habit. As eutrophication progressed throughout the last century, the community was increasingly dominated by these latter growth forms. Diversity was maintained, however, since encroaching reedswamp generated a mosaic of low energy habitats which supported a range of species unable to withstand the hydraulic forces associated with more open water habitat. When the reedswamp disappeared in the 1950s, many of the dependent aquatic macrophytes also declined resulting in widespread macrophyte loss.

The thesis demonstrates not just the complexities of using historical records, but also ways in which these can be overcome. Such records can then permit useful observations and new insights into lake macrophyte community change and ecological integrity that can inform conservation and lake management, both on a site- and lake district level.

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CHAPTER 1 Introduction

1.1 Aquatic plant communities in lakes

Aquatic plants, or macrophytes as they are also termed, are a diverse group defined by their ecology (their growth in water) rather than their taxonomy. They consist largely of vascular plants, but also include bryophytes (liverworts and mosses), and a large group of macroalgae, the charophytes. Where the line is drawn between aquatic and terrestrial species, is not clear cut. Rather it is a gradual transition from largely submerged obligate aquatics, such as *Ceratophyllum demersum*, *Potamogeton pectinatus* and *Myriophyllum spicatum*, through floating-leaved species such as *Potamogeton natans* and *Nuphar lutea*, emergent species such as *Schoenoplectus lacustris*, *Typha latifolia* and *Phragmites australis* to littoral species associated with wet conditions but growing largely outside of the water, such as the marshland herbs, *Mentha aquatica*, *Veronica scutellata* and *Epilobium hirsutum.*

The nature and extent of the aquatic communities found in lakes varies enormously depending on a large suite of biotic and abiotic factors, such as fish community structure, zooplankton densities, bird grazing, water currents, alkalinity, colour, area, altitude and substrate (Sculthorpe, 1967; Spence, 1967; Spence and Chrystal, 1970; Hutchinson, 1975; Jupp and Spence, 1977a, b; Sand-Jensen and Sondergaard, 1979; Spence, 1982; Timms and Moss, 1984; Toivonen and Huttunen, 1995; Scheffer and

Jeppesen, 1998; Vestergaard and Sand-Jensen, 2000b; Heegaard *et al.*, 2001; Jones *et al.*, 2003; Schutten, 2005; Zambrano *et al.*, 2005). The most fundamental are arguably, however, nutrient status and lake bathymetry (Hutchinson, 1975; Moss, 1998; Natural England, 2008). Although macrophytes can occasionally grow at depths of 30 m or more, plants will generally be restricted to shallower depths by levels of light attenuation. Shallow lakes (< 3 m maximum depth) therefore offer more possibility for the colonisation of macrophytes than deep lakes where macrophytes are confined to the shallow margins. The depth to which plants can colonise also depends on the transparency of the water, which itself is often dependent on nutrient concentrations, as the more nutrient-rich a lake, the higher the density of phytoplankton supported by the open water, so the less transparent the water, and the more restricted the aquatic vegetation. The nutrient status of lakes is determined in part by catchment geology which affects nutrient chemistry and alkalinity. In Britain the waters of upland lakes are naturally low in solutes as they lie on hard igneous rock which does not weather easily. Conversely, lowland lakes often lie on mixed glacial drift, or on a variety of older, more eroded rocks, and therefore tend to be richer in solutes, including carbonate. As more productive systems with higher nutrient concentrations, lowland lakes are able to support a larger biomass of macrophytes compared to oligotrophic upland lakes. The species composition also varies considerably between these systems, and can be generalised as being characterised by plants with an isoetid growth form in oligotrophic lakes, and those with an elodeid growth form in eutrophic lakes. Isoetids are generally small in size and stature and are able to persist in low nutrient situations, where competition for light availability and CO_2 (which is used in photosynthesis) is less restricting, e.g. *Isoetes lacustris* (Arts and Leuven, 1988; Maberly and Madsen, 2002; Smolders *et al.*, 2002; Pedersen *et al.*, 2006). Elodeids tend to be larger, taller and faster-growing, better able to exploit high nutrient concentrations quickly by maximising their growth and therefore their potential for competing effectively for light in a crowded water column, e.g. *Elodea Canadensis* (Sand-Jensen and Sondergaard, 1979; Phillips, 1992; Vestergaard and Sand-Jensen, 2000a; Pedersen *et al.*, 2006). They are also able to use HCO_{3^-} as a carbon source, as concentrations of free CO_2 can be naturally very low in productive lakes (Maberly and Madsen, 2002). Plants in more productive lakes also have other effective ways of competing for CO_2 and light, such as *Nuphar lutea*, which has floating leaves thereby enabling it to reach atmospheric CO_2 via stomata on the upper leaf surface, as well as being best placed for light capture (Sculthorpe, 1967).

Although higher nutrient concentrations in lakes allow for a greater biomass of plants, at increasing levels of nutrient enrichment, usually from anthropogenic sources such as treated sewage or agricultural fertilisers, macrophytes start to disappear, becoming replaced by algae. These are reliant on high dissolved nutrient concentrations in the water as, unlike rooted macrophytes, the water column is their primary source of nutrients. Epiphytic algae grow on leaves of submerged macrophytes, severely reducing the amount of light reaching the leaf surface, whilst planktonic algae reduce light penetration beyond the water surface, leading to the loss of macrophytes and dominance of algae at higher nutrient concentrations (Phillips, 1992). In shallow lakes dominated by macrophytes the displacement by phytoplankton can occur at relatively high nutrient concentrations as macrophyte-dominated lakes are stabilised by various positive feedback mechanisms (Scheffer and Jeppesen, 1998). For instance, the macrophyte canopy offers refuge for zooplankton from predation by planktivorous fish, allowing large populations to build up which are able to feed on phytoplankton, maintaining water transparency (Schriver *et al.*, 1995; Jeppesen *et al.*, 1998). Larger macrophytes also provide physical structure within the lake, breaking up erosive forces, thus limiting phytoplankton re-suspension, and reducing the hydraulic shear stress on other rooted plants (Schutten, 2005). When plants do start to disappear, so does their structuring influence, and it may become very hard for them to re-establish. Various counter-factors, such as the change in fish communities, sediment structure and decline in zooplankton, also re-enforce the phytoplankton-dominated state (Scheffer *et al.*, 1993; Scheffer *et al.*, 2003). This phenomenon, encapsulated in the alternative stable states theory, has been widely invoked to explain the difficulty in restoring shallow lakes suffering from eutrophication, even after substantial reduction in nutrient loading (Madgwick, 1999; Phillips *et al.*, 2005).

1.2 Long term change in lake macrophyte communities

Prior to the 1970s there was little systematic national monitoring of macrophyte communities, or of the ecological quality of lakes in England. In more recent years, following concerns over the condition of water bodies in nationally protected areas (Sites of Special Scientific Interest; SSSIs) some of these water bodies have been subject to more detailed survey (Carvalho and Moss, 1995) and subsequently a standardised monitoring programme has been put in place, partly also driven by the data requirements of the Water Framework Directive (WFD) and the Habitats Directive (JNCC, 2005; Williams, 2006). The most recent assessment of the condition of open water in England's protected areas found that 45% were in an unfavourable condition, and amongst the habitats in the worst condition in England (Natural England, 2008; UKTAG, 2009). The main cause identified for this was eutrophication from both point sources (such as sewage outfalls) and diffuse sources (such as run-off of agricultural fertilisers). These are contributory factors to unfavourable condition in 70% and 40% respectively of the total water bodies in unfavourable condition. Lakes are particularly badly affected, and in a survey of over 100 SSSI lakes in England, Carvalho and Moss (1995) found that 84% showed symptoms of eutrophication. They also observed that the symptoms of deterioration were most frequently recorded in the aquatic plant communities.

Since the incorporation of the Water Framework Directive (WFD) into UK legislation in 2005 there has been a statutory requirement for monitoring the quality of all lakes above 50 ha in area, plus smaller water bodies located inside protected areas. The WFD requires that all water bodies in all EU member states be brought into "good ecological status" by 2015 (European Union, 2000). A scoping exercise carried out in preparation for implementation of the WFD found that 41% of water bodies in England and Wales were at risk of failing to meet good ecological status due to phosphorus enrichment (Natural England, 2008; UKTAG, 2009). In order to achieve good ecological status water bodies should not deviate significantly from "reference conditions". These are defined as the conditions expected in water bodies prior to significant anthropogenic impacts (European Union, 2000). Surveying and monitoring of various ecological quality indicators, including macrophytes, will be necessary for the WFD in order to judge how far water bodies deviate from their reference conditions, and to determine whether measures to control various pressures are effective (UKTAG, 2009).

The practical problem with using reference conditions as a baseline for the assessment of lakes is that information on past macrophyte communities is somewhat limited, and most systematic surveys only started after the pressures on these systems, and changes to their flora were already advanced (for example in the Norfolk Broads, George, 1992). Instead of formal survey data, other types of data need to be used in innovative ways to define the composition of macrophytes in reference condition lakes and thus give a clear and unbiased impression of macrophyte community change.

1.3 Palaeolimnology

Palaeolimnology is an established field of research which concerns itself with the study of lake sediments to answer questions about catchment and lake ecosystem histories. By collecting and examining multiple layers of sediment from cores taken from lakes, researchers are able to view a historic record which is both long term and highly resolved. Palaeolimnological techniques can be used to investigate not only physical and chemical characteristics of lakes, but also biological elements, which may in turn provide information about the past chemical and physical environment. There are a whole range of animal and plant taxa that preserve well in lake sediments, and are therefore of use in palaeolimnology, such as diatoms, cladocera, ostracods, molluscs, chironomids, beetles and aquatic mites. Also included are a wide range of macrophyte taxa, which are represented in sediments as plant “macrofossils”. These include any remains of plants that preserve well and are possible to identify under a low powered light microscope, such as seeds, leaf spines, leaf tips and more resistant fragments of leaf or stem (Figure 1.1). In addition to these, macrophyte pollen is often also preserved, although high power light microscopy is required for identification. In Britain there have been a few studies which have successfully investigated past macrophyte communities and macrophyte community change using macrofossils (Sayer *et al.*, 2006; Zhao *et al.*, 2006; Ayres *et al.*, 2008) or a combination of macrofossils with pollen (Davidson *et al.*, 2005).

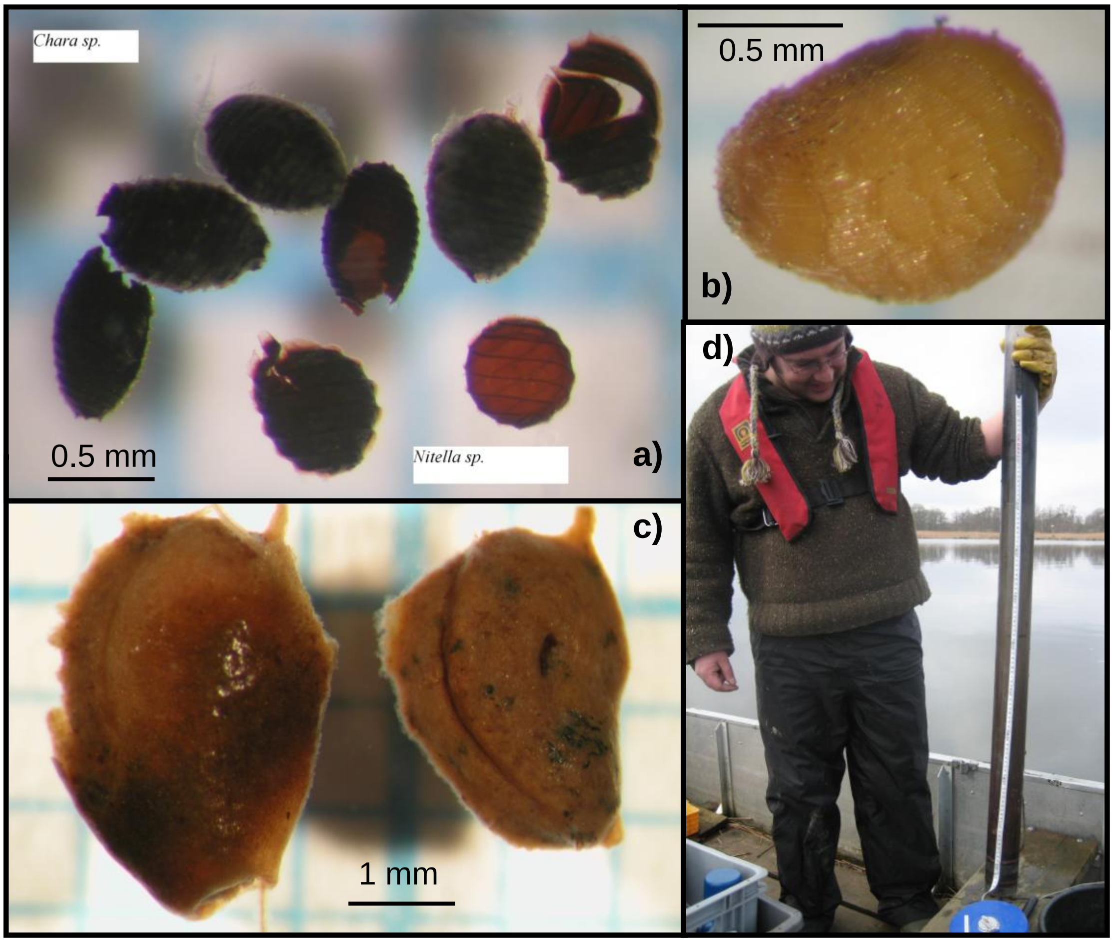

Figure 1.1 Examples of macrofossil remains under x40 light microscope: a) charophyte species oospores, b) *Ranunculus* subgenus *Batrachium* seed, c) *Potamogeton natans* seed, d) core collection on Barton Broad.

1.4 Historic records

Another source of data on long term change in macrophyte communities is historic records. In this thesis, this very general term is used for any recorded observations of macrophytes growing in a lake, besides those obtained through systematic surveys. These records derive from a huge variety of sources such as herbarium specimens (Figure 1.2), county floras, naturalists' notebooks, photographs, guidebooks, journal articles and excursion notes. Whilst this presents a rich data source, often dating back to the early 19th century, it is not without its difficulties as the data quality and quantity varies enormously between lakes, data sources and time periods. Data compilation and interpretation also presents a significant barrier to the use of this sort of data in long term studies of lake macrophytes. Despite the difficulties there are a number of studies from the UK (Jackson, 1978; Davidson *et al.*, 2005; Ayres *et al.*, 2008) and elsewhere which have utilised historic records to investigate long term change in lake macrophyte communities, for example in the Netherlands (Arts and Leuven, 1988; Arts *et al.*, 1990) and Denmark (Sand-Jensen *et al.*, 2000; Sand-Jensen *et al.*, 2008), as well as studies observing changes in macrophytes in rivers (Riis and Sand-Jensen, 2001; Baattrup-Pedersen *et al.*, 2008) and the wider countryside (Simons and Nat, 1996; Auderset Joye *et al.*, 2002; Pedersen *et al.*, 2006). An adequate supply of historic records is a prerequisite for using this approach. Therefore, this study has focussed on two lowland lake districts in England, the Norfolk Broads and West-Midland Meres. Historically these represented some of the botanically most diverse and best recorded groups of lakes in Britain.

Figure 1.2 Herbarium specimen of *Lobelia dortmanna* in the Natural History Museum, collected from Bomere Pool, Shropshire, in 1881.

1.5 England's lowland lake districts: the Norfolk Broads and West Midland Meres.

This thesis is concerned with two lowland lake districts in the UK, both situated in England: the West Midland Meres and the Norfolk Broads (Figure 1.3). Both have been subject to macrophyte community change over the last 200 years (George, 1992; Fisher *et al.*, 2009) and both have relatively large collections of early (pre-1910) botanical records associated with them.

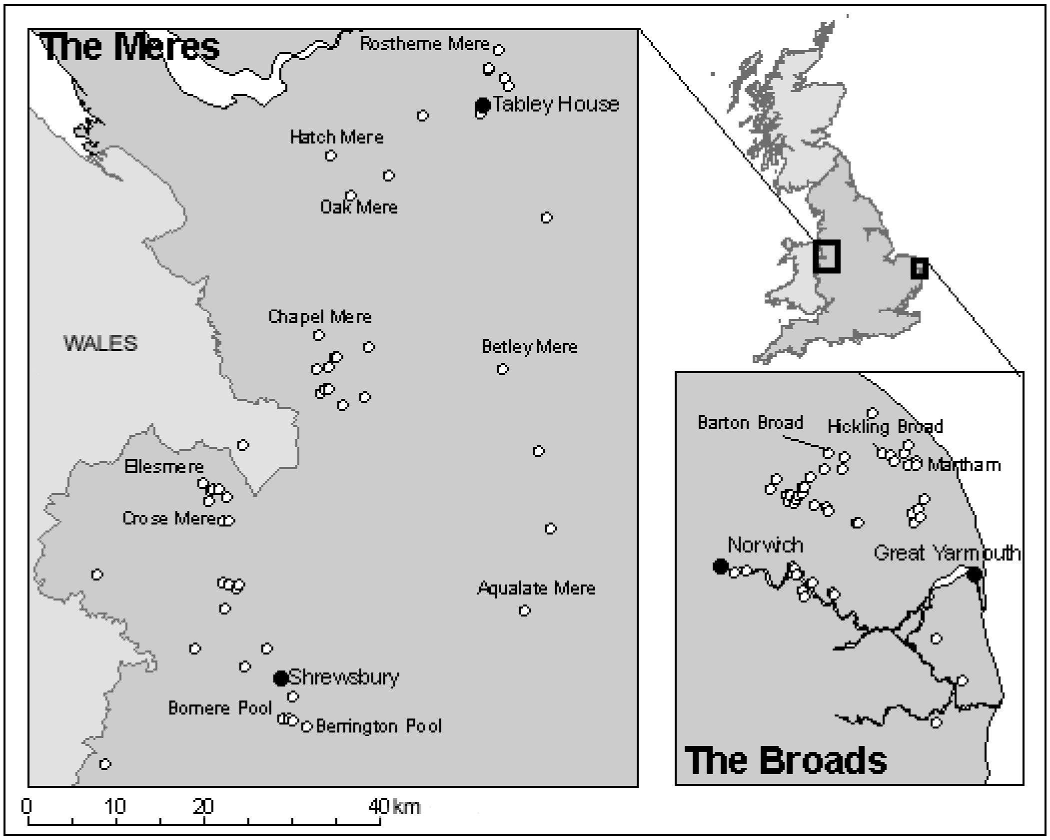

Figure 1.3 Map showing the location of the Norfolk Broads and West Midland Meres, England, UK.

1.5.1 The West Midland Meres

The West Midland Meres are a series of sixty or more small lakes situated in local groupings across the Cheshire/Shropshire/Staffordshire plain (Figure 1.3 and Figure 1.4). The meres were formed less than 18,000 years ago with the retreat of the late Devesian ice sheet. The area is characterised by its substrate, a permeable glacial drift deposited by the glaciers of North Wales and the Lake District during the Pleistocene ice advances. This substrate is predominantly sand and gravel made up of Carboniferous rock deposited by meltwater as the ice sheets retreated. Underlying this is a layer of impermeable boulder clay till laid when the ice sheet was advancing. The meres were formed in a number of ways, either as meltwater lakes, kettle holes, moraine-dammed hollows or post-glacial subsidence hollows (Reynolds, 1979). The majority of the meres were isolated from rivers and streams early in their development, so are dependent on groundwater for supply. The lake water is ion-rich and of wide ranging chemical composition, often including high concentrations of phosphorus and calcium carbonate (Gorham, 1957). The surrounding land is used primarily for agriculture, including dairy and arable farming. The area is currently largely rural but there are a number of small- to moderate-sized towns in the district including Shrewsbury, Chester, Market Drayton, Wem, Stafford, Sandbach, Middlewich, Nantwich, Wellington and Crewe.

The meres have long been heralded as Britain’s naturally eutrophic lakes (Reynolds and Sinker, 1976; McGowan and Britton, 1999) and blue-green algal blooms have been reported since at least the nineteenth century (Phillips, 1884) and probably occurred for centuries before then. Many of the meres contain phosphorus at the level of several hundreds of micrograms per litre, exceeding the levels expected of lowland lakes contaminated by treated sewage effluent (Moss *et al.*, 1995). This feature of the meres was originally attributed to apatite in the drift, through which the groundwater supplying the lakes percolates (Reynolds, 1979). The concentrations of phosphorus in the groundwater supplying Whitemere are, however, much lower than in the lake water. The high levels of phosphorus are now thought to be due to its release from the anaerobic sediments in summer, its recycling to the sediment in winter and limited export of phosphorus due to the small outflow of water (Kilinc and Moss, 2002). Whether the historic productivity and high phosphorus levels are natural (McGowan and Britton, 1999; Kilinc and Moss, 2002), with high initial loads of nutrients coming from freshly weathered glacial deposits, or cultural (Anderson, 1995), with low level anthropogenic eutrophication occurring over a long time period, is uncertain.

The meres vary in depth and bathymetry. About a third are shallow (i.e. less than 3 m deep), but most are quite deep with the average maximum depth being around 8.5 m. They are, however generally small in area for their depth, ranging from about 3 to 75 ha., with a median area of about 16.5 ha. This means there is often a high littoral to open water area ratio, offering potential for macrophyte colonisation. Despite this, the extent of the macrophytic vegetation is quite limited, possibly due to shading caused by the abundant phytoplankton or well wooded margins. Whilst some of the less eutrophic meres such as Bomere and Oak Mere have extensive macrophyte assemblages that include more typically oligotrophic species, such as *Luronium natans, Elatine hexandra* and *Littorella uniflora*, the majority support a low diversity and abundance of macrophytes. Indeed, many have next to no macrophytes at all, or, where a few species persist, these tend to be those associated with highly eutrophic conditions, such as *Zannichellia palustris, Elodea canadensis* or *Nuphar lutea* (Sinker *et al.*, 1985; Moss *et al.*, 1993).

Historical records indicate that species of more oligotrophic conditions have been lost from many of the meres, including *Isoetes lacustris* from Bomere and Ellesmere, *Luronium natans* from Whitemere and Ellesmere, *Potamogeton alpinus* from Bomere and Hatch Mere, and *Potamogeton gramineus* from Berrington Pool and Hatch Mere, to name just a few. Whilst many of the meres have been eutrophic for a long period of time, there is evidence that nutrient concentrations have increased still further over the last 100 years due to intensification of agriculture (Fisher *et al.*, 2009), which may explain some of these losses. Some meres, such as Berrington Pool, Aqualate Mere and Crose Mere, have marginal reedswamp vegetation, comprising *Typha latifolia*, *Typha angustifolia*, *Phragmites australis* and occasionally *Schoenoplectus lacustris*. Again this is limited in its distribution and extent, possibly for a combination of reasons that include steeply shelving lake margins, wind erosion, poaching by livestock and shading by bank side trees (Sinker *et al.*, 1985; Moss *et al.*, 1993).

Figure 1.4 Examples of West Midland Meres: a) Fenemere in Shropshire, b) Bomere Pool in Shropshire, and c) *Persicaria amphibia* growing in the Mere at Mere, Cheshire.

1.5.2 The Norfolk Broads

The Norfolk Broads are a series of about 50 shallow lakes linked with four rivers, close to the East Anglian coast (Figure 1.3 and Figure 1.5). They were dug out as peat pits before the fourteenth century (Lambert *et al.*, 1960) and have since flooded, creating a large wetland of lakes, rivers, floodplains and estuaries. It is thought that human alterations in the 18th and 19th century resulted in the loss of two of the three estuaries, through damming and lock building (George, 1992), leaving only Breydon Water, a large brackish lagoon into which all the rivers discharge. The broads can be divided into three groups (Moss, 1994). Firstly, there are those which are not attached to the river system, such as Upton Broad and Calthorpe Broad. Secondly, there are those broads connected to the main river system, which are normally fresh water, but occasionally become penetrated with sea water, when tidal surges sweep inland beyond the estuary. These are the large majority of the broads and include Barton Broad, Hoveton Broad, Cockshoot Broad and Malthouse Broad. The final group are those associated with the upper reaches of the river Thurne, and include Hickling Broad, Horsey Mere, Heigham Sound and Martham Broad. These waters are slightly brackish because seawater is able to percolate through the underlying permeable rock, the Norfolk Crag. This is exacerbated by the pumping of water from the land adjacent to the sea, into the River Thurne, to drain land for agriculture, thus drawing more sea water into the system (Moss, 1994). Other factors, such as whether boat traffic is permitted, and which river catchment they are positioned on, also influence the character of these lakes

The catchment area is fertile lowland consisting of glacial debris with underlying chalk in the west, and sandstone (Norfolk Crag) in the east. The areas of former river floodplain are underlain with marine clays and freshwater peat. Originally the rivers would have occupied their floodplains during winter, but now are largely confined to embanked channels built to combat flood risk, though some areas of fen and reedswamp remain. The rivers drain a large proportion of East Anglia, most of which is arable farmland. Gradients are very low, as is discharge, and the lower regions experience reverse flow during high tide in the summer months. The broads themselves are shallow (1-2.5 m) and have experienced shallowing and in some cases terrestrialisation through sediment build up and encroachment of swamp and terrestrial vegetation. The water is rich in calcium and magnesium, as well as dissolved salts from underlying rocks and glacier debris, sea spray and, to varying extents, intrusion of seawater.

Palaeolimnological studies (Moss, 1978; Moss, 1979, 1980, 1988; Sayer *et al.*, 2006; Ayres *et al.*, 2008) and historical records (Mason and Bryant, 1975; Jackson, 1978) show that the broads were once dominated by a rich aquatic macrophyte flora notably of charophytes which often formed a dense carpet throughout the shallow lake basins (Gurney, 1904; Nicholson, 1906). Nutrient levels had been increasing since the industrial revolution due to the rise in population and the intensification of agriculture. Treated sewage effluent was also increasingly entering some of the broads. Sometime during the last 100 years or so most of the broads lost their rich macrophyte flora, becoming dominated instead by phytoplankton. Despite attempts to reduce nutrient loading to the rivers and broads in the last 30 years, there was little evidence of macrophyte recovery, partly due to high internal loading of phosphorus from sedimentary sources (Moss, 2001). In fact, the amount of phosphorus which was re-suspended from the sediment often became substantially greater than that coming from the catchment, (Phillips & Jackson, 1990). The restoration of the broads, managed by the Broads Authority, often therefore involves removal of the phosphorus-rich surface sediments by suction pumping (Kelly, 2008).

Today, few of the broads have retained macrophytes and clear water. Upton Great Broad (which is land-locked), has not been subject to the same degree of eutrophication from sewage effluent as most of the broads, and the Martham Broads (North and South) are distant from the other broads on the River Thurne, so are less affected by phosphorus inputs from upstream. Upton Great Broad is dominated by *Najas marina*, a Red Data List species which, in the UK, is confined to the Norfolk Broads. A diverse selection of charophyte species dominate in Martham Broad, forming a dense carpet across the broad, interspersed with other species such as *Najas marina* and *Ranunculus circinatus*. Most of the other broads support only sparse stands of a few species more resilient to eutrophication, such as *Elodea canadensis*, *Potamogeton pectinatus* and *Ceratophyllum demersum*, and, on occasion, have been devoid of aquatic vegetation. Many species previously recorded in the broads, such as *Stratiotes aloides, Utricularia intermedia, Potamogeton alpinus, Potamogeton compressus* and *Littorella uniflora* have all but disappeared (Jackson, 1981b). Although there are areas of fen and reedswamp associated with some of the broads (e.g. Barton Broad and Hickling Broad) reedswamp, consisting primarily of *Phragmites australis, Typha angustifolia* and *Schoenoplectus lacustris,* was previously much more widespread and used to extend into the open water areas of many of the broads. This also disappeared over the last 100 years leaving larger areas of open water which is, at best, surrounded by a much reduced littoral growth of *Phragmites australis* and *Typha angustifolia* with little or no growth extending into the open water (Boorman and Fuller, 1981; Boar *et al.*, 1989).

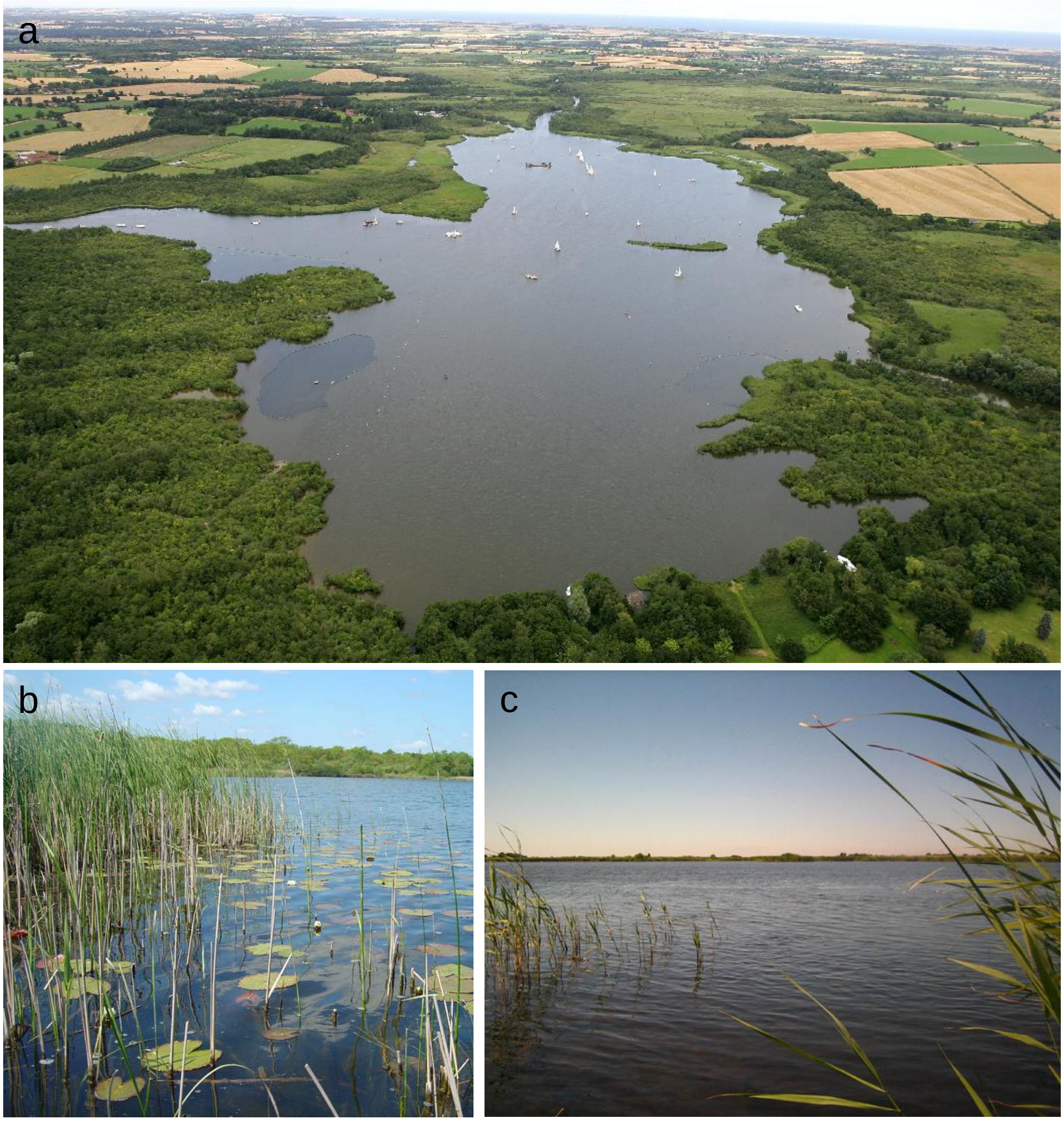

Figure 1.5 Examples of some of the Norfolk Broads: a) Barton Broad (© Mike Page), b) Upton Great Broad (© Ewan Shilland) and c) Martham South Broad.

1.6 Aims and objectives

This study focuses on two lake districts rich in historic records: the Norfolk Broads and West Midland Meres. The primary aim of the study was to compile as many historic macrophyte records for as many of the lakes within these systems as was feasible, and to explore the possibilities of using these data, in combination with macrofossil analysis, to investigate the change in macrophyte communities in these lakes over the last 150-200 years. The objectives of the study were:

- To explore the issues inherent in using historical records
- To investigate means of utilising historic records to inform lake management and lake classification
- To investigate general trends in macrophyte communities in these lake districts over the last 150 years
- To use historic records in combination with macrofossil analysis to make specific observations about a particular lake.

1.7 Outline of the thesis

A large amount of historical macrophyte data was compiled for this thesis, from a variety of sources. In combination with modern macrophyte survey data, compiled records represent a vast data source encompassing over 100 lakes and over 20,000 records. Whilst the potential benefits of this are apparent, there are a large number of issues and constraints inherent in historical data such as this, which need to be identified and tackled before the data are analysed (Chapter 2).

Given the nature of the data, and the constraints described in Chapter 2 a novel technique was developed to identify which species had changed most in their distribution within the Norfolk Broads and West Midland Meres. By developing a so called “change index” for each species, based on its persistence in lakes, those species which declined most in distribution within each lake district could be identified, despite the gaps and irregularities of the historical data (Chapter 3).

Chapter 4 explores the “change index” developed in Chapter 3, in light of published information on plant ecological preferences, in order to identify the factors driving species change over the last 100 years. Non-hierarchical clustering of the species based on their ecological traits was carried out to test whether this would divide them into statistically different mean change index groupings. Individual correlations were also carried out between the change index values and ecological trait values for each of the species in both the meres and broads to see which traits were most important in determining species persistence or decline in these systems.

Chapter 5 illustrates how historical data can be used at a site level, in combination with macrofossil studies, to shed light on the change in macrophyte communities and the causes for this. In this chapter the macrophyte history of Barton Broad spanning the last

200 years is investigated and put into context using a combination of macrofossil and pollen analysis, as well as historical records, descriptions and photographs.

Chapter 6 summarises the key findings of the thesis.

CHAPTER 2 The use of historical macrophyte data to assess community change in freshwater lakes: opportunities and constraints

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2.1 Abstract

This chapter critically examines the use of historical records for assessing macrophyte community change in lakes. It highlights some of the constraints common to such data, as illustrated by extensive long term datasets collected for two sets of lowland lakes in England, the Norfolk Broads and West-Midland Meres. The number of visits made to lakes was found to be highly variable throughout the time span of the datasets, as was the number of records made per visit, both of which were strongly related to the number of species recorded. This variation in recording effort can easily lead to false changes in species richness. Examples of bias in species recording and site selection are illustrated, particularly for earlier records, where recording was more species-focussed as opposed to the typical modern day approach of recording based on systematic surveys of entire water bodies. In conclusion, gathering information about, and understanding the nature and sources of historical datasets is vital in order to analyse them in an ecologically meaningful way, thus ensuring that they fulfil their potential to contribute to freshwater ecology and conservation.

2.2 Introduction

Historical biological records are important in a number of branches of ecology and biogeography, both for understanding the range and variability of community structure prior to modern anthropogenic impacts, and for establishing reference points that can serve as a benchmark against which to assess spatiotemporal trends and variability in individual water bodies. The establishment of a reference condition based on the ecological chronology of selected sites is of particular value to conservation, as it provides evidence-based restoration targets, information on how a site or species might respond to different forms of management in the future (Landres *et al.*, 1999; Swetnam *et al.*, 1999; Egan and Howell, 2001), and perhaps equally importantly, insight into the scale of changes that occur naturally within and between sites when the anthropogenic signal is weak or absent. Establishing reference conditions for water bodies is an important requirement of the EU Water Framework Directive (WFD), since ecological status, the basic currency of the WFD, is a measure of the degree of biological alteration from reference conditions (European Union, 2000). A number of methods are given in the WFD to define biological reference conditions, including establishing a network of high status sites to act as analogues for each water body type, predictive modelling and hindcasting. Among the hindcasting methods given, is the use of available historical data.

Interest in botany in the UK dates back to the 17th century and by the mid 19th century was a popular pastime. Many amateur and professional naturalists gathered wild plants enthusiastically, to augment their collections and swap with other collectors (Allen, 1986, 1987). These naturalists and collectors amassed many thousands of records between them of aquatic plants alone, from right across the UK. Despite the potential utility of historical lake macrophyte records for a range of purposes there are a limited number of studies which have made use of them (e. g. Jackson, 1978; Rintanen, 1996;

Simons and Nat, 1996; Sand-Jensen, 1997; Riis and Sand-Jensen, 1998; Sand-Jensen *et al.*, 2000; Riis and Sand-Jensen, 2001; Davidson *et al.*, 2005; Ayres *et al.*, 2008) and few have been employed specifically in defining reference conditions for the WFD (Blümel *et al.*, 2002; Nielsen *et al.*, 2003; Baattrup-Pedersen *et al.*, 2008). A possible explanation for the under exploitation of such records is that their use requires research of an interdisciplinary nature, involving not only the study of species and their ecology, but also of the history of naturalists and botanical recording that underlies records. Historic records are also, by their very nature, rarely quantitative, which renders them much less attractive for ecological analysis. They require critical scrutiny before they can be investigated for ecological trends, to ensure that any conclusions drawn relate to genuine ecological patterns rather than being an artefact of the bias often inherent in this sort of data. Nevertheless, this concern has not prevented their use in other fields, and there is an extensive literature on the analysis of historical records to map distributions or changes in, for example beetles (Desender and Turin, 1989), butterflies (van Swaay, 1990; Thomas and Abery, 1995) and vascular plants (McCollin *et al.*, 2000; Telfer *et al.*, 2002). There are also discussions of some of the problems inherent to this type of data in relation to botanical recording (Rich and Woodruff, 1992; Rich and Smith, 1996; Delisle *et al.*, 2003; Rich, 2006; Rich and Karran, 2006) and butterfly surveys (Dennis *et al.*, 1999).

With the current emphasis in conservation and management being on restoring sites back to a more sustainable and less impacted condition, and with developing interest in the long term responses of aquatic ecosystems to climate change (Mooij *et al.*, 2005;

Heino *et al.*, 2009), it is timely for aquatic ecologists to identify the hurdles to using historic macrophyte records and to find ways of overcoming these. In order to do this, there must be a strong understanding of the nature of historic records, the effect that this has on the qualities of datasets and the constraints imposed on analysis and interpretation. This paper considers some of these issues, drawing examples from long term macrophyte data collected for two English lake districts, the Norfolk Broads and West Midland Meres. In turn it seeks to demonstrate ways in which pitfalls in interpretation can be minimised so that the rich potential of the historical archive can be exploited more effectively in the fields of freshwater ecology and conservation.

2.3 Methods

2.3.1 Study area

The Norfolk Broads are a series of over 50 shallow, eutrophic, lowland lakes, associated with five major rivers, lying near the east coast of England, in Eastern Norfolk (Figure 1.3). They are water filled medieval peat diggings and vary in area from 1-140 hectares, with depths rarely exceeding 2 m. Once famous for clear waters and diverse communities of aquatic plants, they have since suffered significant eutrophication and have now lost many of their original macrophytes and some have become dominated by phytoplankton (George, 1992; Moss, 2001). The West Midland Meres are a series of mesotrophic or eutrophic lakes formed by the filling of pits and sinks in the glacial moraine deposited at the end of the last glacial period (Figure 1.3). Scattered across the English counties of Shropshire, Cheshire and Staffordshire, they range in area from <1-75 hectares, and are generally deep for their surface area, with depths ranging from <1-50 m (Reynolds, 1979). Although they are mostly groundwater fed, many are highly eutrophic with particularly high phosphorus concentrations thought to be due to phosphorus-saturated sediments and long water residence times (Reynolds and Davies, 2001; Moss *et al.*, 2005). Termed Britain's "naturally eutrophic" lakes, they have experienced some of the earliest recorded algal blooms (Reynolds, 1979; Anderson, 1995; McGowan and Britton, 1999). Nevertheless, there is strong evidence that eutrophication has intensified over the last century (Carvalho and Moss, 1995; Brooks *et al.*, 2001; Fisher *et al.*, 2009), including the loss of macrophyte species (Chapter 3).

2.3.2 The broads and meres dataset

The dataset utilised here is a compilation of macrophyte records from the lakes within the Norfolk Broads and the West Midland Meres. It spans two centuries, with records from 1798 to the present day. The records were collated from original sources and previous, published and unpublished compilations of historical records. Most of the meres records were compiled by Lockton on behalf of the Shropshire Botanical Society (www.shropsbotdata.org.uk) and many of those from the broads by Jackson (1978; 1981a; 1981b). These were complemented and verified by checking original sources, such as antiquarian books (e.g. Christopher Davies, 1882, 1883; Emerson, 1893), county floras (e.g. Leighton, 1841; Trimmer, 1866), articles in journals (e.g. *Transactions of the Norfolk and Norwich Naturalists' Society, Journal of Botany*), records collected from herbarium specimens at the Natural History Museum, London, and the Castle Museum, Norwich, and from the Botanical Society of the British Isles (BSBI) Vascular Plants database, accessed via the National Biodiversity Network gateway (data.nbn.org.uk). Modern surveys contributing macrophyte records include those carried out routinely since 1983 by the Broads Authority (Broad Authority unpublished data), and a series of surveys of the meres from 1978 onwards, carried out for the Nature Conservancy Council (now the Joint Nature Conservation Committee - JNCC), English Nature (now Natural England) and the Environment Agency (Wigginton, 1980, 1987; Moss *et al.*, 1993; Whild Associates, 2001, 2002, 2003 & 2005, Goldsmith *et al.*, in prep.). For the purposes of this study, macrophytes were defined as plants with Ellenberg F (moisture) values of 10 or above (Ellenberg *et al.*, 1991; Hill *et al.*, 2004, Chapter 3). Further details of the dataset are presented in Table 2.1.

Table 2.1 Details of the broads and meres macrophyte dataset

Area	**Year span**	**No. records**	**No. visits**	**No. lakes**	**No. species**
Broads	1805-2006	5151	1377	51	95
Meres	1798-2006	5202	1016	50	99
	Total:	10353	2393	101	120

2.3.3 Analysis

Linear regression was used to demonstrate the relationships between numbers of recorded species and various parameters of recording effort (e.g. number of visits).

Where relationships were logarithmic, data was log transformed ($\log_e X$) prior to entry into regression equations. All correlations reported are Pearson's correlation coefficient (r). For the purposes of this study, a visit was defined as a unique combination of recorder, lake and date attached to one or more macrophyte records. A record was defined as a unique combination of recorder, lake, date and species. All statistical analysis was performed using Minitab (Release 14).

Distribution of species and visits in the meres was visualised by plotting number of records against sites along the x-axis, ordered by distance from Shrewsbury, Shropshire and distance to Tabley House near Knutsford, Cheshire (distance to Shrewsbury/distance to Tabley House), the two places where the authors of the early Shropshire and Cheshire floras respectively, were based. Two fifty year time periods were plotted, 1830-1880 and 1950-2000, to capture the main recording activity of each era. The former captures the records published in the first floras of Shropshire and Cheshire (Leighton, 1841; Warren, 1899), and the latter captures major surveys in 1979-80, 1987 and 1991 carried out for the JNCC and Natural England (Wigginton, 1980, 1987; Moss *et al.*, 1993).

2.4 Results and Discussion

Before long term data sets containing historical records can be used to illustrate ecological trends (Chapter 4) they must be fully understood in terms of the data sources from which the records derive, the nature of the records and the habits and motives of recorders, so that any bias in the dataset can be recognised and overcome where possible. Major sources of error can be summarised as those associated with recording effort, record distribution, and selective recording of species. Examples of these are illustrated here using the broads and meres datasets and further problems encountered when collecting and analysing historical records are also discussed.

2.4.1 Recording effort

There is a large variation in recording effort throughout the period of the combined broads and meres dataset, with modern surveys tending to be both more frequent and more comprehensive than the generally more *ad hoc* historical records. There are many factors contributing towards recording effort, with the number of visits within a time period likely to be a significant one. Figure 2.1 a shows the increase in both number of recorded species and number of visits over the time span of the dataset. Indeed, the number of species recorded in the broads and meres within ten year periods is highly correlated with the number of visits in each period ($\log_e$ (no. of visits)) (Pearson's $r = 0.915$, $p < 0.0001$) (Figure 2.1 b). The number of visits fluctuated substantially throughout the recording period, with number of visits being low prior to 1880 and around the period of the two world wars (1910-1950). The lower numbers of species recorded in those periods reflects this reduced effort (Figure 2.1 a).

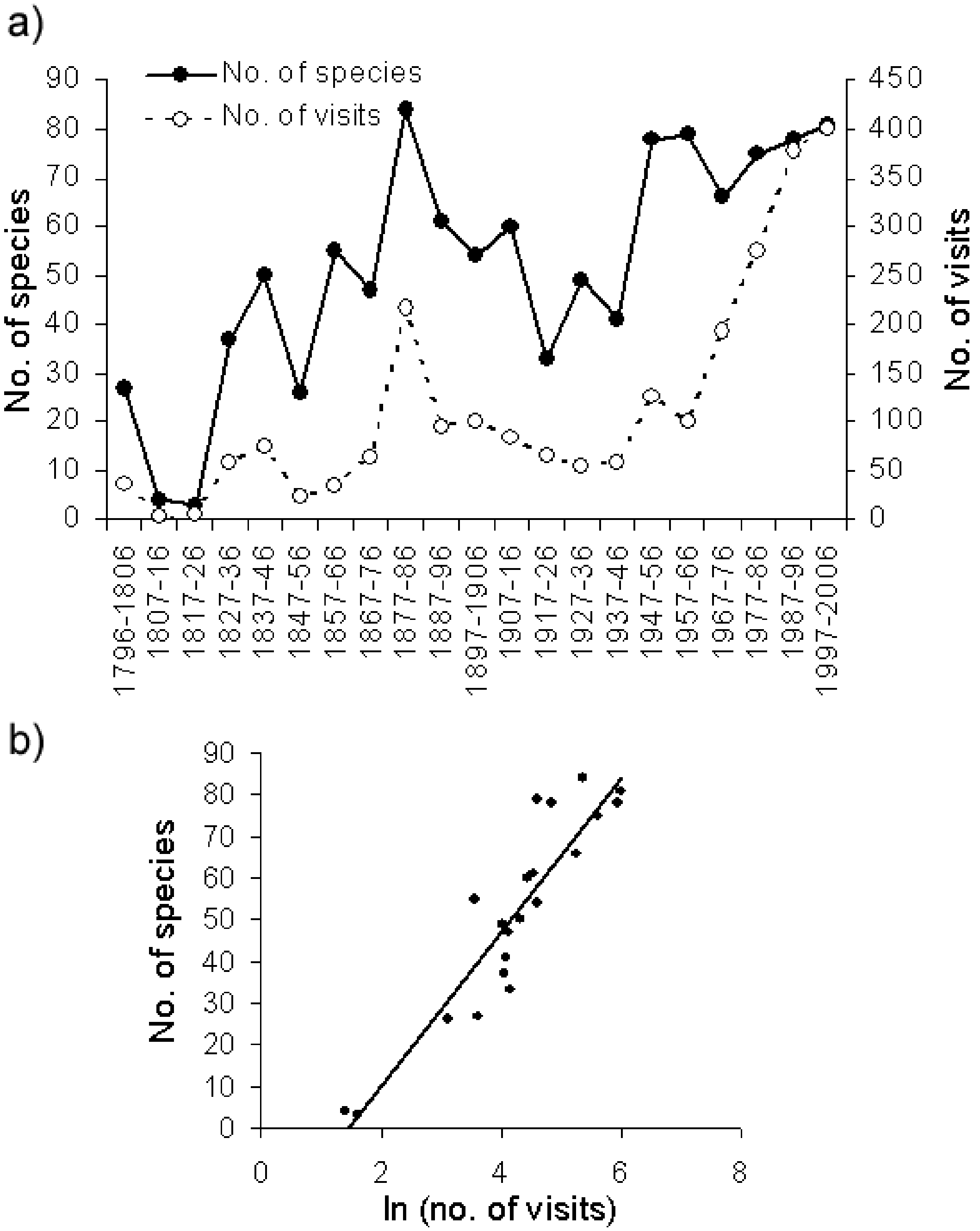

Figure 2.1 Plot showing a) number of visits to lakes within the broads and meres and total number of species found within ten year time periods, and b) the logarithmic relationship between number of species and number of visits.

The nature of recording also varies substantially throughout the time period of the dataset, with visits after 1940 yielding higher numbers of records collected per visit than visits pre-1940, and many of the earlier visits contributing only one record (Figure 2.2 a). This is because later records are generally obtained as part of surveys designed to sample the full flora, whereas older records largely comprise herbarium specimens or references to a single occurrence of a species in the literature. Lists of species found at a lake on a single day are much less common among the earlier records, and collectors for herbaria would often target specific species, rather than a range of species at one site. It is therefore not possible to use number of visits alone to reflect recording effort. The number of species recorded in ten year periods is also highly correlated with the average number of records per visit over ten year periods ($\log_e$ (no. records per visit)) ($p < 0.0001$), demonstrating, as expected, that higher numbers of records per visit (i.e. increased comprehensiveness of survey) also results in more species being found within a given time period (Figure 2.2 b). Trends observed in macrophyte species richness or diversity using historical records are often subject to this kind of bias leading to underestimates in the level of decline. For example, Sand-Jensen *et al.* (2000) compared species richness between an early period (1870-1927) and a late period (1983-1997) in Danish lakes and streams, and found that species richness in vegetated lakes had not changed, whereas in streams it had declined. They concede, however, that their results may be underestimates of decline as the modern surveys were probably more comprehensive than the early records, especially in the lakes where they were aided by scuba diving.

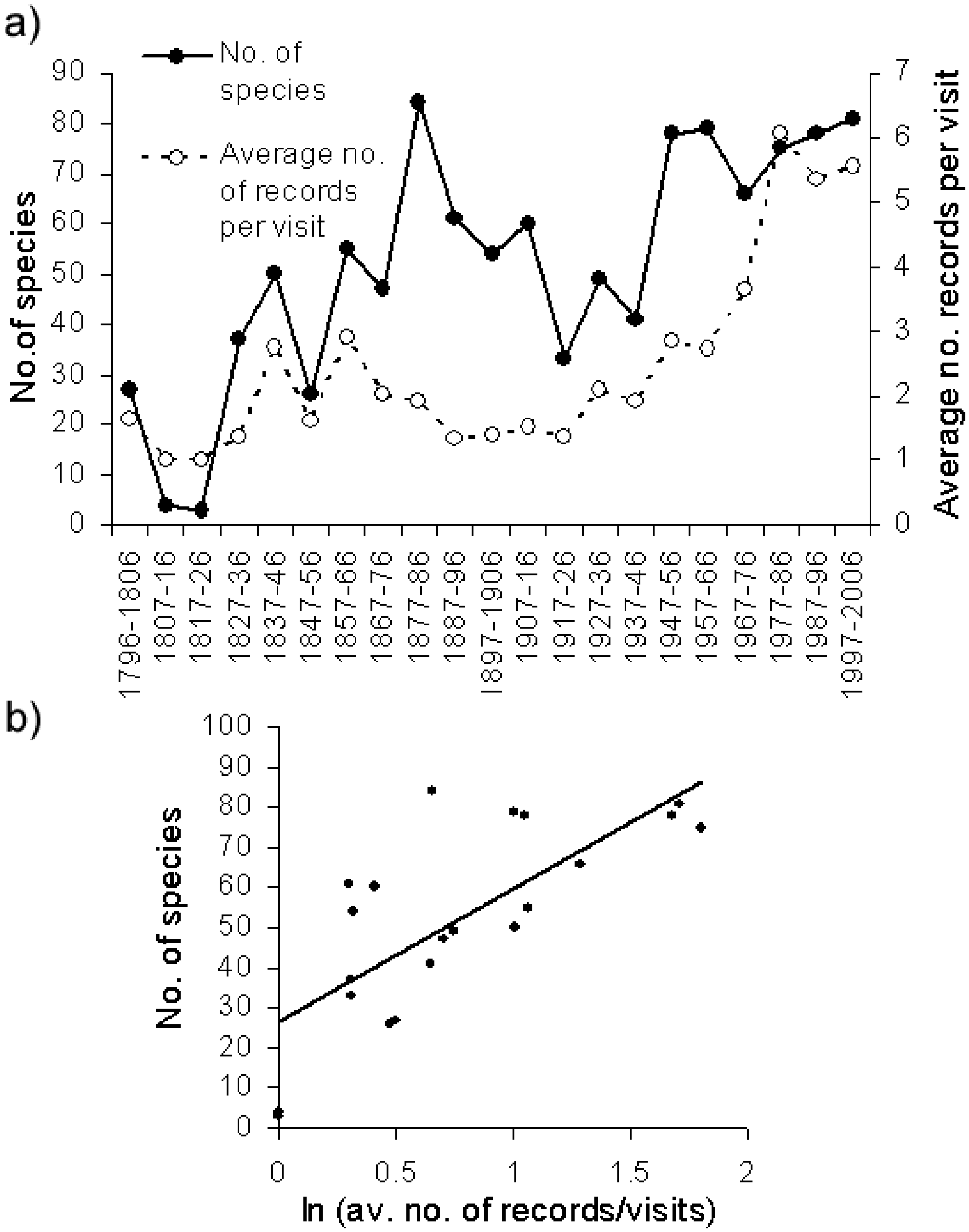

Figure 2.2 Plot showing a) number of species within the broads and meres and average number of records per visit within ten year time periods, and b) the logarithmic relationship between number of species and average number of records.

2.4.2 Record distribution

In botanical recording there is often a tendency for the distribution of plant records to reflect the distribution of botanists, and for less accessible sites to receive less attention than more accessible ones (Rich and Woodruff, 1992). The distribution of visits to meres over a 50 year period in the 19th century is certainly more heavily biased towards particular sites and areas than in recent times (Figure 2.3). These biased distributions in early records reflect the botanical recording activity of the time, which in Shropshire was dominated by W.A. Leighton, who collected material for his *Flora of Shropshire* (1841), and, being based in Shrewsbury, Shropshire, favoured nearby sites, such as Berrington Pool and Bomere Pool. Other sites that feature prominently, such as Hatch Mere and Rostherne Mere, are those recorded as part of the *Flora of Cheshire* (Warren, 1899), the principle recorder being J. B. L. Warren, who was based at the nearby Tabley House, near Knutsford, Cheshire, and worked within the same time period. This bias is also probably more pronounced for the earlier period as the records tend to be fewer and derive from fewer recorders. In the latter half of the 20th century, site visits were more evenly distributed across the meres. This is not just because there were more site visits in total, but also because the recording culture changed, with recorders tending to visit many sites (often for comparative purposes) rather than repeatedly visiting the same sites and ignoring others. There was a shift from an interest in individual species, which prompted early botanists like Leighton to return to the same location where a species was known to grow, to an interest in lake plant communities and species associations driven by the emerging discipline of vegetation science.

Interestingly, despite the differences in visit frequencies between lakes in the early and late period, there is still a strong correlation between number of visits to each lake in the early period and numbers of visits to each lake in the late period ($p = 0.001$), suggesting that lakes surveyed frequently in the earlier period were more likely to be surveyed frequently in the later period. Number of visits is not significantly correlated to lake size or distance from the nearest road in either period (all $p = >0.05$), so a likely explanation is that these lakes became known as sites worth visiting, perhaps because they were known to be species-rich or supported rare species, or even because the aim of some surveys was to document a change in flora, making previous recording a prerequisite. There is a correlation between number of species in the early period and number of visits in the late period ($p = 0.001$), but as number of species is so dependent on number of visits in the earlier period it is impossible to say whether it is the intensity of earlier recording or number of species which influenced the future recording at sites, although it is most likely both.

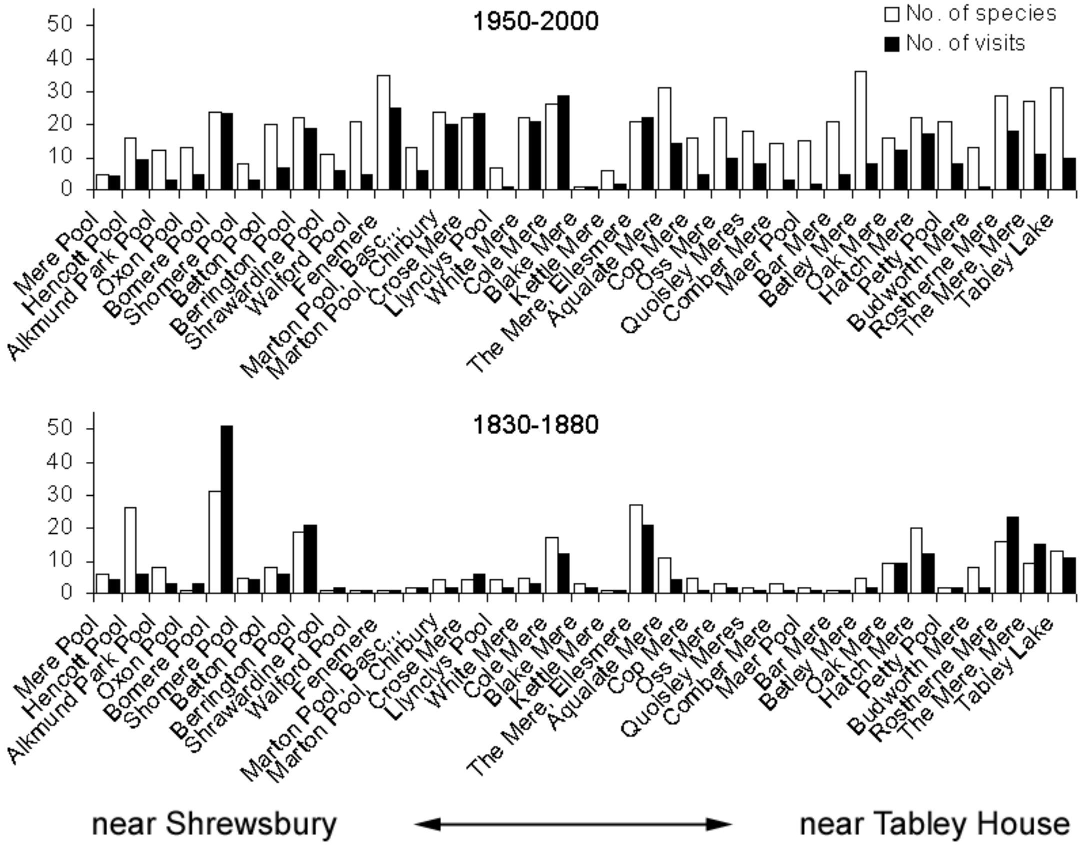

Figure 2.3 Plot of the number of visits to meres and the numbers of species found in two 50 year time periods. Lakes are ordered by distance from Shrewsbury/distance from Tabley House.

2.4.3 Species bias

The factor most difficult to overcome when interpreting historical datasets is the tendency for earlier collections of records to be biased towards particular species. One potential problem is that common species tend to be under-represented, and rare species over-represented. This is partly due to the tendency for earlier collectors to be species-orientated rather than vegetation-orientated, focussing on rare species at the expense of the commoner and probably ecologically more important ones. It is also due to the nature of the sources from which earlier records are extracted. These are largely entries in county floras and herbarium specimens. Entries in county floras were much more likely to name a site when a species was uncommon, for example *Littorella uniflora*, which is referred to as "not common" and occurring at "Filby Broad" in Trimmer's *Flora of Norfolk* (1866). In contrast, the common species *Potamogeton pectinatus*, is described in the same flora as being "frequent in rivers, canals, ponds, and marsh ditches", and a list of some of the parishes in which it is found is given, but with no specific locations. This results in few early site-specific records for common species giving the impression that they were rarer in the lakes than was probably actually the case based on more general descriptions of their distribution.

In the 19th century botany was a popular pastime, one principal concern being the identification and collection of plants to create comprehensive personal herbaria (Allen, 1986). There was a network of botanical exchange clubs (e.g. the Watson Botanical Exchange Club), where amateur botanists could exchange specimens to complete their collections. When a rare species was found, its location became a hotspot for botanical collectors, with multiple specimens collected and distributed to different herbaria through the exchange clubs. An example of this occurred at Hickling Broad, where the scarce *Najas marina* was first discovered in 1883 (Bennett, 1884). The site and its surrounds were intensively visited after this date, and so many specimens were collected that measures had to be taken to protect the population. This is clearly illustrated by Bennett's 1909 account of events in the *Transactions of the Norfolk and Norwich Naturalists' Society*:

> "Passing (…) near the keeper's house to Hickling Broad, (…) my daughter at the bow of the boat brought up a lot of aquatics in the "drag." (…) I at once saw we had *Naias*! Giving a good "Hallo," and making the boat rock considerably, I knew we had the new British plant. Curiously enough three days after Mr. H. Groves went over the same ground and found the *Naias*, being accompanied by the same lad. He said to Mr. Groves: "Be ye from Lon'on after weeds? Ah, yer too late." He knew the plant again as I had pointed it out to him. (…) Afterwards I heard the plant has been so "raided" as to be hardly found, and I asked Mr. Coton to buy the land. On August 8th, 1888, Mrs Coton wrote me that "her husband has bought the rand (…) where *Naias* grows, as you suggested to him at the *Linnean*." This was done with a view to preserve the plant" (Bennett, 1909).

The resultant records create the misleading impression that *Najas marina* was actually more common and consistently present than probably more widely distributed and abundant species such as, for example, *Potamogeton pectinatus* and *Myriophyllum spicatum* (Figure 2.4). However, *Najas* is known from the above description to have been scarce and, in Hickling Broad was confined to the south-east corner (Bennett, 1909), whereas *Potamogeton pectinatus* is recorded in Hickling as early as 1868 and, although not formally recorded again until much later, is described as being one of the dominant submerged plants of the Thurne valley broads, of which Hickling Broad is the largest (Pallis, 1911). Similarly, *Myriophyllum spicatum*, although not recorded in Hickling Broad until 1934, is described as abundant in the Thurne Broads in 1911 (Pallis, 1911) and "not uncommon" in the county and present in Hickling parish (Trimmer, 1866). This example demonstrates the importance of putting historical records into the context of other contemporary accounts, even where these are not lake-specific. Additional information can be gained by comparing historical records to macrophyte chronologies assembled through analysis of macrofossil remains in sediment cores (Davidson *et al.*, 2005; Ayres *et al.*, 2008). Macrofossil sequences generally provide a good representation of common species, as their remains are likely to be prevalent in the sediment, although rare or local species may often be missed by this approach (Davidson *et al.*, 2005; Zhao *et al.*, 2006).

There are also discrepancies in methods and criteria for inclusion of species between modern surveys (see Goulder, 2008). For example, recent mere surveys have tended to record marginal species more thoroughly than equivalent investigations of the broads by the Broads Authority, which only record plants growing in open water (Wigginton, 1980; Jackson, 1983; JNCC, 2005; Goldsmith, in prep.). These discrepancies must be understood when comparing results of different survey regimes. Issues of detection bias between species (e.g. caused by abundance, conspicuousness or size) are similarly likely to be amplified by variations in survey method, survey personnel or conditions at the time of survey. Consequently the true loss of a species may be very difficult to confirm with certainty; it merely becomes more probable as the length of period or number of surveys increase in which the species is not found.

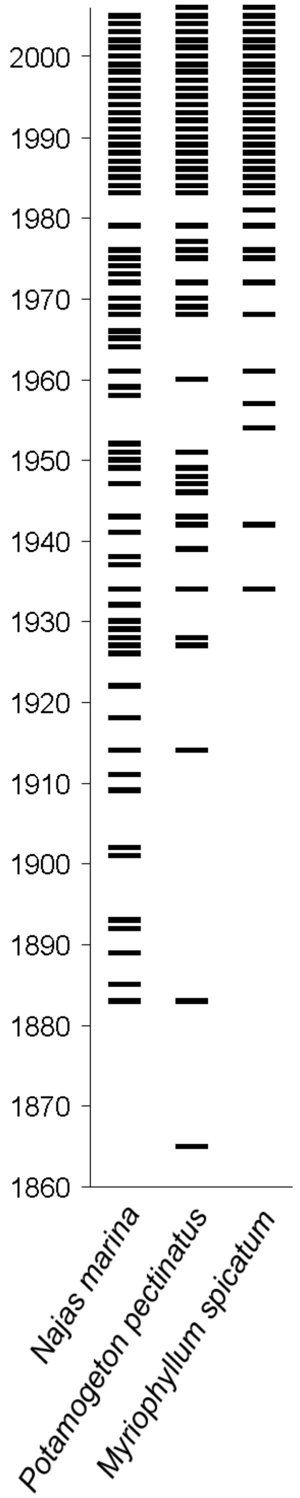

Figure 2.4 Chronology of species records for *Najas marina*, *Potamogeton pectinatus* and *Myriophyllum spicatum*. A mark is shown for each year which has one or more records for that species.

2.4.4 Species names

Historical records often refer to synonyms which need to be converted to current nomenclature, such as that of Stace (1997). Where authorities are given, this can usually be done via the literature and there are several websites which can facilitate this (e.g. TROPICOS and the International Plant Names Index). In instances where renaming has been simple and unambiguous it is usually clear to which species a synonym refers, even where the authority is not given (e.g. *Littorella lacustris* L. is now *Littorella uniflora* (L.) Asch.). Herbarium specimens, which constitute a large part of the older records, have often been checked and renamed on the specimen sheets, or where they have not, can easily be verified by specialists. There are still instances however, where naming and identification is notoriously difficult and therefore often confused, with multiple synonyms. For example, among the genus *Callitriche*, species are vegetatively very similar, exhibit marked phenotypic plasticity, and have reduced flowers, making taxonomy difficult (Lansdown and Jarvis, 2004; Lansdown, 2006). It is difficult to be confident that misidentification, or mistranslations of synonyms have not occurred, and consequently earlier records may have to be discarded or degraded, e.g. to genus level. There are also instances of common misidentification. For example in Britain, *Potamogeton berchtoldii* has often been confused with *Potamogeton pusillus*, or the distinction between closely related taxa had not been described when records were made, for example *Ceratophyllum demersum* and *Ceratophyllum submersum*, whose distinction was not properly understood in the UK until 1927 (Preston and Croft, 1997). In these instances records have to be merged under one name which covers both species as the two cannot be confidently distinguished over the full duration of a recording period. Consequently the whole species list must be subject to the same scrutiny when comparing old and new records.

2.4.5 Site locations

Identifying specific locations for species records is perhaps easier for lakes than it is for rivers or many terrestrial habitats, as lakes are relatively discrete entities which usually retain the same name. Despite this, caution is still required, and old maps must be checked to confirm that the old names and locations agree with contemporary ones. Furthermore, with older records it is not always clear whether a name refers to a lake, or the church parish area with the same name. Thus, for example, in his *Flora of Norfolk* (1866), Trimmer often refers to locations such as “Hickling” or “Horsey”, but does not clarify whether this refers to the parish, the broad with the same name, or either interchangeably. Where this degree of ambiguity exists, records cannot safely be assumed to be from the lake.

2.4.6 Dates

Dates attached to records vary in their precision, from full dates including the day of the year, to just the year. The exceptions are records from books (e.g. county floras) which may be referring to records in lakes collected any time before the date of publication (where not specified), sometimes spanning ten years or more. Occasionally this can be refined by checking primary sources, where they are given, or, when no other references exist, dates must be estimated based on the date of publication, or excluded. Amalgamation of records over a number of years is common in studies using historical records which removes this uncertainty to an extent, and also reduces the problems of record scarcity and recording bias. For example, Davidson *et al*. (2005) compared chronological trajectories of macrophyte community change in Groby Pool, Leicestershire as inferred by palaeolimnology (macrofossil and pollen analysis) and historical records collected from herbarium and literature sources, by combining these data and splitting them into *ca.* 50 year intervals from 1740 to 2000. More often studies using historical macrophyte records tend to compare an early period spanning a number of years, with a modern survey or surveys. For example Riis and Sand-Jensen (2001), compared macrophytes collected in Danish streams between 1876-1920, with a comprehensive survey conducted in 1996. They aimed to capture the maximum number of early records by merging records collected around 1896 which was considered a particularly comprehensively surveyed year. There is undoubtedly a trade-off to be reached between temporal resolution and quantity of data, and this should be based on the characteristics of each individual dataset (Rich and Karran, 2006).

2.4.7 Pre-compiled data

Many of the records within the broads and meres dataset were not collected directly from their primary source, but are a synthesis of various pre-compiled records such as those of Jackson (1981b), the Shropshire Botanical Society (Lockton pers. comm.) and the BSBI Vascular Plants database accessed via the NBN gateway. A clear understanding of the criteria for record collection is required so that any bias relating to collection criteria can be eliminated. For example in the broads, Jackson's literature review (1981b) focussed on a subset of aquatic species (74 in total) so care had to be taken to check original sources for those species which he excluded (e.g. *Schoenoplectus lacustris*). In the broads and meres dataset the pre-compiled data used was well referenced, so duplication of records could be largely avoided and additional searches could be focussed on sources not previously investigated.

2.4.8 Analysis

Once all the issues associated with historical macrophyte records have been identified, the data need to be analysed and interpreted in ways which avoid or at least minimise the various sources of error so that remaining patterns are not an artefact and can be interpreted ecologically. Most previous studies using historical macrophyte data have tended either to treat the data in a descriptive, qualitative or semi-quantitative manner, (Jackson, 1978; Arts *et al.*, 1990; Simons and Nat, 1996; Sand-Jensen, 1997; Nielsen *et al.*, 2003), or have used other techniques, such as macrofossil analysis, to complement the historical records (Orth and Moore, 1984; Davidson *et al.*, 2005; Ayres *et al.*, 2008). Where direct quantitative comparisons of early and late record sets have been made, authors have acknowledged some of the associated problems. Auderset Joye *et al*. (2002) compared the distribution of Characeae in Switzerland before 1930 and after

1975 using herbarium specimens for the older period, and field survey data for the recent period. They observed changes in the frequency of different species by looking at numbers of records in each period as a percentage of the total number of records for that period, in order to counteract changes in recording effort. They also looked at the change in geographical distribution by observing changes in species percentages per 10 km grid squares. It was acknowledged that at this scale, observed distributions and species richness of grid squares were directly related to number of records and botanical activity. Sand-Jensen *et al*. (2000) used a randomisation procedure to allow them to compare historical and recent surveys of lakes and streams in Denmark, despite there being more sites covered in the recent survey. The contemporary frequency of each species was calculated by randomly sampling the same number of sites covered by the historical study from the larger pool of modern sites. This was done 1000 times to obtain 95% confidence intervals. They also estimated that similar recording effort was used in each period per stream based on the number of days the historical survey took. Despite this, they still acknowledge that the modern surveys of the larger lakes were more comprehensive than the historical ones. Occasionally, historical data is deemed sufficiently comprehensive and survey methods well documented enough to allow direct comparisons using quantitative analysis techniques. For example Rintanen (1996) observed the changes in macrophyte communities in 113 Finnish lakes between the 1930s and 1980s by comparing a comprehensive and well documented early survey, with a modern survey carried out using the same methods. In a study of change in submerged macrophytes in Lake Fure, Denmark, Sand-Jensen *et al*. (2008) compared macrophyte records collected in 1911-13, 1951-52, 1983 and 87, and every second year since 1990. They obtained relative abundance measures for each species in each period by calculating the number of sampled sites in which it was found (n_i) as a proportion of the total number of site and species combinations (Σn_i). These relative abundances were then used to measure dissimilarity in macrophyte communities between the time periods.

In most cases however, the statistical assumptions of quantitative analysis (for example the consistency of survey method and recording effort), particularly of some widely used ordination techniques, are not properly met and the output is consequently difficult to interpret, the effect of changes in recording methods or recording bias between observers being virtually inseparable from ecological changes. Historical data itself is also rarely sufficiently comprehensive or well documented enough to overcome many of its associated biases. In addition, zero values arising from the lack of records would be treated as an absence of that species, strongly influencing the outcome of community ordinations when, in reality, there are significant biases in what is recorded which can result in common species being treated as absent, despite most likely having been present (Figure 2.4).

The quantitative analysis of ecological trends in species compositions and distributions using historical records is an advanced field of study (Desender and Turin, 1989; van Swaay, 1990; Rich and Woodruff, 1996; Warren *et al.*, 1997; McCollin *et al.*, 2000; Telfer *et al.*, 2002; Graham *et al.*, 2004; Lutolf *et al.*, 2006). Many of these studies analyse data from biological atlas datasets, most of which have a combination of collated historical records as well as various modern surveys (Telfer *et al.*, 2002). For example, van Swaay (1990) assessed changes in the abundance of butterfly species in the Netherlands by dividing atlas data collated for the Dutch Butterfly Mapping Scheme into five year periods (1901-1980) and observing the change in number of grid squares each species occupied in each period, as a percentage of the total number of recorded grid squares in that period. Telfer *et al*. (2002) used a mixture of collated historical data and survey data to calculate an index of relative change in range size for vascular plants and beetles by using the standardised residuals of each species from a linear regression of counts of 10-km grid cells between an early and a late time period. These analytical methods are designed to minimise bias associated with the data and there are also many studies within this wider field which specifically tackle the problems inherent in the use of historical records (Rich and Smith, 1996; Dennis *et al.*, 1999; Rich, 2006) and ways in which to overcome them (Delisle *et al.*, 2003; Lutolf *et al.*, 2006; Rich and Karran, 2006). These techniques, developed mainly for analysing the large amounts of fairly coarse scale (e.g. hectad level) historical and modern survey data used in distribution mapping, can equally be applied to the study of aquatic macrophytes at finer spatial scales, but need to be tailored to the specific attributes of historical records. For example, a useful approach which neutralises many sources of bias, would be to measure the proportion of lakes in which each species was historically found and which still contained that species in the modern period (Chapter 3). The most important starting point for any analysis of historic records is, however, an understanding of the dataset and its sources, and recognition of its inherent biases, so that appropriate methods of analysis can be devised while over-interpretation or false conclusions are avoided.

2.5 Conclusion

The biases associated with historical records can be summarised as those relating to recording effort, record distribution, and species. All were pertinent to the broads and meres dataset presented here, and are likely to be common influences in any dataset containing historical records. These biases largely reflect the change in recording ethos over the last 200 years, from *ad hoc* collection of interesting species, to comprehensive whole lake surveys. Additionally there is scope for error from other factors such as misidentifications, confusion about site names and the logistics of combining data from widely different sources.

The analysis of a dataset containing historical records, whether quantitative or qualitative, requires caution and a strong understanding of the source and nature of those records, so that the various sources of bias are acknowledged and, where possible circumvented, leaving behind patterns that can be interpreted ecologically. Only then can historical records provide new insights to community change and its underlying causes, or be used reliably to inform future restoration and management.

CHAPTER 3 Deriving an index to quantify long term changes in aquatic vegetation in lowland lakes using historical records

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3.1 Abstract

This paper uses historical macrophyte data from two groups of principally eutrophic lowland lakes in the UK (the Norfolk Broads and the West Midland Meres), to develop a change index, based on species persistence over the last 200 years within individual lakes. The use of a change index enables the robust interpretation of datasets based on a large variety of historic sources and incorporating a number of known and unknown biases. Species persistence, measured as the proportion of lakes still containing a species that occurred historically, was found to have a linear relationship with present day levels of occupancy across all lakes. This relationship was used to derive change index scores for species with limited historical data. Species with high change index values were most characteristic of nutrient-enriched lakes. Species with low index scores, which showed several periods of steep decline in the broads and meres, were not, however, confined to those associated with less fertile conditions. Averaging of change index scores in present day survey data served to identify the lake whose current flora suggests the least historical change, and to rank lakes in order of degree of botanical change over the last century. Thus the index may be a useful tool in assessing restoration measures or in guiding the selection of reference sites.

3.2 Introduction

Historical macrophyte records, although sparse and inconsistently collected, are often the only readily available data from which to reliably reconstruct the past aquatic flora of highly impacted lakes which are now the norm over most of lowland Europe. For the purposes of the Water Framework Directive (2000/60/EC), information on former plant communities is essential for establishing how far a contemporary lake deviates from its pre-impacted, "reference" state, and therefore for judging the ecological status of a lake. Historical records are also essential in helping to characterise the range of community structures which can be expected for a particular lake type in its reference state, information which is lacking for many lowland lakes types where un-impacted analogues are scarce (Bennion and Batterbee, 2007). Such information is important in setting suitable targets for restoration or conservation and as a benchmark against which to measure progress. The catchments of lowland lakes have been subjected to a higher intensity and earlier onset of human impact than those in the uplands. However, the proximity of human habitation has also ensured a long recording history, with some lowland lakes being subject to extensive botanical interest since the early 19th century, when field botany was growing in popularity (Morton, 1981).

There is a large and expanding literature on the use of museum records or other historical data to interpret change in species distribution and composition (van Swaay, 1990; Rich and Woodruff, 1996; Graham *et al.*, 2004; Braithwaite *et al.*, 2006; Rich and Karran, 2006). Where survey methods and recording effort are comparable between time periods, direct comparisons between them are possible (Kennison *et al.*, 1998; Sand-Jensen *et al.*, 2000; von Numers and Korvenpää, 2007). However, this is rarely the case, especially with collections of older records, so in these situations different forms of bias associated with the data must be carefully considered, and analysis methods used which overcome them. These problems have been widely acknowledged (Rich and Woodruff, 1992; Rich and Smith, 1996; Rich, 2006; Rich and Karran, 2006, Chapter 2).

Historical records have been used before to characterise changes in the aquatic plant communities of standing waters (e.g. Rintanen, 1996; Simons and Nat, 1996; Sand-Jensen *et al.*, 2000; Auderset Joye *et al.*, 2002; Körner, 2002; Davidson *et al.*, 2005), but either more complete survey datasets have been used (Rintanen, 1996; Körner, 2002) than in the present study, or the limitations have been discussed but ignored for the sake of the analysis (Auderset Joye *et al.*, 2002). Often historical data have been used to characterise past macrophyte communities, but in a more descriptive way (Jackson, 1978; Sand-Jensen, 1997; Davidson *et al.*, 2005; Ayres *et al.*, 2008). This paper uses historical macrophyte data for two sets of lowland lakes, the Norfolk Broads and the West Midland Meres, to develop a quantitative change index comprising a continuous gradient from species which have declined through to those which have persisted or increased, over the last 150 years. The index is then considered in terms of its ecological significance and is used to interpret changes in the vegetation of both the broads and meres over the period of the datasets.

3.3 Methods

3.3.1 Geographic area

This study makes use of two historical macrophyte datasets, one from the Norfolk Broads, and the other from the West Midland Meres. These are both sets of lowland, typically base-rich and predominantly freshwater lakes in England. The broads are a series of flooded medieval peat workings associated with a number of rivers in the East of England. They range in area (from 1 ha. to 140 ha.) and are shallow (most sites are <2 m deep) and highly alkaline (2-4 meq/L) (George, 1992; Moss, 2001). The meres of the English West Midlands are a series of natural water-filled hollows in the glacial drift, grouped in local clusters. They are of varying alkalinity (0.03-5.88 meq/L), with the majority being highly alkaline (>2 meq/L). They vary in depth (from less than 1 m to ~50 m) and area (from less than 1 ha. to 75 ha.) and are largely ground water fed (Reynolds, 1979). Both sets of lakes are surrounded by intensive agriculture and are near to centres of human population so have consequently been subjected to anthropogenic eutrophication over the last 150 years. Current nutrient concentrations are typically high in the broads (the majority have TP values of >100 μg L^{-1}) and in the meres (average TP values in most meres are over 100 μg L^{-1} in summer and may exceed 1500 μg L^{-1}; NO_3-N up to 6 mg L^{-1}) (George, 1992; Fisher *et al.*, 2009).

3.3.2 Sources of historical macrophyte data

The Norfolk Broads data were compiled from various sources including the Botanical Society of the British Isles' (BSBI) Vascular Plants Database accessed via the NBN gateway (www.data.nbn.org.uk), records collated from various published and unpublished sources and museum herbarium specimens, by Jackson (1978; 1981a; 1981b) and supplemented by searches done for this study. Records were also obtained from regular surveys carried out since 1982 by the Broads Authority (Broads Authority unpublished data). The meres data was compiled by A. Lockton on behalf of the Shropshire Botanical Society's Shropshire Flora database (www.shropsbotdata.org.uk at) and supplemented by records compiled for this study, largely from the Natural History Museum herbarium. All records were stored in an MS Access database with taxon name, date of record, lake, recorder, and source of record as fields. Each record represents the confirmation of a species growing in a particular lake at a particular date, although the source of the records, method of collection, frequency of records, and sites recorded varies greatly throughout the time span of the datasets (Chapter 2). Both datasets were checked by the respective county recorders (B. Ellis and A. Lockton) and species names were changed to conform to the nomenclature of Stace (1997). Where there were uncertainties over nomenclature or identification, or where an aggregate name was used widely in some sources of records, species were merged into groups, e.g. all the *Callitriche* were merged under "*Callitriche* spp.", *Potamogeton berchtoldii* and *pusillus* were merged under "*Potamogeton pusillus* agg.", and all the Ranunculaceae of the subgenus Batrachium were merged under "*Ranunculus* subgenus

Batrachium” except *Ranunculus circinatus* which was considered sufficiently distinctive for identifications to be generally reliable.

3.3.3 Criteria for species and site selection

For the purposes of this study, macrophytes were broadly defined as having an Ellenberg F (moisture) value of ten or above (Ellenberg *et al.*, 1991; Hill *et al.*, 2004). In the broads dataset, with two exceptions (*Littorella uniflora* and *Hippuris vulgaris*), species with an Ellenberg F value of ten were ignored as they were considered unlikely to be recorded by Broads Authority boat surveys which do not systematically record marginal vegetation (Jackson, 1983). *Littorella uniflora* is sufficiently rare in the Broads region that it is likely to have been recorded as a species of interest were it present, while *Hippuris vulgaris* routinely grows fully submerged in the open water of the broads and thus is recorded by the surveys. In the meres dataset, four additional species, *Limosella aquatica*, *Lythrum portula*, *Ranunculus hederaceus* and *Ranunculus omiophyllus* were included despite having Ellenberg values of less than ten, as they were considered to have a sufficiently aquatic habit to be treated as macrophytes in this study. The Ellenberg classification deals only with vascular plants. Since charophytes are well represented in the historical record and are an important component of the aquatic vegetation of base-rich lakes, they were included. Aquatic bryophytes, with the exception of the floating liverwort *Riccia fluitans*, were excluded as they were virtually absent from the historical record. All the lakes were distinct recognisable water bodies (either broads or meres) and clearly identifiable as the same lake throughout the time span of the dataset. Where records referred to a part of a larger lake set (e.g. north and south basins of Martham Broad), all records were merged under the name of the set (e.g. Martham Broad), so that records which did not specify a basin could be included.

Table 3.1 Number of lakes, species and records in the broads and meres datasets including breakdown of these in the two time periods: pre-1921, and post-1979 for the broads, and pre-1911 and post-1969 for the meres.

			Early period			Late period		
Dataset	Year span	Total no. records	No. lakes	No. species	Total no. records	No. lakes	No. species	Total no. records
Broads	1805-2006	4510	24	55	538	37	50	3159
Meres	1798-2006	4661	38	88	900	44	71	3282

Two time periods were identified for each set of lakes; an early and a late period. The earlier time period was chosen to capture the maximum number of records without sacrificing temporal resolution, and the later time period to coincide with the onset of comprehensive modern surveys (Wigginton, 1980; Jackson, 1983; Kennison *et al.*, 1998). In the broads these periods were pre-1921, and post-1979, and in the meres pre-1911 and post-1969. Lakes which had no records in the later period were deleted as they were assumed to have either disappeared, or not been surveyed at all in the later period and therefore could not be used for comparison. Further details of the datasets are presented in Table 3.1. Note that the numbers in Table 3.1 differ from those in Table 2.1, chapter 2, due to the exclusion and merging of species and sites detailed in the above in sections 3.3.2 and 3.3.3.

3.3.4 Developing a change index

The number of lakes occupied by each macrophyte species in the early period were enumerated, as were the number of these lakes which still supported each species in the late period. An empirical change value (P_{em}) was calculated for each species as the proportion of early period lakes still occupied by the species in the late period. This was done separately for each set of lakes (broads and meres). All subsequent calculations were performed using the statistical software package Minitab (release 14).

P_{em} = Number of these lakes which are still occupied by species X / Number of lakes with species X in early period

P_{mod} = Number of modern lakes occupied by species X / Total number of modern lakes

E.g. Species X currently grows in 10 out of 20 lakes surveyed. It was historically recorded in 8 lakes, of which 5 still contain the species. The P_{em} and P_{mod} values would be as follows:

$P_{em} = 5/8 = 0.625$

$P_{mod} = 10/20 = 0.5$

When plotted, P_{em} was revealed to have a strong linear relationship with the total number of modern sites occupied by each species (P_{mod}) ($p<0.001$ for both broads and meres; $n = 61$ and $n = 100$ respectively), which was expressed as a proportion of the total number of modern sites surveyed (Figure 3.1).

Both sets of proportions were logit transformed to ensure normal distribution: logit (P) = ln[P/(1-P)] where P is the proportion (either P_{em} or P_{mod}) (Williamson and Gaston, 1999; Telfer *et al.*, 2002), (Anderson-Darling normality test, $p>0.05$ for both broads and meres). To avoid zero values proportions were calculated as $P_{em} = (x + 0.5)/(n + 1)$, where x is the number of early period lakes still containing a species in the late period, and n is the number of lakes containing the species in the early period, and $P_{mod} = (x + 0.5)/(n + 1)$ where x is the number of lakes with a species in the late period and n is the total number of late period lakes surveyed. Where the number of early period lakes containing a species was very low, limited information could be inferred for that species. Thus only species occupying 4 or more lakes in the early period were used in the calculation. Logit transformed P_{em} and P_{mod} then had an even stronger linear relationship with each other (Figure 3.2), ($p=<0.0001$ for both broads and meres; $n = 25$ and $n = 45$ respectively).

An inverse linear regression model was constructed with the same logit-transformed proportions, again using only those species occurring in four or more lakes in the early period (Figure 3.3). The inverse regression equations were then used to model the change index for all the species in each data set from the proportions of modern lakes containing each species (P_{mod}). This allowed a change index value to be given not only for those species with an empirical change value, (P_{em}), but also for those that were rare, absent, or unrecorded in the early period.

In order to check the relationship between the change indices derived from the two separate lake district datasets, a Pearson's correlation was carried out between the change index values obtained from the broads dataset, and those obtained from the meres dataset, for species common to both broads and meres.

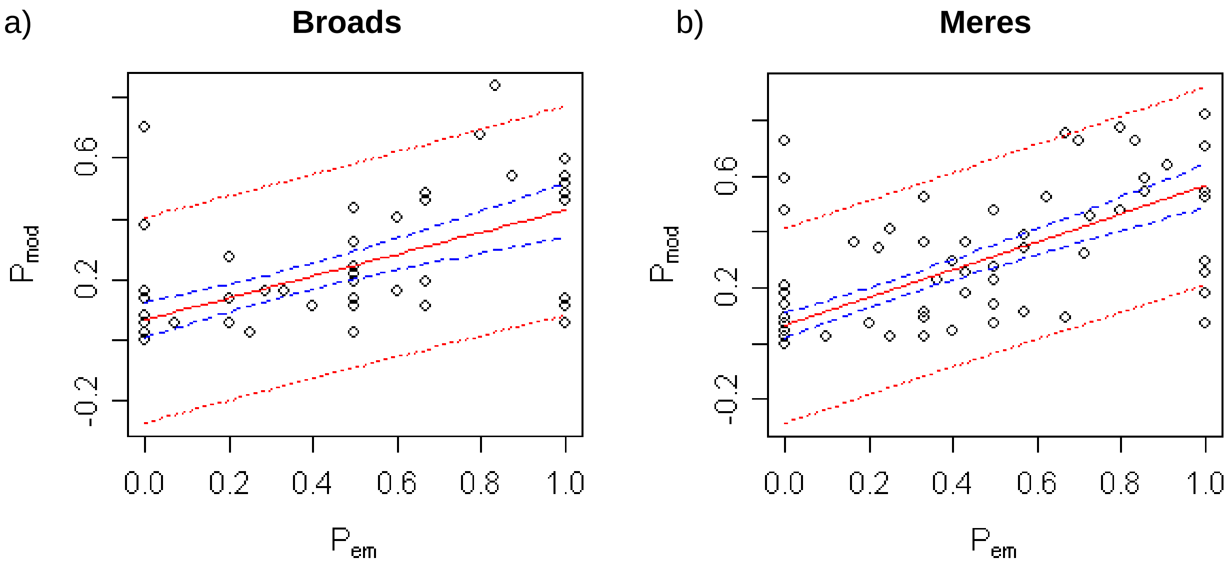


Figure 3.1 Total number of modern sites occupied by each species as a proportion of total number of modern sites (P_{mod}) against proportion of early period lakes still being occupied by a species in the late period (P_{em}), for a) the broads and b) the meres data. The fitted regression line (solid), the 95% confidence (blue, dashed) and prediction intervals (red, dotted) are also shown.

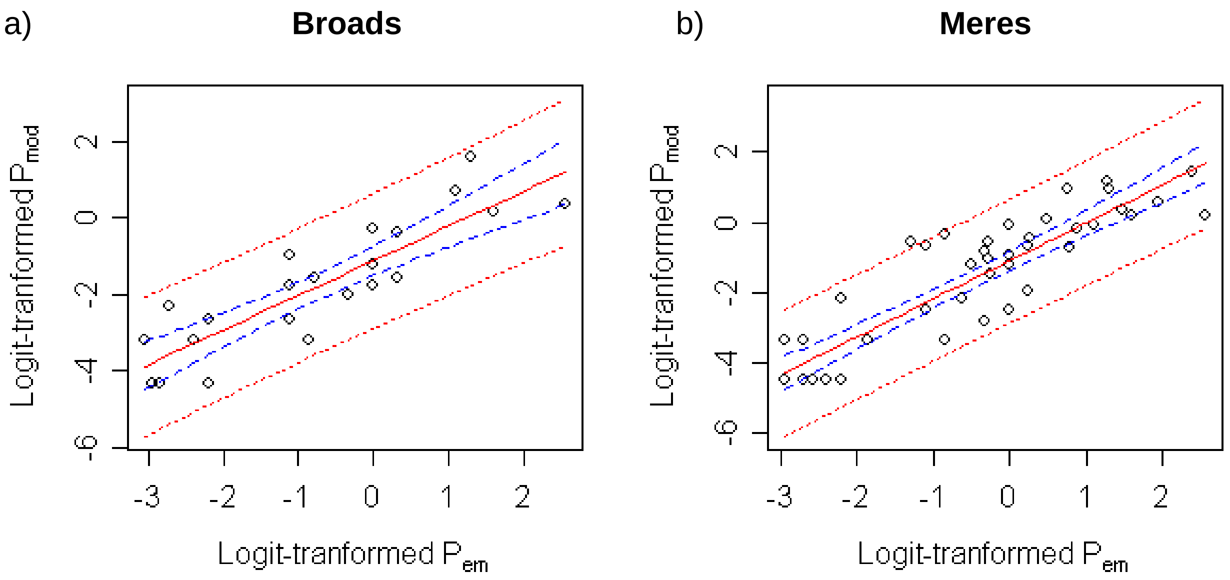


Figure 3.2 Logit-transformed number of modern sites occupied by each species as a proportion of total number of modern sites (P_{mod}) against logit-transformed proportion of early period lakes still being occupied by a species in the late period (P_{em}), for a) the broads and b) the meres data. The fitted regression line (solid), the 95% confidence (blue, dashed) and prediction intervals (red, dotted) are also shown. Only species with 4 or more early period sites were used.

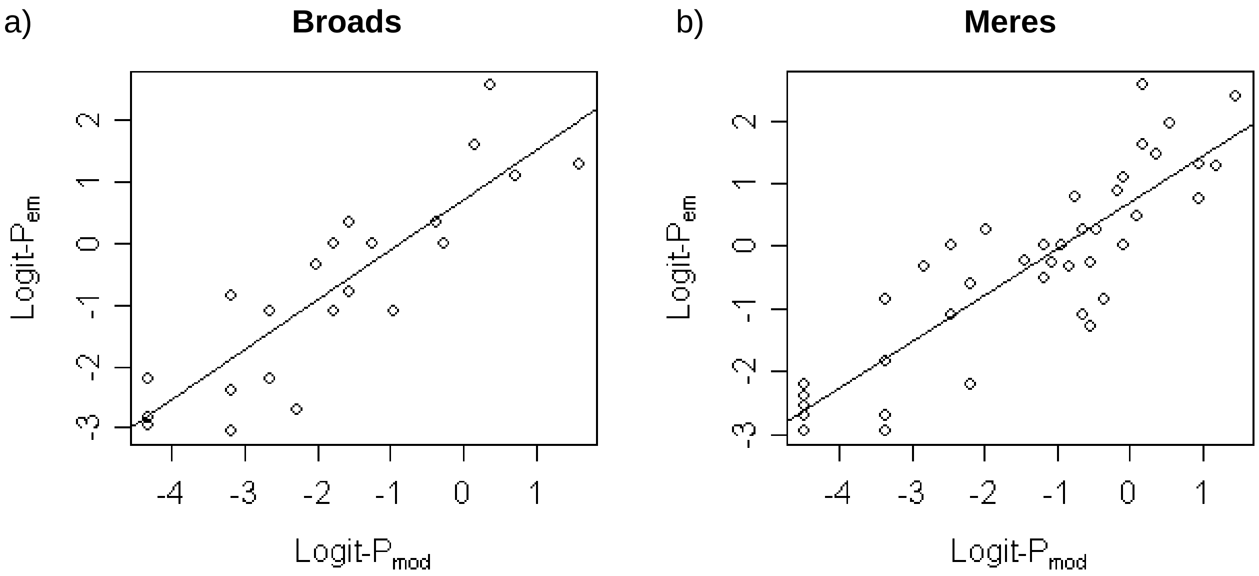


Figure 3.3 Inverse regression models of logit-transformed proportion of early period lakes still being occupied by a species in the late period (P_{em}) against Logit-transformed proportions of modern sites occupied by each species as a of total number of modern sites (P_{mod}), for a) the broads, (inverse regression equation $P_{em} = 0.7075 + 0.813\ P_{mod}$, adjusted R^2: 0.724, F-statistic: 63.96, degrees of freedom: 23, p-value: <0.001) and b) the meres, (inverse regression equation $P_{em} = 0.698 + 0.7412\ P_{mod}$, adjusted R^2: 0.7975, F-statistic: 174.3, degrees of freedom: 43, p-value: <0.001).

3.3.5 Establishing an ecological basis for the change index

Eutrophication is probably the most significant anthropogenic influence on lowland lakes in Europe (Carvalho and Moss, 1995; Gulati and van Donk, 2002; Sondergaard and Jeppesen, 2007). A test was therefore carried out to determine whether the macrophyte change index was related to species nutrient affinity. This was done by observing the relationship between the change index and the Lake Macrophyte Nutrient Index (LMNI) scores of the corresponding species (Willby *et al.*, 2009). The LMNI index is based on an adjustment of Ellenberg N scores specifically for aquatic macrophytes, undertaken following the algorithmic approach described by Hill *et al.* (1999). The LMNI scores are derived from a compilation of 4500 macrophyte surveys of lakes distributed across Britain and Ireland. Spearman's rank correlations were used to test correlations between change index and LMNI as the data were not normally distributed.

3.3.6 Reconstructing changes in lake vegetation

In order to overcome the problem of sporadic recording before the advent of modern surveys, the first and last appearance of each species in each lake was noted and an assumption was made that species were continuously present in lakes between these two dates. A timeline was constructed of numbers of lakes containing, or assuming to contain each species based on first and last observations. Species were then subdivided into three groups of index scores; those falling within the standard error of the change index mean (Group 2), and those falling below (Group 1) or above (Group 3) this range. The mean was weighted by the number of early period lakes in which a species occurred in order to give less weight to rare species. Changes in the representation of each group over the recording period were then assessed graphically.

3.3.7 Use of the change index to compare contemporary lakes

The change index values were subsequently applied to a set of contemporary survey data for a suite of sites in each group of lakes. Lakes were chosen which were known to have been comprehensively surveyed for macrophytes within the last 20 years. A value was derived for each lake by summing the change index of all species found in each lake since 1990, and dividing it by the total number of species found in the lake during that period, to obtain an average species change index for each lake. These values were then compared in order to rank lakes from most to least changed.

3.4 Results

3.4.1 The change index and its interpretation

The macrophyte change index values for all species in each lake dataset are given in Table 3.2 and the mean and standard deviation for each lake group are shown in Table

3.3. Species suffering the most decline in distribution within the lakes, were represented by low index scores, whereas those with an apparently increasing or stable distribution were represented by higher change index scores.

Table 3.2 List of species, their modelled logit- P_{em} (change index) values and change index groups for the broads and meres datasets. The three change index groups were: Group 2, those falling within the standard error of the change index mean; Group 1, those falling below; or Group 3, above this range. Where index values are missing, these species were not found in the late or early period of that particular dataset.

Species	**Broads Index**	**Meres Index**	**LMNI value**	**Change index group**	
				Broads	**Meres**
Acorus calamus		-0.94	8.16		2
Alisma plantago-aquatica		1.55	7.25		3
Apium inundatum		-2.70	5.69		1
Apium nodiflorum		0.66	7.70		3
Azolla filiculoides	-2.80		9.28	1	
Baldellia ranunculoides		-2.70	5.58		1
Berula erecta		0.32	7.48		3
Butomus umbellatus	-2.80	-1.84	8.46	1	2
Callitriche sp.	0.13	1.85	6.90	3	3
Carex elata		1.15	5.48		3
Carex lasiocarpa		-1.84	4.87		2
Carex limosa		-2.70			1
Carex rostrata		0.32	4.46		3
Carex vesicaria		0.32	5.02		3
Ceratophyllum demersum	1.99	-0.18	8.67	3	2
Chara aspera	-0.92	-2.70	7.10	2	1
Chara baltica	-0.92		8.60	2	
Chara canescens	-2.80		8.13	1	
Chara connivens	-0.43		7.92	2	
Chara contraria var. *contraria*	-0.74	-1.84	7.47	2	2
Chara curta	-1.45		6.52	2	
Chara globularis	0.58	-0.95	7.34	3	2
Chara hispida	-0.30		6.87	2	
Chara intermedia	-0.74		8.00	2	
Chara rudis		-2.70	6.94		1
Chara virgata	-1.15	-0.95	5.55	2	2
Chara vulgaris	0.41	-0.08	7.19	3	2
Crassula helmsii		-1.43	6.18		2
Damasonium alisma		-2.70	4.64		1
Elatine hexandra		-0.95	5.41		2
Eleocharis acicularis		-0.77	6.75		2
Eleocharis multicaulis		-2.70	1.93		1
Eleocharis palustris		1.01	5.48		3
Eleogiton fluitans		-1.84	3.45		2
Elodea canadensis	1.29	0.94	7.14	3	3
Elodea nuttallii	0.32	-1.16	6.92	3	2

Species	**Broads Index**	**Meres Index**	**LMNI value**	**Change index group**	
				Broads	**Meres**
Equisetum fluviatile		0.80	5.15		3
Glyceria fluitans		0.80	6.17		3
Glyceria maxima		-0.63	8.24		2
Glyceria x pedicellata		-1.43	6.88		2
Hippuris vulgaris	-0.58	-1.84	6.40	2	2
Hottonia palustris	-1.89	-0.38	7.33	1	2
Hydrocharis morsus-ranae	-0.58	-2.70	8.26	2	1
Hypericum elodes		-1.84	4.95		2
Isoetes lacustris		-2.70	3.09		1
Juncus bulbosus		0.09	3.72		2
Lemna gibba	-1.89	-1.43	9.24	1	2
Lemna minor	1.39	2.09	7.58	3	3
Lemna minuta	-0.58	-0.63	8.64	2	2
Lemna trisulca	0.75	0.80	7.82	3	3
Limosella aquatica		-2.70	6.49		1
Littorella uniflora	-2.80	-0.95	4.70	1	2
Lobelia dortmanna		-2.70	2.46		1
Lythrum portula		-2.70	5.56		1
Menyanthes trifoliata		-0.18	4.76		2
Myriophyllum alterniflorum		-2.70	4.54		1
Myriophyllum spicatum	-0.58	-0.38	7.84	2	2
Myriophyllum verticillatum	-0.74	-2.70	8.67	2	1
Najas marina	0.58		8.84	3	
Nitella flexilis agg.	-0.43	-1.16	5.60	2	2
Nitella mucronata	-0.74		8.42	2	
Nitellopsis obtusa	-0.74		7.62	2	
Nuphar lutea	1.01	1.74	6.92	3	3
Nuphar pumila		-1.84	5.33		2
Nuphar x spenneriana		-1.16	5.61		2
Nymphaea alba	0.49	0.87	5.54	3	3
Oenanthe aquatica		0.09	8.31		2
Oenanthe fluviatilis	-2.80		7.67	1	
Persicaria amphibia		1.46	7.25		3
Phragmites australis		1.46	7.19		3
Pilularia globulifera		-2.70	5.18		1
Potamogeton acutifolius	-1.89		7.48	1	
Potamogeton alpinus	-2.80	-1.84	5.79	1	2
Potamogeton coloratus	-1.89	-2.70	6.70	1	1
Potamogeton compressus	-2.80		8.00	1	
Potamogeton crispus	0.67	0.32	7.64	3	3
Potamogeton friesii	-0.07	-2.70	7.64	2	1
Potamogeton gramineus		-2.70	5.51		1
Potamogeton lucens	-1.89	-1.84	7.02	1	2
Potamogeton natans	-1.45	-0.63	5.16	2	2
Potamogeton obtusifolius	-0.92	-0.63	6.72	2	2
Potamogeton pectinatus	0.84	0.09	8.25	3	2
Potamogeton perfoliatus	-0.74	-1.43	5.83	2	2
Potamogeton polygonifolius		-1.43	3.50		2
Potamogeton praelongus	-2.80	-2.70	5.77	1	1
Potamogeton pusillus	0.84	0.60	7.61	3	3
Potamogeton trichoides	-1.89		8.39	1	
Potamogeton x angustifolius		-2.70	5.69		1

Species	**Broads Index**	**Meres Index**	**LMNI value**	**Change index group**	
				Broads	**Meres**
Potamogeton x cooperi		-2.70	5.67		1
Potamogeton x salicifolius	-1.45		6.89	2	
Potentilla palustris		0.60	4.59		3
Ranunculus circinatus	-0.19	-0.18	8.64	2	2
Ranunculus lingua		-0.08	7.61		2
Ranunculus subgenus Batrachium	-1.89	0.24	6.86	1	3
Riccia fluitans		-2.70	6.63		1
Rorippa microphylla		-0.95			2
Rorippa nasturtium-aquaticum		1.01	7.58		3
Rumex hydrolapathum		0.24	7.70		3
Sagittaria sagittifolia	-1.89		7.88	1	
Scheuchzeria palustris		-2.70			1
Schoenoplectus lacustris	-0.92	0.39	7.59	2	3
Schoenoplectus tabernaemontani		-0.38			2
Sparganium emersum	-0.58	-0.77	6.59	2	2
Sparganium erectum		1.85	7.54		3
Sparganium natans		-2.70	4.84		1
Spirodela polyrhiza	-1.89	-0.95	8.79	1	2
Stratiotes aloides	-1.45	-2.70	8.51	2	1
Subularia aquatica		-2.70	2.93		1
Typha angustifolia		0.87	7.12		3
Typha latifolia		1.46	7.83		3
Utricularia australis	-2.80		4.65	1	
Utricularia intermedia	-2.80		2.74	1	
Utricularia minor	-2.80	-2.70	2.97	1	1
Utricularia vulgaris	-1.15	-2.70	5.39	2	1
Veronica anagallis-aquatica		-1.16	7.60		2
Veronica beccabunga		1.46	6.98		3
Veronica catenata		-0.63	8.07		2
Zannichellia palustris	0.67	0.73	8.49	3	3

Table 3.3 The mean and standard deviation of the macrophyte change index scores for all species the broads and meres. The weighted mean was weighted by the number of early period lakes in which a species occurred in order to give less weight to rare species.

	Mean change index	S.E. mean	Weighted mean change index
Broads	-0.924	0.789	-0.834
Meres	-0.888	0.673	-0.513

The change index values derived from each of the broads and meres datasets for species common to both areas, were found to be highly correlated (Pearson's r = 0.656, n = 42, p < 0.0001, Figure 3.4). Although the general trend was for species to have equivalent index scores whether calculated from the broad or meres data, there were a few species which did not fit this pattern. There was only one taxon (*Ranunculus* subgenus Batrachium) whose index scores fell below the standard error of the weighted mean of the change index (group 1) in one set of lakes (the broads) but above the standard error of the weighted mean (group 3) in the other (the meres). This is perhaps not surprising as the species aggregated under *Ranunculus* subgenus Batrachium differ between the broads and meres, making it difficult to make general statements about the taxon as a whole.

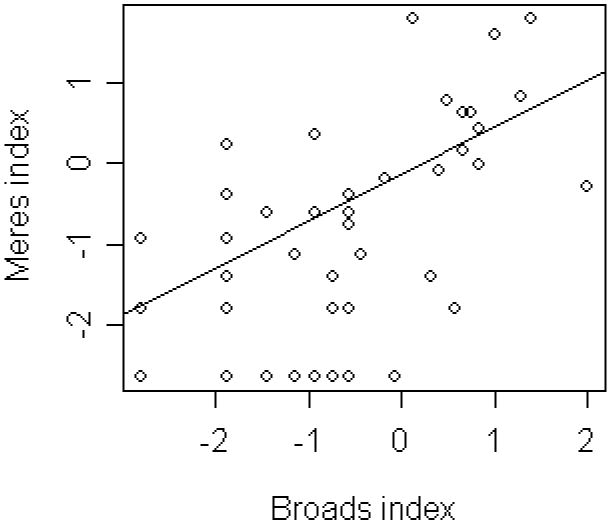


Figure 3.4 The relationship between change index values obtained for species common to both broads and meres (Pearson’s r = 0.656, n = 42, p < 0.0001).

3.4.2 Ecological basis for the change index

There was a correlation between the change index and Lake Macrophyte Nutrient Index (LMNI) scores ($p = 0.169$ and $p = 0.002$ in the broads and meres respectively), suggesting that the change index is related to nutrient affinity. However, this correlation was not significant in the broads. This was because, as was also the pattern in the meres, species with lower change index scores covered a large range of LMNI scores, whereas those species with high change index scores, tended to have high LMNI values, consistent with tolerance of fertile conditions (Figure 3.5).

3.4.3 Temporal changes in vegetation over the recording period

The macrophyte change index was applied to the historical macrophyte datasets of the broads and meres in order to interpret changes in macrophyte community structure over the period spanned by the datasets. The overall change in status of each change index group (those above, below or within the standard error of the mean) over the time period of the datasets is summarised in Figure 3.6. Figure 3.7 provides examples of changes in the status of selected representatives of each change index group.

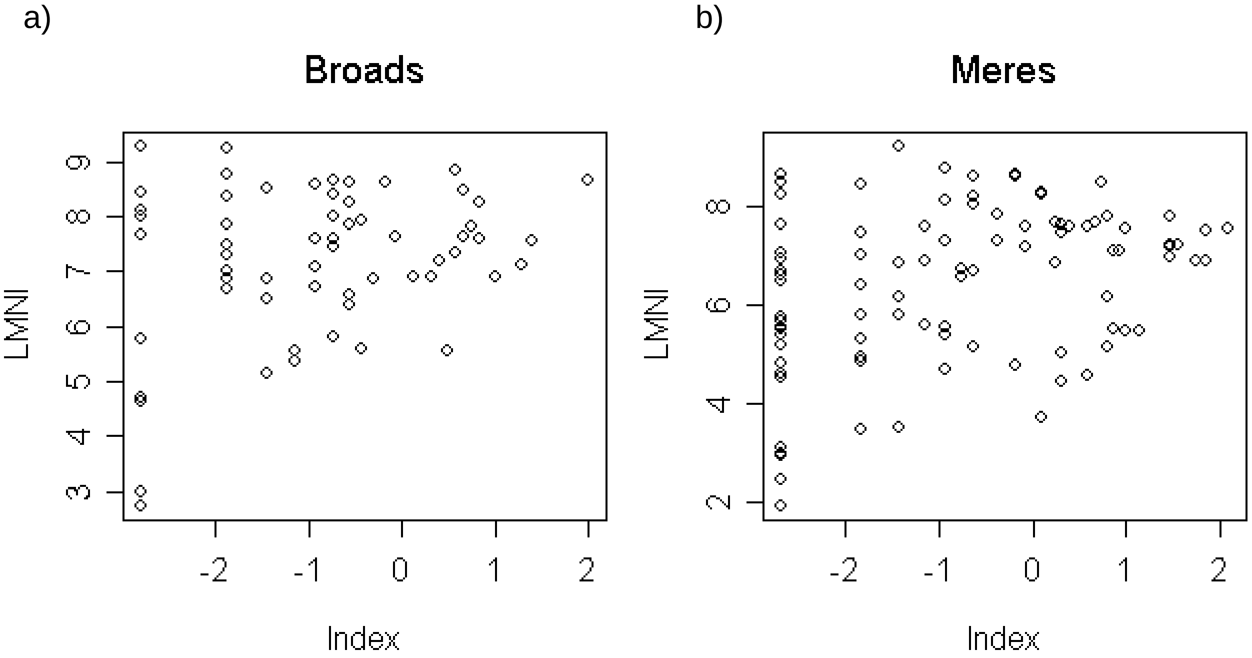


Figure 3.5 The relationship between Lake Macrophyte Nutrient Index (LMNI) and the change index in the broads a) and the meres b).

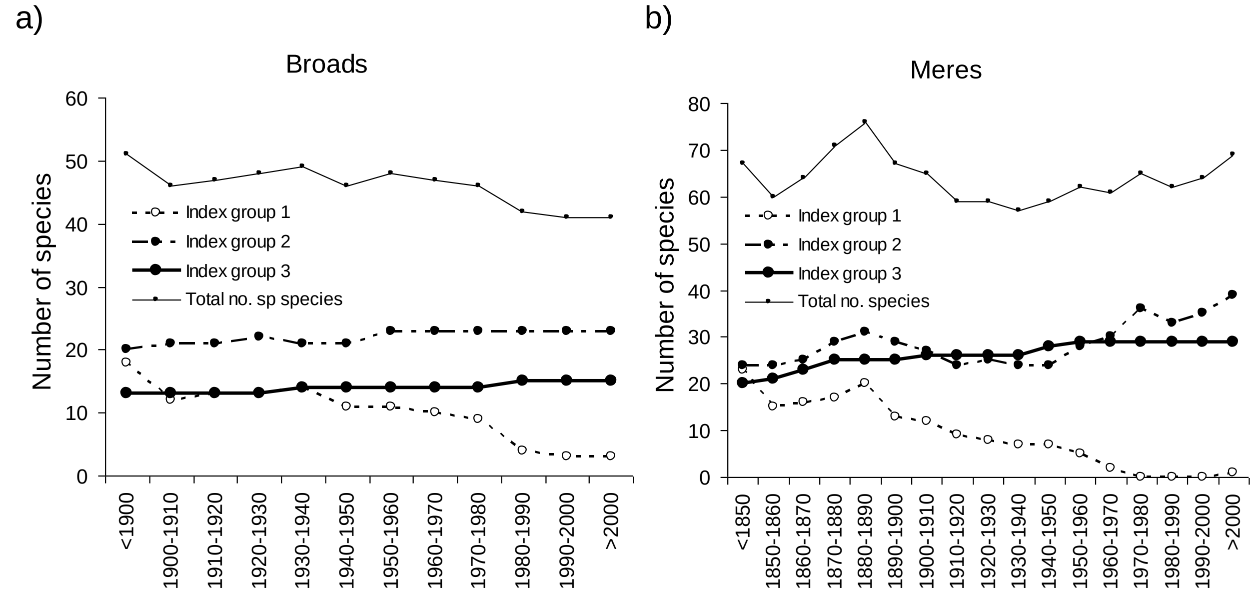
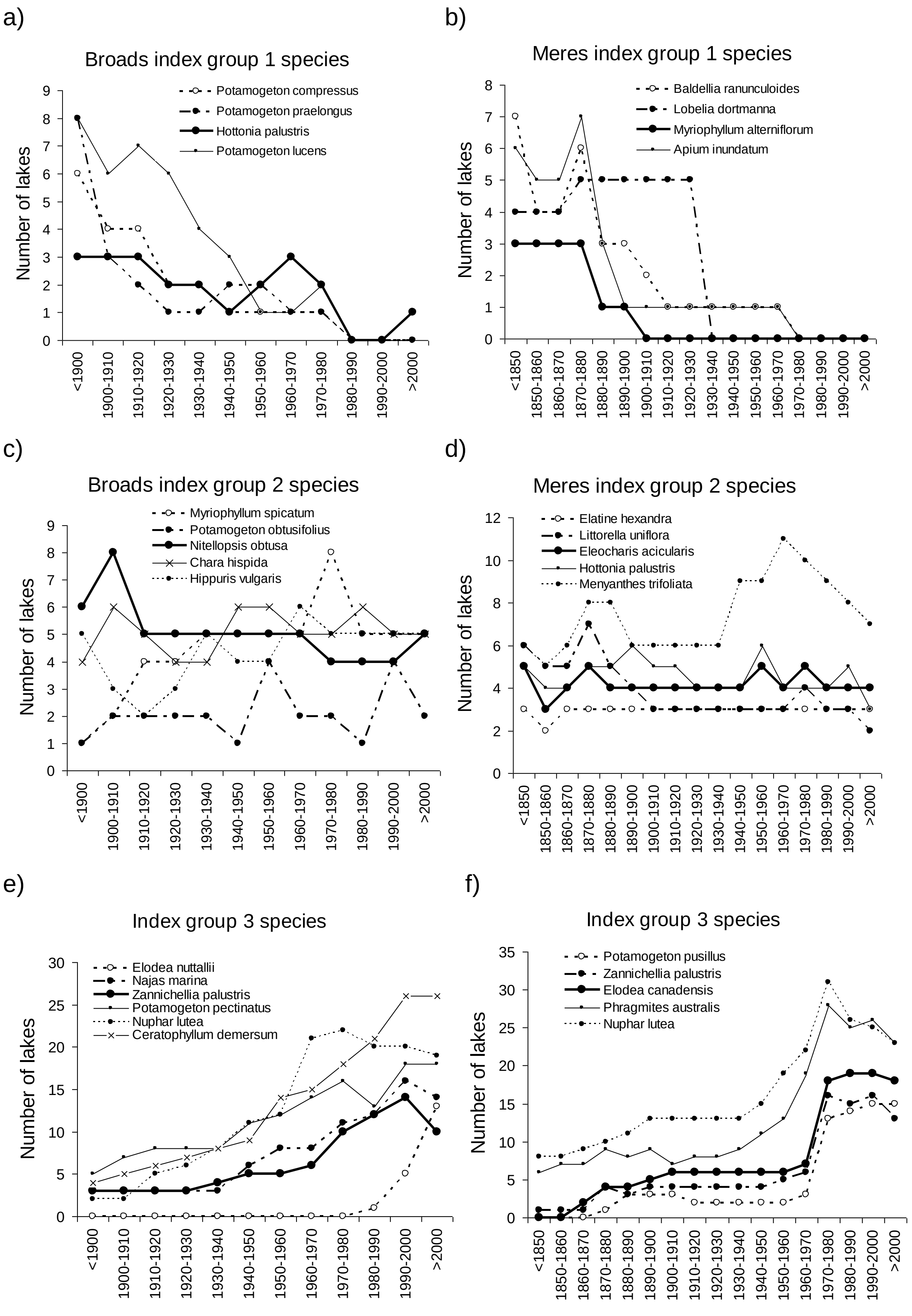


Figure 3.6 Number of species belonging to each index group within ten year periods throughout the time span of the broads a) and meres b) datasets.

Figure 3.7 (on following page) Change in number of lakes a species is recorded in within ten year periods, assuming continuous coverage between first and last observation dates for each species in each lake. A selection of species representative of index groups 1, 2 and 3 are shown for both the broads, a), c) and e), and the meres, b), d) and f), datasets.


a)
Broads index group 1 species
Potamogeton compressus
Potamogeton praelongus
Hottonia palustris
Potamogeton lucens
Number of lakes
<1900
1900-1910
1910-1920
1920-1930
1930-1940
1940-1950
1950-1960
1960-1970
1970-1980
1980-1990
1990-2000
>2000
b)
Meres index group 1 species
Baldellia ranunculoides
Lobelia dortmanna
Myriophyllum alterniflorum
Apium inundatum
Number of lakes
<1850
1850-1860
1860-1870
1870-1880
1880-1890
1890-1900
1900-1910
1910-1920
1920-1930
1930-1940
1940-1950
1950-1960
1960-1970
1970-1980
1980-1990
1990-2000
>2000
c)
Broads index group 2 species
Myriophyllum spicatum
Potamogeton obtusifolius
Nitellopsis obtusa
Chara hispida
Hippuris vulgaris
Number of lakes
d)
Meres index group 2 species
Elatine hexandra
Littorella uniflora
Eleocharis acicularis
Hottonia palustris
Menyanthes trifoliata
Number of lakes
e)
Index group 3 species
Elodea nuttallii
Najas marina
Zannichellia palustris
Potamogeton pectinatus
Nuphar lutea
Ceratophyllum demersum
Number of lakes
f)
Index group 3 species
Potamogeton pusillus
Zannichellia palustris
Elodea canadensis
Phragmites australis
Nuphar lutea
Number of lakes

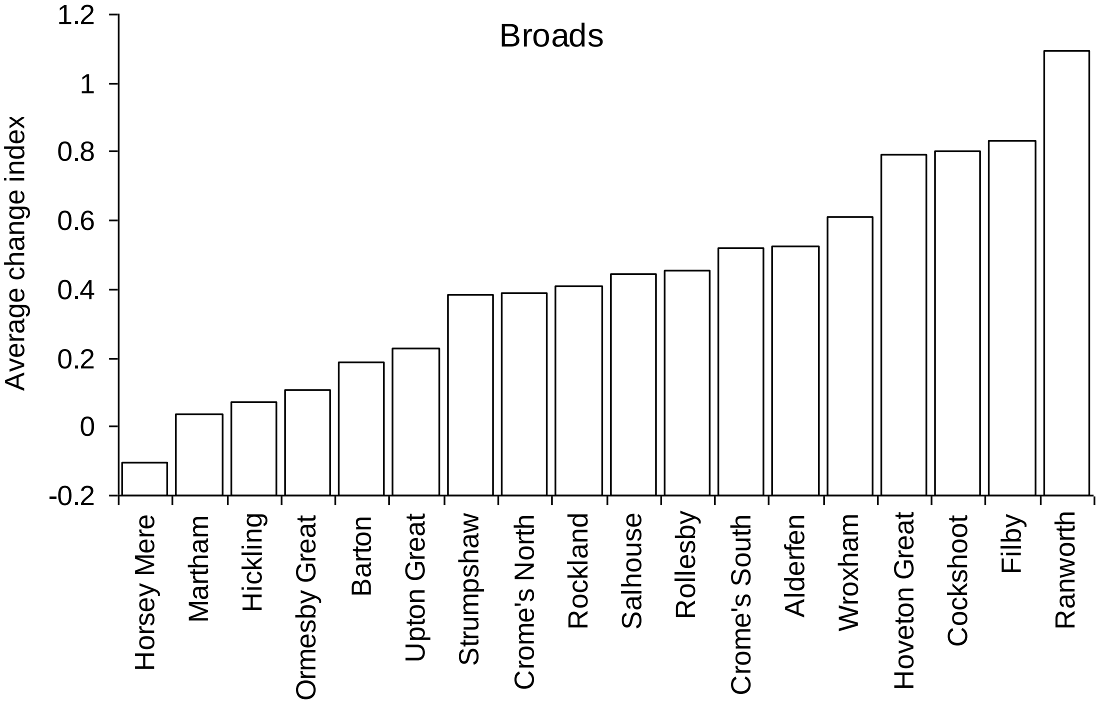
In both lake districts, the numbers of index group 1 species, such as *Potamogeton compressus* and *Potamogeton lucens* in the broads and *Lobelia dortmanna* and *Apium inundatum* in the meres, decreased as expected. In the broads they dropped from 18 to 3 species, and in the meres from 23 to 1 species. The periods of most rapid decline in this group occurred before 1910, and between 1940 and 1950, and 1980 and 1990 in the broads, and before 1850 and between 1890 and 1920 in the meres (Figure 3.6). In contrast the observed numbers of species within the other two groups increased, in both the broads and, especially the meres. This increase was sufficient to buffer the change in total numbers of observed species which consequently dropped by a smaller amount (by 19.6 % in the broads and 9.2 % in the meres). Some species within group 2 showed a slight decline or increase in the number of lakes in which they were observed, for example *Littorella uniflora* which decreased in the meres and *Myriophyllum spicatum*, which increased in the broads, but the majority of species in this group showed little change (e.g. *Chara hispida* in the broads and *Hottonia palustris* in the meres). All species in group 3 showed an increase in the number of lakes occupied over the time-span of the dataset. Although some of this increase could be due to increased sampling effort and more comprehensive survey methods, some increases will reflect a genuine expansion in distribution. Invasive alien taxa, such as *Elodea nuttallii*, that were absent historically, offer a good example. In the examples of group 3 species in the meres, there appears to be an abrupt increase in the number of lakes occupied between 1970 and 1980. This is almost certainly due to increased recording effort associated with the onset of surveys by the Nature Conservancy Council (Wigginton, 1980, 1987). Nonetheless, the decrease in group 1 species still indicates a real decline, as modern recording regimes would be likely to detect these species if they were present. Indeed, many of the group 1 taxa have declined so severely across lowland Britain (and elsewhere) that they are now protected by national or international legislation, and considerable recording effort is devoted to assessing changes in their status (e.g. Stewart and Church, 1992; Edwards and Pearman, 2004; Lockton and Whild, 2005)

3.4.4 Application of the index

One straightforward application of the index is to provide a measure of the integrity of contemporary sites using comprehensive biological survey data to reflect the degree of similarity between modern sites and their historical analogue. Such an index would be based on the average change index values of the species recorded. For the purposes of comparing values between different sites it is necessary to employ a change index that has been trained on the sites to which it is to be applied, or which is based on sites of a similar type and geographical distribution, in order to minimise the influence of environmental and biogeographical elements on species composition.

When applied to a set of contemporary (post 1990) data for each group of lakes (Figure 3.8) the change index indicates that Horsey Mere and the Martham Broads represent the historically least changed broads in terms of their composition, whilst Ranworth Broad and Filby Broad appear to be the most degraded. Within the meres, Whitemere and Mere Mere stand out as those sites whose current composition converges most closely on the historical baseline.

a)



b)

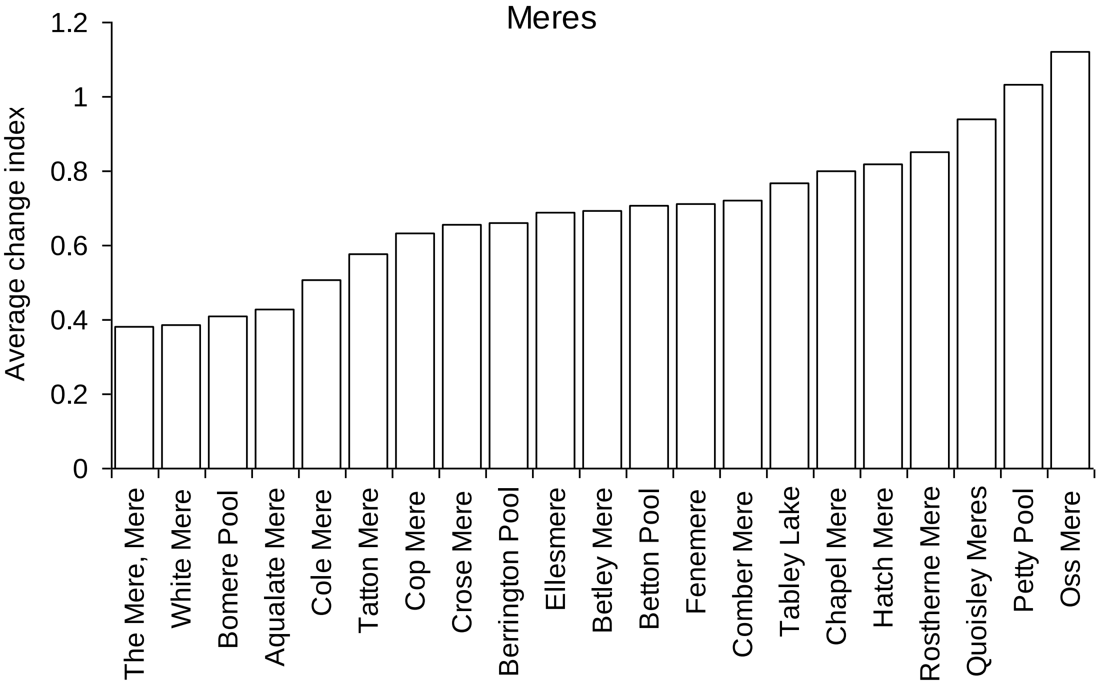


Figure 3.8 A selection of lakes in a) the broads and b) the meres ranked according to the average index scores of the macrophyte species found growing in them since 1990.

3.5 Discussion

3.5.1 Using historical data to interpret macrophyte compositional changes

The change index proposed here seeks to characterise those species which have declined in distribution within lowland lakes. It is essentially a measure of the proportion of lakes in which a species was recorded historically and which still contain that species in the late period, as modelled from empirical data. As such, the lower the index value for a species, the fewer individual lakes it has persisted in (and hence the fewer lakes it is found in presently). The higher the index value, the closer it is to persisting in all of the lakes in which it was historically recorded. Although there are many more lakes with records of high index value species (e.g. *Elodea canadensis*) recorded in the modern period compared to the early period (5 and 6 in the early period in the broads and meres respectively, compared to 25 in the late period for *Elodea canadensis*), the index can only go as far as saying that a species persists in those lakes in which it was first recorded. Thus it cannot be used to indicate an increase in the distribution of a species from an historical baseline. This is inevitable given the nature of the data used to generate the index; within the late period the records come mainly from surveys designed to be much more inclusive than early period recording. Common species were undoubtedly under-recorded in the early period due to a bias in historical recording towards rarer, more noteworthy species (Chapter 2). Equally, the apparent increase in the number of lakes containing common, widely distributed species is likely to be an artefact of more comprehensive modern surveys. For example, *Nuphar lutea* was known to be widespread in the broads and meres in the late 19th century (Leighton, 1841; Trimmer, 1866; Christopher Davies, 1883), but was rarely noted on botanical expeditions or collected for herbaria. The increase in number of lakes in which it is recorded today compared to historically is likely to be due, in part, to changes in recording strategy (Chapter 2).

Since the index value for each species is modelled as opposed to being strictly empirical, some species recorded in very few or no lakes in the early period may still have high index values, as the index is derived from the number of modern lakes containing a species (and the model is only based on species present in four or more early period lakes). This means that in some cases (e.g. *Elodea nuttallii* and *Lemna minor* in the broads, and *Apium nodiflorum* and *Veronica beccabunga* in the meres), high index values do not necessarily mean that a high proportion of lakes retain this species, but may simply mean that a species has changed from being uncommon, to widespread, or from being unrecorded (or overlooked) to well recorded. *Elodea nuttallii* is a good example of a species which was definitely not present in the broads in the early period, being first recorded in Britain in 1966 (Stace, 1997), but which is now widespread and hence has a higher than average index score. These species are an exception but must be considered when interpreting the index.

Another group of species to consider are those with potentially high site turnover. These species may show little persistence in individual lakes, but still retain a high or persistent overall distribution among the group of lakes as a whole. Ruderal species with high reproductive output and efficient dispersal mechanisms would be expected to dominate this group (Willby *et al.*, 2000). If there are many such cases it could affect the assumption that low change index scores indicate species decline. This was checked by looking at the index scores of those species which had occupied more early period lakes than modern ones (i.e. where there is an unequivocal decline in distribution). This revealed that all the below average change index (group 1) species in both the broads and meres occurred in fewer lakes in the modern period than historically. Of the average index score (group 2) species, 23% in the broads and 33% in the meres species occupied fewer lakes in the modern period than historically, while all species with an above average index score (group 3) had more modern sites than historic ones. This means that one can say conclusively that the species with a below average index score have declined in absolute terms within that group of lakes. In summary, low change index values indicate a species characterised by decline and restricted modern distribution. Conversely species with high change index values indicate a large modern distribution, and either high levels of persistence or a genuine increase in distribution since the early period, although these two possibilities cannot be distinguished by the index.

This study is unique among those previously using historic macrophyte data in that it utilises a change index and is thereby able to classify species by the level of their change in lake occupancy whilst avoiding the problems of recording bias and insufficient data. The change index approach has, however, been used for numerical assessments of change in the distribution of other species (van Swaay, 1990; Thomas and Abery, 1995; Pearman, 1997; Warren *et al.*, 1997; Preston *et al.*, 2002; Telfer *et al.*, 2002; Braithwaite *et al.*, 2006). The index in this study follows a similar principle to that of Pearman (1997) who calculated a “decline rating” for vascular plants based on the number of recorded post-1970 10-km squares (hectads) divided by the number of recorded post-1930 hectads, expressed as a percentage. In the change index presented here it is the ratio of early period lakes still holding a species in the late period, to the number of early period lakes in which the species was recorded. However, the principle was then extended by identifying the relationship between this ratio and the current distribution of aquatic plant species, expressed in terms of the number of individual lakes occupied, this relationship was used to infer the index for all species, even where historical data were very sparse or lacking. The advantage of this approach is that it allows the use of a limited amount of data within specific areas (the broads and the meres), from a large variety of historical sources and yet still can indicate which species have declined, and identify periods of more rapid decline. As lakes are usually identifiable as a discrete location, even in older records, the number of lakes occupied could be used as a measure of decline. This allows for a more sensitive index than one based upon hectads, where losses within one site within a hectad may be obscured by persistence at other sites within the same hectad. This is particularly important when assessing decline in lake macrophytes in those areas with a high density of aquatic habitat, as species lost from lakes may potentially persist in other aquatic habitats nearby. In Broadland, for example, many species lost from the broads have continued to thrive in adjacent drainage dykes (George, 1992).

One limitation of the index is that it is impossible to tell from this method whether species are increasing or staying stable; it can only provide information on species decline. Telfer *et al.* (2002) were able to calculate an index of relative change in range size (both increase and decline) by using the standardised residuals of each species from a linear regression of counts of 10-km grid cells occupied in an early and a late time period. Such an approach could not be applied to the data in this study, however, as there was no relationship between number of lakes occupied in early and late recording periods. This may be because, compared to their datasets which incorporated data from intensive recording of >1500 species across Britain (2800 hectads), this dataset was relatively small (fewer species and fewer sites). This meant that the data from the early recording period was more sensitive to inconsistent recording as a site scale was used, rather than the much larger hectad scale, as the basis for analysis. Additionally, the early period used was much earlier than that of Telfer *et al.* (2002), being designed to capture the nineteenth century condition of these lakes, and therefore relied on much more sporadic data compiled from different sources, with associated bias. The most noticeable bias was the tendency for common species to be under recorded in the early time period (Chapter 2). These changes in recording activity could not be easily corrected for as attempted in some other studies (Rich and Karran, 2006), as the sources used in this study were so varied (Chapter 2). Another limitation, common to many indices based on presence only data, is that they take no account of abundance. For example, in the broads the index suggests that charophytes show good persistence, as they are still found in most of the lakes in which they were historically recorded. This conceals that fact that their extent within the lakes is generally much lower now than it was historically; the sparse and fragmented growth of charophytes found in many broads today is far removed from the luxuriant charophyte lawns referred to in early accounts (Gurney, 1904; Pallis, 1911). Additionally, it cannot be assumed that probability of detection is related to abundance, since earlier surveys often specifically sought out rare species, which were likely to have limited cover (Bennett, 1909).

In global terms, based on the reconstructions there was a slight decrease in total number of species recorded in the broads and meres over the time period of the dataset (Figure 3.6). This probably underestimates the true extent of species loss, as some species present were probably not recorded in the earlier time periods. Thus, the apparent stability or increase in groups 2 and 3 may be illusory rather than real. There is an unequivocal loss of group 1 species, with periods of rapid decline in this group before 1910, and between 1940 and 1950, and 1980 and 1990 in the broads, and before 1850 and between 1890 and 1920 in the meres (Figure 3.6). This indicates early (pre-1910) eutrophication impacts in both sets of lakes, associated with a growth in rural populations, increased agricultural mechanisation, land drainage, increased fertiliser use and stocking densities (Rowley, 1972; Reynolds, 1979; George, 1992; Williamson, 1997).

3.5.2 Characterising changed species

Change index values derived separately for species common to both broads and meres were significantly correlated ($p < 0.0001$). This suggests that the index is not highly specific to an individual group of lakes but rather may be generally applicable to lowland base-rich lakes in Britain. It also suggests that similar species have declined or remained widespread in both lake districts, pointing towards common drivers of change. Species associated with lower tolerance to eutrophication, such as *Littorella uniflora* and *Potamogeton alpinus* in the broads, and *Myriophyllum alterniflorum* and *Apium inundatum* in the meres, were found to have below average index scores. Historical studies in other European countries replicate these findings (Rintanen, 1996; Sand-Jensen *et al.*, 2008). In contrast, many of the species with above average scores, such as *Myriophyllum spicatum*, *Zannichellia palustris* and *Nuphar lutea*, are generally quite tolerant of nutrient-rich situations (Preston and Croft, 1997). Observation of the relationship between Lake Macrophyte Nutrient Index (LMNI) scores and the change index confirms that species with high change index scores consistently have high nutrient affinity. This is not surprising, since cultural eutrophication, driven by agricultural intensification, has been a major influence on both groups of lakes (George, 1992; Fisher *et al.*, 2009). However, it is notable, especially in the case of the broads, that low change index values are not at all confined to those species normally associated with less fertile conditions, thus implying that species tolerating more nutrient-rich conditions have also declined significantly (e.g. *Hydrocharis morsus-ranae*, *Stratiotes aloides*). It is likely that some of the lakes considered here were already quite enriched by the time of the earliest records, meaning that some species present historically had relatively high LMNI scores, e.g. *Sagittaria sagittifolia* and *Potamogeton lucens* in the broads, and *Myriophyllum verticillatum* and *Butomus umbellatus* in the meres. Nevertheless, parish records indicate that land cover and rural population densities have changed sufficiently over the last century for nutrient loading to most of the lakes in this study to have increased significantly on average (Sinker *et al.*, 1985; George, 1992; Williamson, 1997; Greenwood, 1999; Fisher *et al.*, 2009). Subsequent losses of some species may therefore be due more to other factors only indirectly linked to eutrophication, such as the changes in physical habitat structure that are likely to have accompanied reedswamp dieback in the broads (Boorman & Fuller, 1981), expansion of invasive species (Ellis, 1963), or increased densities of benthivorous cyprinid fish (Timms and Moss, 1984; Scheffer *et al.*, 2003). In exploring the underlying basis of a general change index constructed for British vascular plants Preston *et al.* (2002) also noted that many rather nutrient tolerant species had declined significantly alongside more nutrient sensitive ones.

3.5.3 Application of the index

The index has the potential to classify lakes into those least changed and those most impacted, based on current macrophyte assemblages, as illustrated in Figure 3.8. Those lakes which are thought to be in a better ecological condition generally have relatively low average index scores, such as the Martham Broads and Whitemere, whereas those known to have impacted macrophyte communities, such as Ranworth Broad and

Rostherne Mere, have high scores. Whilst this has the potential to provide a very useful tool for lake classification, it must be remembered that species composition is only one aspect of the vegetation community, and that the average lake index in its simplest form does not say anything about species richness or abundance of species. For example, Horsey Mere has the lowest index score of all the broads, but is known to have a low abundance of a few species, reflecting its often turbid state, so is not generally thought of as being in good ecological condition. It still has a low average score, however, as those species which it does possess, such as *Chara baltica* and *Potamogeton x salicifolius* have low index scores. The low diversity of the lake also means that it has few of the higher scoring species which are ubiquitous in many of the other lakes, such as *Nuphar lutea* and *Ceratophyllum demersum*. It is important to note that the use of a change index in this way cannot measure how much any individual site has changed over time, since the baseline for each site is generally unknown (due to the incompleteness of the historical record) or it would naturally have varied between sites within a region due to site-specific factors. The average change index therefore effectively reflects the relative importance at a site of species that have declined across a complex of lakes as a whole.

Visualisation, based on physical examples, is an important part of developing an appropriate guiding image for restoration (Palmer *et al.*, 2005). Ecologists have struggled to identify the biology that equates with reference conditions when most or all examples of a habitat type are impacted. Hence the robust use of historical recording data offers significant potential in this area. It may also serve to provide targets for, or indicators of successful restoration. Diagnosing the full causes of historic changes in lake vegetation will prove challenging in systems exposed to multiple stressors. The use of a change index to identify declining species, when allied to knowledge of species' ecological requirements, could aid interpretation of macrophyte community change, without making assumptions which cannot be supported by a dataset characterised by gaps and inconsistent recording methods.

CHAPTER 4 The use of historical macrophyte records to identify causes of long term change in lowland lakes.

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4.1 Abstract

Lake macrophytes are often surveyed in order to determine the ecological status of lakes, the distribution of individual species over environmental gradients commonly being used to infer general or specific causes of degradation. This ecological information can also shed light on past environmental conditions in those lakes for which historical records are available. This study analyses the underlying ecological basis for an index of macrophyte change derived from historical records for two lake districts in England, the Norfolk Broads and West Midland Meres. The change index, based on the modern day survival of each species in individual lakes in which they were historically recorded, provides a measure of the extent of species decline within each lake district over the last 100-150 years. Functional groups determined from morphological and regenerative traits displayed significant differences in change index values in both groups of lakes, but declining taxa occurred across a wide range of plant growth forms. The change index was analysed in light of published information on plant ecological associations in order to identify the main factors driving long term compositional change. Non-hierarchical clustering of species based on their ecological traits resulted in groups with distinct change index values, indicating that changes in the status of species could be partly explained by their ecological preferences. Of these traits, trophic preference was consistently the most important, with species of less fertile habitats consistently experiencing the greatest declines. However, some characteristically eutrophic species have also declined significantly. In these cases increasing loss of shallow water, low energy habitats, or fluctuating water levels, appear to have been contributory factors.

4.2 Introduction

Macrophytes play an important part in the functioning of lakes, particularly shallow lakes or those with relatively small circumference to area ratios where the colonisation potential and thus influence of aquatic plants is likely to be greatest (Jeppesen *et al.*, 1998; Moss, 1998). Different attributes of macrophytes, such as richness, cover, general community composition, or the presence or absence of indicator species can therefore give information on the ecological quality of a lake (Seddon, 1972; Palmer *et al.*, 1992; Moss *et al.*, 2003; Duigan *et al.*, 2007; Willby *et al.*, 2009). Macrophytes are one of several biological quality elements that must be considered in the ecological classification of lakes, required under the WFD, as well as being a feature of interest in many designations of freshwater sites as Special Areas of Conservation, under the EU Habitats Directive. To this end, extensive sampling programs have been initiated to gather contemporary data on species distributions and lake attributes in order to type lakes and to devise systems to classify lake status or conservation value, based on their macrophyte assemblages (Moss *et al.*, 2003; Duigan *et al.*, 2007, 2008; Penning *et al.*, 2008a; Penning *et al.*, 2008b; Willby *et al.*, 2009). Although macrophyte assemblages can vary systematically along recognised pressure gradients, such as nutrient concentrations (Penning *et al.*, 2008b; Willby *et al.*, 2009), knowledge of the trophic status of a lake does not necessarily equate to its ecological status as defined in the WFD. Thus, the Directive requires that status is evaluated by assessing the amount to which the biology deviates from that expected under “undisturbed conditions” (European Union, 2000), regardless of the cause of that deviation. Assessments of biotic integrity undertaken with respect to the US Clean Water Act follow a similar rationale (Patrick and Palavage, 1994).

The question of what constitutes a macrophyte community characteristic of "undisturbed conditions" is pivotal in terms of assessing ecological status, yet such conditions may prove elusive, especially so in the case of highly impacted lowland lakes for which un-impacted modern day analogues are scarce or lacking on a European scale (Bennion and Batterbee, 2007). Historical macrophyte records collected from lakes >100 years ago could thus offer an important insight into the composition of past macrophyte communities, complementing information that can be extracted from more conventional palaeoecological sources, such as pollen or macrofossils (Davidson *et al.*, 2005; Ayres *et al.*, 2008). By comparing the past and present distributions of a species in particular lakes, a change index can be assigned to each species (Chapter 3), which then can be interpreted in relation to species ecological traits. Other studies investigating change in the British Flora have also attempted to identify drivers of change by correlating change indices against various known attributes of species (e.g. Preston *et al.*, 2002; Telfer *et al.*, 2002; Braithwaite *et al.*, 2006). For example, Braithwaite *et al.* (2006) used BSBI repeat survey data at a tetrad scale (2 km x 2 km) to calculate a "change factor" for each species. They then divided the flora into "Broad Habitat" types (e.g. wetland, aquatic habitats, calcareous grassland, etc) and took the mean change factor of species within each group and correlated this to various known ecological attributes of the species, such as Ellenberg values for light (L), acidity (R) and fertility (N). They also used one-way analysis of variance to look for differences in the change factor across various categorical variables, such as whether species are native to Britain, perennation habit and level of north-south distribution. The disadvantages of this coarse-grained approach may be more pronounced in the case of aquatic habitats than other Broad Habitats as changes within waterbodies could be masked by changes in the number and nature of waterbodies in the countryside as a whole.

This study explores the underlying ecological basis of an index based on the change in distribution of macrophytes in two sets of lowland lakes in England, over the last 150 years (Chapter 3). By analysing the ecological profiles of those species whose distributions have shown the greatest change within these two lake districts this study attempts to identify the main environmental drivers of macrophyte change in shallow lowland lakes.

4.3 Methods

4.3.1 Geographic area

This study focuses on two groups of lowland, predominantly base-rich lakes in England: the Norfolk Broads and the West Midland Meres. The broads are a series of flooded medieval peat workings associated with a number of rivers near the East Anglian coast. They range in area (from 1 ha to 140 ha) and are very alkaline (2-4 meq/L) and shallow (mostly <2 m deep) (George, 1992; Moss, 2001). The meres of the English West

Midlands are a series of water-filled hollows in the glacial drift, grouped in local clusters. Alkalinity may be as low as 0.05 meq/L but most sites are base-rich (>2 meq/L). The meres vary in depth (from less than 1 m to ~50 m maximum depth) and area (from < 1 ha to 75 ha) and are largely ground water fed (Reynolds, 1979). Both groups of lakes have been subjected to eutrophication over the last 150 years and, given their lowland situation, are surrounded by intensive agriculture and are near to centres of human population.

4.3.2 The species change index

A change index was derived using a dataset compiled of macrophyte records collected from *ca.* 90 lakes in the Norfolk Broads and West Midland Meres spanning a period of over 200 years. The dataset contained historical plant records collected from a variety of sources, including herbarium specimens, published records, county floras and naturalists' notes, as well as records from modern surveys and sampling regimes. For more detail on the sources or the issues encountered in collecting and using these data see Chapter 2 and Chapter 3.

The change index was based on species persistence over the last 200 years, within individual lakes. Species persistence, measured as the proportion of those lakes which historically supported a species, and which still contained that species in the modern period, was found to have a linear relationship with current day levels of occupancy across all lakes within a lake district (i.e. the number of lakes occupied as a proportion of all lakes surveyed). This relationship was used to derive change index scores for species with limited historical data. A separate index was calculated for the broads and meres, though these were subsequently found to be highly correlated. Low index values represent species which have declined (i.e. have been lost from a high proportion of the lakes in which they occurred historically) and have restricted modern distributions (i.e. occur in a small proportion of the available lake resource), whereas high index values are an indication of species persistence and large modern distribution. For more details on the calculation of the index see Chapter 3.

4.3.3 Species selection

For the purposes of this study, macrophytes were broadly defined as having an Ellenberg F (moisture) value of ten or above (Ellenberg *et al.*, 1991; Hill *et al.*, 2004). In the broads dataset, with two exceptions (*Littorella uniflora* and *Hippuris vulgaris*) species with an Ellenberg F value of ten were ignored since contemporary surveys do not systematically record marginal vegetation (Jackson, 1983). In the meres dataset, four additional species, *Limosella aquatica* and *Lythrum portula* (with Ellenberg F values of 8), and *Ranunculus hederaceus* and *Ranunculus omiophyllus* (with Ellenberg F values of 9) were also included, as they were considered to have a sufficiently strongly aquatic habit to be treated as macrophytes for the purposes of this study. The Ellenberg classification deals only with vascular plants. Since charophytes are well represented in the historical record for these lakes, and are an important component of the aquatic vegetation of base-rich lakes, they were also included in this study. Aquatic bryophytes, with the exception of the floating liverwort *Riccia fluitans*, were excluded as they were virtually absent from the historical record. Where there were uncertainties over nomenclature or identification, or an aggregate name was used widely in some sources of records, species were merged into groups, e.g. all the *Callitriche* were merged under "*Callitriche* spp.", *Potamogeton berchtoldii* and *pusillus* were merged under "*Potamogeton pusillus*", and all the Ranunculaceae of the subgenus Batrachium were merged under "*Ranunculus* subgenus Batrachium" with the exception of *Ranunculus circinatus* which was considered sufficiently distinctive for identifications to be generally reliable. All other nomenclature conformed to Stace (1997) and Bryant *et al* (2002). The list of species analysed contained 118 species in total across the broads and meres: 61 in the broads and 100 in the meres (Table 4.1).

Table 4.1. Macrophyte species included in the analysis showing: *k* - mean group membership in both broads and meres, change index values derived from both the broad and meres historical data, Ellenberg R (acidity) and Ellenberg S (salinity) values, Lake Macrophyte Nutrient Index (LMNI) values, and functional group membership (FG) as detailed in Willby *et al.* 2000.

	K-mean group		Change index		Ellenberg			
	Broads	Meres	Broads	Meres	R	S	LMNI	FG
Acorus calamus		6		-0.946	7	0	8.157	21
Alisma plantago-aquatica		4		1.550	7	0	7.255	13
Apium inundatum		1		-2.696	6	0	5.693	22
Apium nodiflorum		4		0.665	7	0	7.702	22
Azolla filiculoides	2		-2.802		8	0	9.278	1
Baldellia ranunculoides		1		-2.696	6	0	5.578	13
Berula erecta		4		0.316	7	0	7.482	22
Butomus umbellatus	2	6	-2.802	-1.840	7	0	8.457	13
Callitriche sp.	1	4	0.128	1.847	6	0	6.899	
Carex elata		3		1.151	7	0	5.483	19
Carex lasiocarpa		1		-1.840	6	0	4.874	19
Carex limosa		3		-2.696	4	0		19
Carex rostrata		1		0.316	4	0	4.459	19
Carex vesicaria		4		0.316	5	0	5.021	19
Ceratophyllum demersum	4	2	1.991	-0.176	7	1	8.666	5
Chara aspera	4	2	-0.924	-2.696	7	1	7.098	2
Chara baltica	4		-0.924		8	2	8.599	2
Chara canescens	1		-2.802		8	2	8.133	2
Chara connivens	4		-0.432		8	1	7.924	2
Chara contraria var. *contraria*	4	2	-0.736	-1.840	8	0	7.469	2
Chara curta	4		-1.449		8	1	6.516	2
Chara globularis	4	2	0.579	-0.946	7	1	7.342	2
Chara hispida	3		-0.304		7	1	6.867	2
Chara intermedia	4		-0.736		8	1	7.998	2
Chara rudis		5		-2.696	8	0	6.935	2
Chara virgata	4	2	-1.152	-0.946	5	0	5.550	2
Chara vulgaris	4	2	0.405	-0.084	7	0	7.194	2
Crassula helmsii		1		-1.432	6	0	6.176	5
Damasonium alisma		4		-2.696	5	0	4.639	13
Elatine hexandra		3		-0.946	5	0	5.409	11
Eleocharis acicularis		4		-0.773	7	1	6.749	4
Eleocharis multicaulis		3		-2.696	4	0	1.925	4
Eleocharis palustris		4		1.008	6	1	5.484	20
Eleogiton fluitans		1		-1.840	4	0	3.452	15
Elodea canadensis	4	2	1.288	0.938	7	0	7.139	5
Elodea nuttallii	4	2	0.315	-1.156	7	1	6.923	5
Equisetum fluviatile		1		0.801	6	0	5.153	20
Glyceria fluitans		4		0.801	6	0	6.170	13
Glyceria maxima		6		-0.626	7	0	8.242	21
Glyceria x pedicellata		4		-1.432	7	1	6.880	13
Hippuris vulgaris	1	6	-0.575	-1.840	6	1	6.405	7
Hottonia palustris	3	5	-1.887	-0.380	7	0	7.327	7
Hydrocharis morsus-ranae	4	2	-0.575	-2.696	7	0	8.261	8
Hypericum elodes		3		-1.840	3	0	4.950	11
Isoetes lacustris		1		-2.696	4	0	3.090	4
Juncus bulbosus		1		0.086	4	0	3.717	4
Lemna gibba	2	6	-1.887	-1.432	7	1	9.240	1
Lemna minor	2	6	1.387	2.093	7	0	7.579	1
Lemna minuta	2	6	-0.575	-0.626	7	0	8.640	1
Lemna trisulca	2	6	0.751	0.801	7	0	7.815	1
Limosella aquatica		3		-2.696	5	0	6.494	11
Littorella uniflora	1	1	-2.802	-0.946	5	0	4.701	4
Lobelia dortmanna		1		-2.696	5	0	2.460	4
Lythrum portula		3		-2.696	5	0	5.562	11
Menyanthes trifoliata		3		-0.176	4	0	4.764	10
Myriophyllum alterniflorum		1		-2.696	5	0	4.537	7
Myriophyllum spicatum	2	6	-0.575	-0.380	7	0	7.845	7
Myriophyllum verticillatum	2	6	-0.736	-2.696	7	0	8.667	7
Najas marina	4		0.579		9	0	8.835	14
Nitella flexilis agg.	4	2	-0.432	-1.156	4	0	5.604	2
Nitella mucronata	4		-0.736		6	0	8.421	2
Nitellopsis obtusa	4		-0.736		8	1	7.617	2
Nuphar lutea	4	2	1.011	1.741	7	1	6.924	12
Nuphar pumila		5		-1.840	6	0	5.327	12
Nuphar x spenneriana		2		-1.156	6	0	5.610	12
Nymphaea alba	4	2	0.493	0.869	6	0	5.540	12
Oenanthe aquatica		4		0.086	7	0	8.306	22
Oenanthe fluviatilis	2		-2.802		8	0	7.665	22
Persicaria amphibia		6		1.463	6	0	7.254	10
Phragmites australis		6		1.463	7	2	7.192	21
Pilularia globulifera		3		-2.696	4	0	5.179	4
Potamogeton acutifolius	4		-1.887		7	0	7.485	14
Potamogeton alpinus	1	2	-2.802	-1.840	6	1	5.788	16
Potamogeton coloratus	1	1	-1.887	-2.696	8	0	6.697	16
Potamogeton compressus	4		-2.802		7	0	7.998	14
Potamogeton crispus	2	6	0.665	0.316	7	1	7.644	17
Potamogeton friesii	4	2	-0.075	-2.696	7	0	7.643	14
Potamogeton gramineus		1		-2.696	6	0	5.512	16
Potamogeton lucens	4	2	-1.887	-1.840	6	0	7.017	17
Potamogeton natans	1	2	-1.449	-0.626	6	0	5.158	16
Potamogeton obtusifolius	4	2	-0.924	-0.626	6	0	6.718	14
Potamogeton pectinatus	2	6	0.837	0.086	7	2	8.247	15
Potamogeton perfoliatus	4	2	-0.736	-1.432	6	1	5.825	17
Potamogeton polygonifolius		1		-1.432	4	0	3.497	16
Potamogeton praelongus	4	2	-2.802	-2.696	7	1	5.765	16
Potamogeton pusillus/berchtoldii	4	2	0.837	0.597	7	1	7.608	14
Potamogeton trichoides	2		-1.887		7	0	8.389	14
Potamogeton x angustifolius		2		-2.696	6	0	5.693	16
Potamogeton x cooperi		2		-2.696	7	1	5.669	17
Potamogeton x salicifolius	4		-1.449		7	0	6.886	17
Potentilla palustris		3		0.597	5	0	4.591	10
Ranunculus circinatus	3	5	-0.185	-0.176	7	0	8.645	5
Ranunculus lingua		4		-0.084	6	0	7.613	10
Ranunculus subgenus *Batrachium*	1	6	-1.887	0.242	6	0	6.862	
Riccia fluitans		5		-2.696	8	0	6.632	1
Rorippa microphylla		6		-0.946	7	0		11
Rorippa nasturtium-aquaticum		6		1.008	7	0	7.583	11
Rumex hydrolapathum		4		0.242	7	0	7.705	10
Sagittaria sagittifolia	2		-1.887		7	0	7.877	12
Scheuchzeria palustris		3		-2.696	3	0		20
Schoenoplectus lacustris	1	2	-0.924	0.388	7	0	7.592	20
Schoenoplectus tabernaemontani		4		-0.380	8	3		20
Sparganium emersum	2	6	-0.575	-0.773	7	0	6.588	13
Sparganium erectum		6		1.847	7	0	7.536	21
Sparganium natans		1		-2.696	6	0	4.841	13
Spirodela polyrhiza	3	5	-1.887	-0.946	7	1	8.791	1
Stratiotes aloides	3	5	-1.449	-2.696	7	1	8.506	8
Subularia aquatica		1		-2.696	5	0	2.932	4
Typha angustifolia		6		0.869	7	1	7.124	21
Typha latifolia		6		1.463	7	0	7.827	21
Utricularia australis	3		-2.802		5	0	4.647	9
Utricularia intermedia	3		-2.802		4	0	2.741	9
Utricularia minor	3	3	-2.802	-2.696	4	0	2.972	9
Utricularia vulgaris	3	5	-1.152	-2.696	6	0	5.386	9
Veronica anagallis-aquatica		4		-1.156	7	0	7.598	11
Veronica beccabunga		4		1.463	6	0	6.981	11
Veronica catenata		4		-0.626	7	0	8.067	11
Zannichellia palustris	2	6	0.665	0.733	8	2	8.492	15

4.3.4 Analysis

A matrix of the ecological profiles of the species was compiled from the literature (e.g. Sledge, 1949; Spence and Chrystal, 1970; Haslam *et al.*, 1975; Moore, 1986; Clapham *et al.*, 1987; Grime *et al.*, 1988; Hultgren, 1989; Blindow, 1992; Stewart and Church, 1992; Fitter and Peat 1994; Preston, 1995; Vandenbrink *et al.*, 1995; Hroudova *et al.*, 1996; Preston and Croft, 1997; Stace, 1997; Luo *et al.*, 2008), as well as personal observation of species at these and other lake sites in the UK. These included 17 attributes distributed across 4 multistate-ordered habitat variables: Water depth, water level fluctuation, water flow and trophic status. These variables were chosen because they are relatively well covered in the literature, and were expected to be factors which have changed in the broads and meres over the last 100 years (George, 1992; English Nature, 1998; Fisher *et al.*, 2009). Categorical scores were assigned to each species for for each habitat attribute, with '0' indicating no recorded association, '1' indicating a weak or variably reported association, and '2' indicating a strong association of that species with that habitat attribute. In addition to the categorical variables, two ordinal and one continuous variable describing species-environment associations were also included. These were the Ellenberg's indicator values for acidity (R) and salinity (S), adjusted for the British flora (Ellenberg *et al.*, 1991; Hill *et al.*, 1999; Hill *et al.*, 2004) and the Lake Macrophyte Nutrient Index (LMNI), an algorithmic adjustment of Ellenberg's N scores specifically for aquatic macrophytes (Willby *et al.*, 2009), undertaken following the approach described by Hill *et al.* (1999). Since most vascular plant hybrids, plus all charophytes, lack Ellenberg scores suitable values were derived for these taxa based on published accounts (e.g. Stewart & Church, 1992, Preston, 1995; Preston & Croft, 1997). The 22 habitat characteristics are given in Table 4.2.

Table 4.2. The 22 habitat characteristics used in correlations, including 17 which are subdivisions of 4 multistate habitat variables which were used in the k-means cluster analysis.

Multistate variables	**Characteristics**
Water depth	<0.5 m 0.5-2 m 2-4 m >4 m
Water level stability	Permanent/stable Permanent/fluctuating Intermittent exposure Prolonged exposure
Water speed	Sluggish/standing Slow Moderate Fast
Trophic status of water column	Oligotrophic Oligo-mesotrophic Meso-eutrophic Eutrophic Hypereutrophic
Other variables:	Lake macrophyte nutrient index (LMNI) Ellenberg R (acidity) Ellenberg S (salinity)

Species were partitioned into groups sharing similar habitat characteristics by non-hierarchical *k*-means cluster analysis based on the 4 multistate habitat variables, using the algorithm of Hartigan and Wong (1979) and the statistical software R (2008). The habitat variables were first standardised by making the sum of each of the 4 multistate variables for each species equal to one. Species were chosen at random to act as group centroids. This ‘random starts’ procedure was carried out 100 times and the solution which minimised the total error sum of squares, i.e. the distance between cluster members and the cluster centroid, was chosen (Legendre and Legendre, 1998). The number of groupings was determined by plotting the within groups sum of squares against the number of clusters extracted (Everitt and Hothorn, 2006). By doing this, the number of groups could be chosen which maximised the within group sum of squares, whilst retaining enough species in each group for meaningful analysis. Cluster analysis was performed separately for the broads and meres as they contained different species and different numbers of species. The broads species were clustered into four groups, and the meres, which contained more species, into six groups.

The results of *k*-means cluster analysis were visualised on a biplot after principal component analysis (PCA) of the species environmental preferences used in the cluster analysis (Fig. 4.1).

In order to test whether the species change index was related to habitat characteristics, species were divided into their *k*-mean groups. Kruskal-Wallis tests were carried out on both broads and meres index values, to test for differences between the cluster groups, using the statistical software package MINITAB 14. Groups were then tested against each other using the Mann–Whitney test to check for equal probability distributions (i.e. that the two samples are drawn from a single population), in order to ascertain which groups differed most in relation to the change index. The frequency and distribution of change index values within each of the *k*-mean groups (for both the broads and meres separately) were visualised using histogram plots.

Species were also ordered into functional groups composed of species sharing homogenous collections of attributes for a range of morphological and regenerative traits (Willby *et al.*, 2000). These functional groups are detailed in Table 4.3. The variation in within-group relative to between-group change index values was then tested for each group of lakes by ANOVA. Given that there was no significant heterogeneity of variances in change index values between these groups, (Bartlett's test, p=0.459 and p=0.92 for the broads and meres respectively), a one-way ANOVA was carried out on both broads and meres index values. Since Willby *et al.*, (2000) did not consider charophytes and some emergent species in their analysis these species were assigned to new groups based on growth form characteristics, as indicated in Table 4.1 and Table 4.3.

The relationship between the change index and the habitat preferences in Table 4.2 was further explored using Spearman's rank correlations. As the relationship between the change index and trophic niche was found previously to break down for those species with higher LMNI values (Chapter 3), the correlations were also performed independently on an exclusive group of more eutrophic species (LMNI >6) to determine if different trends in relation to habitat characteristics existed within this group

Table 4.3. Functional groups based on morphological features and habitat use (see Willby *et al.*, 2000).

Functional group code	Name	Growth form and morphology
1	lemnids and ricielids	Very small, free floating plants
2	charophytes	Small-medium, predominantly submerged perennials or annuals with simple branched structure of capillary leaves, high reproductive output
4	isoetids	Small-medium sized, submerged or amphibious, rosette forming plants with stiff, tubular evergreen leaves
5	elodeids and ceratophyllids	Medium-large, submerged, canopy forming, multi-branched perennials with densely arranged small laminar or rigid dissected leaves. Mainly vegetative
7	myriophyllids and herbids	Medium-large, submerged or partially emergent, rhizomatous perennials with flexible, dissected-leaved submerged foliage
8	hydrocharids and stratiotids	Medium-large, free-floating rosettes of mainly floating or aerial leaves linked by stolons
9	utricularids	Small-medium, submerged, loosely or unanchored perennial with multiple branches and small, dense, flaccid, capillary-leaves. Conspicuous aerial flowers
10	magno and parvonymphaeids	Large, mostly emergent or floating leaved, stand-forming, stoloniferous or rhizomatous perennials with large, insect-pollinated aerial flowers
11	herbids and elodeids	Small-leaved, amphibious or submerged, annual or perennial, prostrate plants
12	magnonymphaeids and sagittarids	Large-very large, unbranched, rhizomatous perennials with large expanded, submerged and floating leaves
13	vallisnerids and sagittarids	Medium-sized, perennial, basal rosette of submerged elongate leaves with expanded or strap-shaped floating and/or emergent foliage
14	parvopotamids	Small-medium, submerged, fine, linear leaved pondweeds with multiple branched foliage
15	magno- and parvopotamids	Submerged, medium-sized, rhizomatous perennials with fine or tubular leaves
16	parvonymphaeids and magnopotamids	Medium-large, branched, submerged rhizomatous perennials with expanded medium submerged and floating leaves
17	magnopotamids	Medium-large, branched, submerged rhizomatous perennials with expanded medium-large submerged laminar leaves.
19	carices	medium sized, linear leaved, spreading plants with rosette growth form
20	rushes and horsetails	medium sized, linear-or tubular-leaved, erect, rhizomatous emergent plants
21	large, emergent monocots	large-very large, rhizomatous emergent plants
22	aquatic/semi aquatic umbellifers	facultative submerged plants with capillary or dissected leaves, and expanded emergent leaves

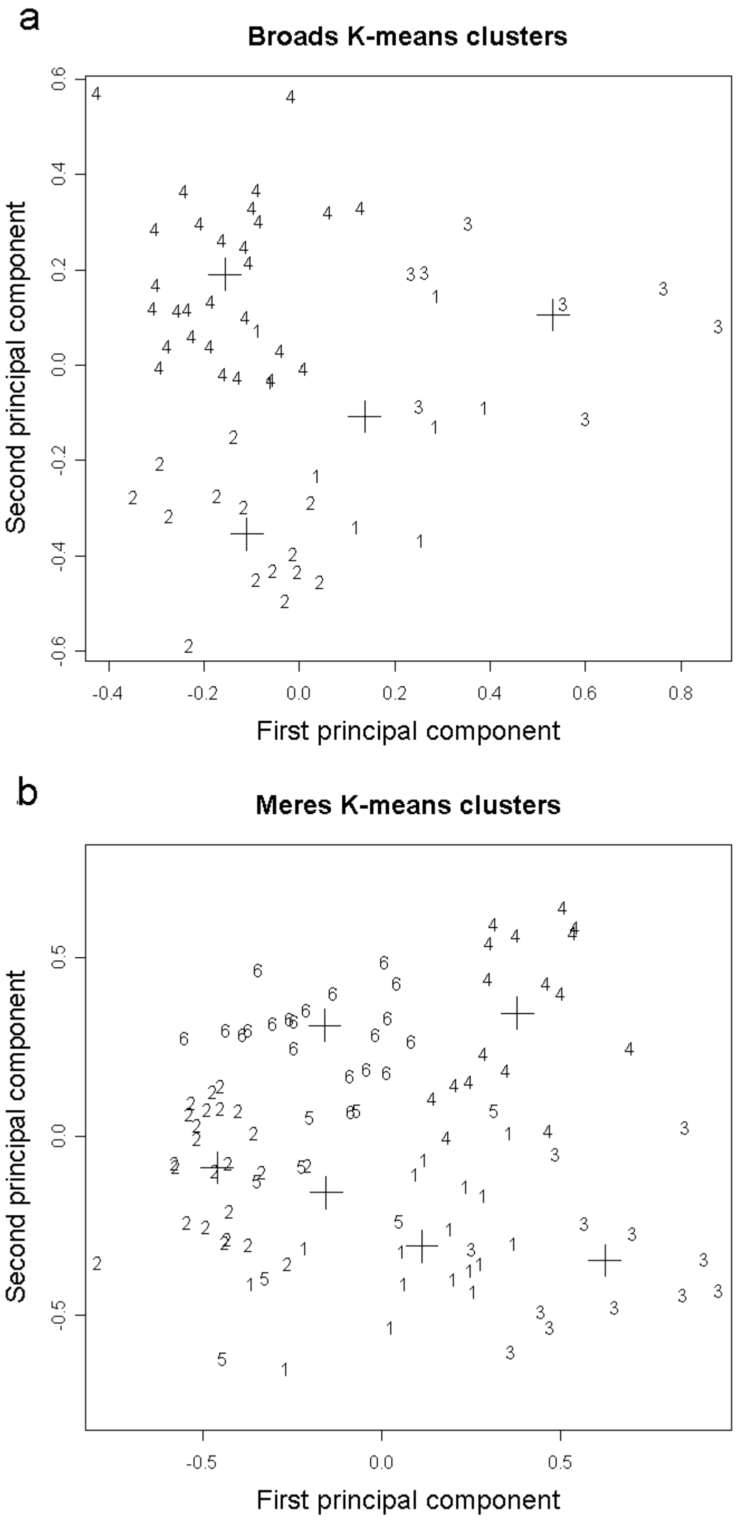

Figure 4.1 *K*-mean cluster analysis of the species in the a) broads and b) meres, based on a set of their habitat associations (see Table 4.2). Cluster centers are indicated with a cross. Species associated with each *k*-mean numbered group are detailed in Table 4.1.

4.4 Results

The *k*-means clustering split the broads species into four groups with 9, 9, 15 and 28 members respectively. The meres species were split into six groups of 8, 12, 17, 17, 22 and 24 members respectively. The group memberships of the species are given in Table 4.1. The results of the *k*-means cluster analysis are also shown on a biplot of the ecological trait data, using principal components analysis (PCA) (Figure 4.1). The grouping pattern and dispersion differs slightly between the broads and meres on account of the differing numbers of species being clustered, and the different number of groups they were being clustered into. Despite this, groups 4, 3 and 2 in the broads held many of the same species as groups 2, 5 and 6 in the meres (Table 4.1).

The mean ranks of the change index values were significantly different among the *k*-mean cluster groups in the broads (Kruskal–Wallis H = 8.95, 3 d.f., P = 0.03) and meres (Kruskal–Wallis H=27.78, 5 d.f., P = 0.000). This indicates that the change index, and thus the change in macrophyte species distribution in the broads and meres over the last 100 years, is influenced by one or more of the four environmental variables used in the classification.

Mann-Whitney U test probabilities are displayed in Table 4.4. Figure 4.2 and Figure 4.3 show the difference in change index between the *k*-mean groups. In the broads, significant differences in probability distributions of change index values were found between group 4, and groups 1 and 3 (Table 4.4 and

Figure 4.2). Groups 1 and 3 had very little difference in probability distribution of the change index, as did groups 2 and 4 (Table 4.4 and Figure 4.2). In the meres, the groups with the most significantly different probability distributions of the change index were groups 4 and 6 in relation to the other groups, with groups 4 and 6 also not significantly different from one another (Table 4.4 and Figure 4.3). None of the other groups had significantly different change index probability distributions, although very low change index values were most prevalent in groups 1 and 3 (Figure 4.3).

Table 4.4. Mann-Whitney U test comparing the probability distribution of the species change index between the k-mean cluster groups. Numbers are P values, with * representing significance at the 95% level.

		Broads				
	Group No.	1	2	3	4	5
Meres	1		0.1641	1.0000	0.0149*	
	2	0.0589		0.1939	0.7013	
	3	1.0000	0.1686		0.0142*	
	4	0.0004*	0.0100*	0.0048*		
	5	0.9498	0.2234	1.0000	0.0034*	
	6	0.0002*	0.0108*	0.0033*	0.8984	0.0055*

There was a highly significant difference in the mean index values for the functional groups of Willby *et al.* (2000) for both the broads and meres (ANOVA p=0.007 and p=0.006 respectively) (Figure 4.4), suggesting that the index values of species relate strongly to their functional and morphological characteristics.

The results of Spearman’s correlation between the change index in the broads and meres and the ecological characteristics of species (Table 4.2) are presented in Table 4.5. In both groups of lakes, significant positive correlations were found between the species change index and association with hypertrophic conditions, and significant negative correlations were found with association with oligotrophic and oligo-mesotrophic conditions. Additionally, in the broads, significant positive correlations were found between the species change index and species associations with 2-4 m depth water and permanent/stable water level, and significant negative correlations were found with associations with water depth less than 0.5 m and intermittent exposure. In the meres, significant positive correlations were also found between the change index and environmental preferences towards sluggish/standing water, eutrophic conditions, LMNI, and Ellenberg's indicator values for acidity (R).

Table 4.5. The results of Spearman's correlation between the species change index in each lake district and species environmental preferences.

	All species		LMNI>6	
Change index:	Broads	Meres	Broads	Meres
<0.5 m	-0.28*	0.19	-0.29*	0.13
0.5-2 m	-0.08	-0.11	-0.13	0.00
2-4 m	0.3*	-0.15	0.34*	-0.14
>4 m	0.12	-0.15	0.17	-0.13
Permanent/stable	0.29*	-0.08	0.22	-0.20
Permanent/fluctuating	0.13	0.15	0.06	0.14
Intermittent exposure	-0.38**	0.08	-0.31*	0.15
Prolonged exposure	-0.19	-0.10	-0.18	0.02
Sluggish/standing	-0.11	-0.26*	-0.08	-0.41**
Slow	0.12	0.16	0.02	0.24
Moderate	0.04	0.17	0.11	0.36**
Fast	0.01	0.15	-0.02	0.14
Oligotrophic	-0.29*	-0.36***	0.00	-0.16
Oligo-mesotrophic	-0.31*	-0.35***	-0.07	-0.08
Meso-eutrophic	-0.06	-0.05	-0.22	-0.06
Eutrophic	0.10	0.25*	-0.24	-0.15
Hypereutrophic	0.42**	0.48***	0.32*	0.32*
LMNI	0.18	0.32**	-0.09	0.01
Ellenberg R (acidity)	0.15	0.27*	-0.09	-0.05
Ellenberg S (salinity)	0.20	0.13	0.22	0.07

* p<0.05, ** p<0.005, *** p<0.0005

For those species associated with more eutrophic conditions (species with LMNI>6), there was still a significant positive correlation between the change index and association with hypertrophic conditions in both the broads and meres. In the broads, there was still a positive correlation with the 2-4 m depth preference. Significant negative correlations were still found with species preferences of water depth less than 0.5 m and intermittent exposure. In the meres, species with LMNI>6 also retained a negative correlation between the change index and association with sluggish/standing water. The only additional significant correlation here was a positive one with association with moderate water velocity.

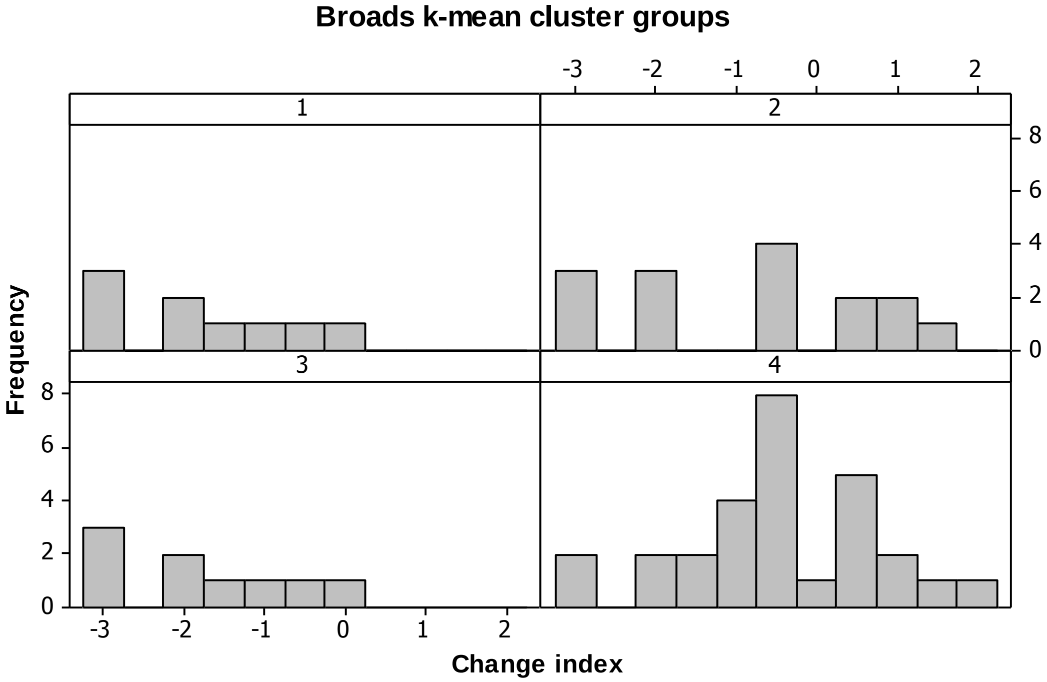

Figure 4.2 Histograms of the change index values found in each of the 4 broads *k*-mean cluster groups.

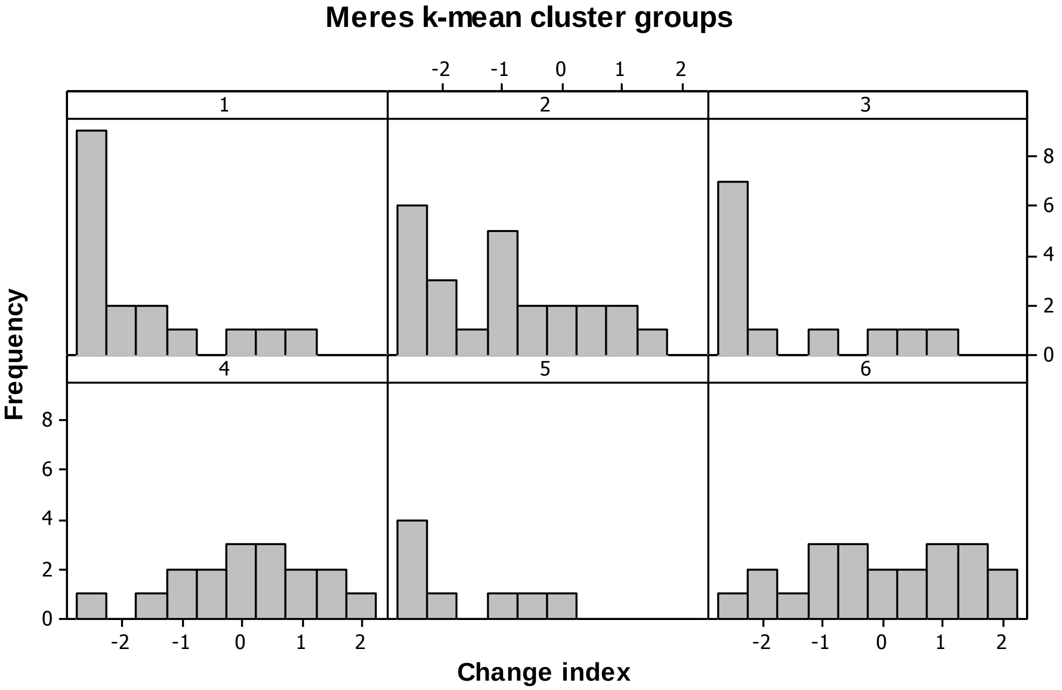

Figure 4.3 Histograms of the change index values found in each of the 6 meres *k*-mean cluster groups.

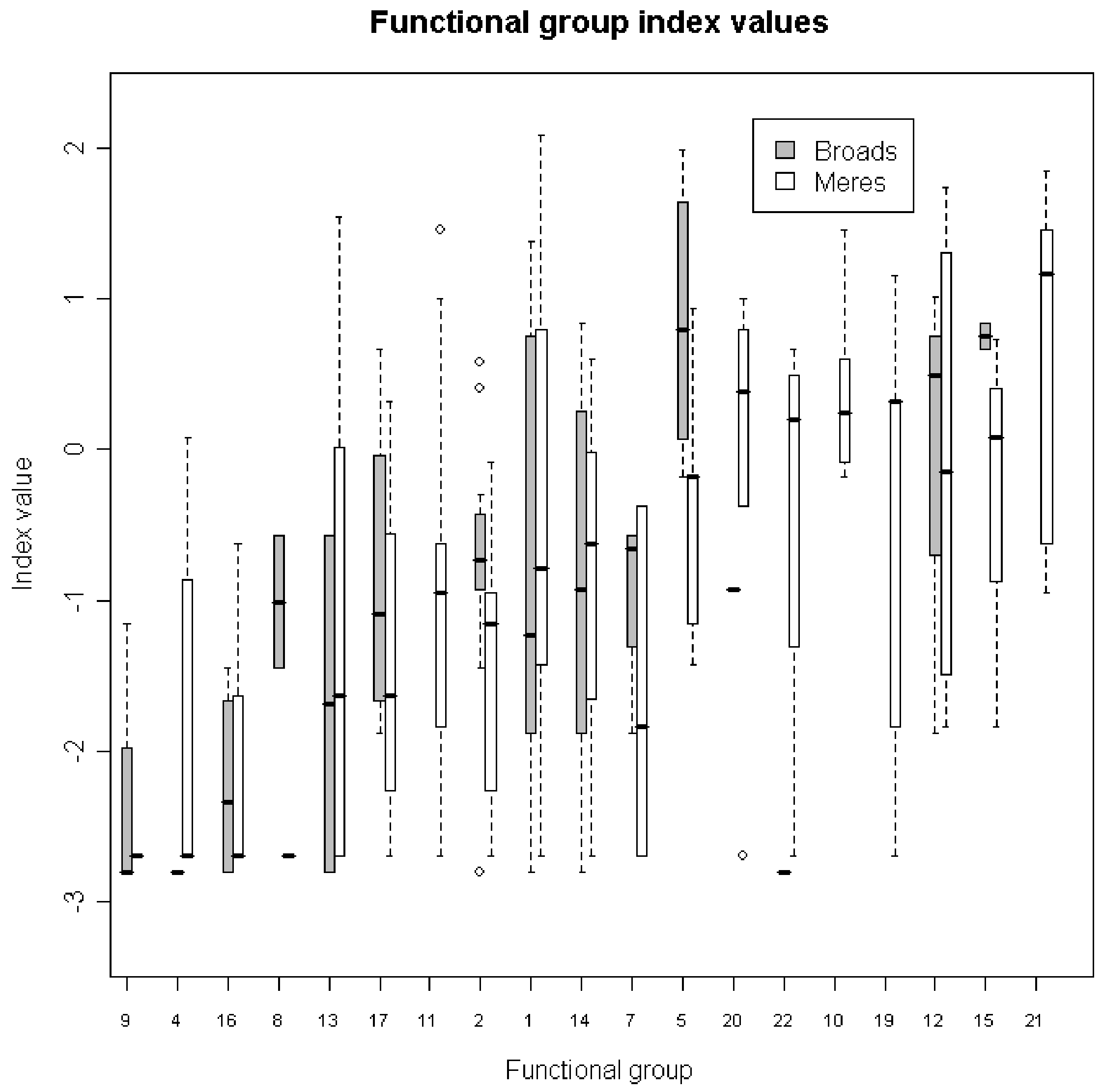

Figure 4.4 A boxplot of change index values for species within each functional group for both data sets, ordered by average change index value of species in each group.

4.5 Discussion

The lake district-specific species change indices used in this study are based on the survival of species in the lakes in which they were found ~100 years ago, ascertained using historical records (Chapter 3). By analysing these species change indices in the broads and meres this study hoped to link ecological attributes of these species to their level of decline or their persistence in these lakes over the last 200 years. Not only would this enable objective assessment of the main pressures on macrophyte species in these lake districts, but it would also help interpret the ecological context of an index based on historic records. This in turn would assess the effectiveness of the change index in gauging the ecological quality of lakes based on contemporary macrophyte records.

K-mean clustering based on species environmental preferences (water depth, water level stability, water speed and trophic status) identified distinct groups of species which varied significantly in their change index values. In the broads, group 4 (Table 4.1), which contained species such as *Ceratophyllum demersum*, *Elodea canadensis*, *Najas marina* and *Nuphar lutea*, showed significantly higher change index values, and hence less decline, than groups 1 and 3, (which included species such as *Littorella uniflora, Potamogeton alpinus, Schoenoplectus lacustris, Hottonia palustris, Stratiotes aloides* and *Utricularia vulgaris*), indicating that the four environmental variables; water depth, water level fluctuation, water movement and trophic state, together were important in influencing the amount of species change. In the meres, groups 4 and 6, which included high index score species such as *Apium nodiflorum, Glyceria maxima, Lemna minor*, *Myriophyllum spicatum, Typha latifolia* and *Zannichellia pulustris*, were the groups which had significantly higher change index values than groups 1, 2 and 3, with groups 1 and 3 being the most different. Groups 1 and 3 in the meres included those species with the lowest change index, and hence those which have suffered the greatest decline, such as *Baldellia ranunculoides, Myriophyllum alterniflorum, Potamogeton coloratus* and *Elatine hexandra*.

The index values were also strongly related to an established functional grouping based on morphological characteristics (Willby *et al.*, 2000) in both broads and meres. The functional groupings of (i) isoetids, (ii) hydrocharids and stratiotids, (iii) utricularids, and (iv) parvonymphaeids and magnopotamids (groups 4, 8, 9 and 16 respectively) (Table 4.3), were those with the lowest average index scores, suggesting that these species had declined the most in both lake districts during the period of the datasets. These functional groups contain many species which are generally regarded as being associated with less nutrient-rich conditions, such as *Isoetes lacustris*, *Littorella uniflora, Lobelia dortmanna, Utricularia* species and *Potamogeton gramineus,* but also species which typically favour more sheltered conditions such as *Utricularia vulgaris*, *Potamogeton coloratus, Stratiotes aloides* and *Hydrocharis morsus-ranae,* or species associated with deeper water, such as *Isoetes lacustris* and *Potamogeton praelongus* (Preston and Croft, 1997).

Eutrophication is the most important factor affecting community composition of macrophytes in lowland lakes in Europe (Carvalho and Moss, 1995; Sand-Jensen *et al.*, 2000; Penning *et al.*, 2008b). Therefore, it would be expected to find some correlation between the degree to which the distribution of a species has changed, and the nutrient profile of the species. Correlations between the change index and the ecological traits showed that the trophic niche of species was indeed an important factor influencing changes in the status of species in both the broads and meres. Thus, characteristically oligotrophic and oligo-mesotrophic species (e.g. *Littorella uniflora, Isoetes lacustris, Lobelia dortmanna* and *Utricularia minor*) were negatively correlated to the change index, while hypertrophic species (e.g. *Zannichellia palustris, Potamogeton pectinatus, Rorippa nasturtium-aquaticum, Rumex hydrolapathum* and *Typha latifolia*) were positively correlated, as expected. This confirms that species with oligo and oligo-mesotrophic preference have declined in both the broads and meres, and there are now a very limited number of lakes in both regions that continue to support such species. Conversely, those species associated with hypertrophic conditions have persisted or expanded over the last 100 years, and currently are widely distributed among the lakes of the broads and meres. Similar trends were observed in other studies of vegetational change in lakes across Europe (Arts and Leuven, 1988; Arts *et al.*, 1990; Rintanen, 1996; Sand-Jensen, 1997; Sand-Jensen *et al.*, 2000; Sand-Jensen *et al.*, 2008). For example, in Denmark, studies of macrophyte changes in lakes over the last 100 years also showed decline in some similar typically oligotrophic species, such as *Littorella uniflora* and *Utricularia sp*., and an increase in typically eutrophic species, such as *Potamogeton pectinatus* (Sand-Jensen *et al.*, 2000; Sand-Jensen *et al.*, 2008).

Given the pervasiveness of cultural eutrophication of lowland lakes, the evidence that species of low fertility habitats have been lost is affirming but unremarkable. More surprising is that, whilst the mere-specific species change index showed a positive correlation with the fertility rank of all macrophyte species (LMNI), the broads change index did not. Similarly, in the meres there was a correlation between the eutrophic attribute and the change index that was not replicated in the broads. The broads have suffered significant and well documented cultural eutrophication over the last 100 years, caused principally by the intensification of agriculture and the development of central sewerage systems in Norwich, the region's main centre of population (George, 1992; Williamson, 1997; Moss, 2001). It was therefore expected that the change in macrophytes would closely reflect this in their trophic niche. Since this is not entirely the case it raises the question of why some species of typically eutrophic habitats have persisted, whilst others have declined.

Chapter 3 has previously shown that species with high index scores (i.e. those that have not declined), are universally associated with highly fertile conditions, but that species with low change index scores (i.e. which have declined), are associated with fertility ranging from very high to very low. This is because some of the species which have declined in the broads, and hence have low change index values, such as *Hottonia palustris*, *Stratiotes aloides,* and *Potamogeton compressus*, are also strongly associated with eutrophic conditions. There is conclusive evidence, based on historical record data, for the decline of these and other associated species on a national scale (Preston *et* *al.*, 2002). It is notable however, that many of the species lost from the broads themselves continue to thrive in drainage ditches in the adjacent grazing marshes (George, 1992), or elsewhere in similar habitats, such as canals with low boat traffic (Willby *et al.*, 2001). Clearly niche characteristics, other than fertility, must be influencing historical changes in the status of plants in shallow lakes.

Interestingly, the variable persistence of aquatic plants of naturally fertile habitats appears to replicate a trend observed by Preston *et al.* (2002) in an analysis of possible causes for changes in the entire British vascular plant flora over the period 1930-1990. A variety of mechanisms have been invoked to explain the coexistence of species in fertile habitats. These include niche partitioning on alternative axes, establishment lotteries, physical patchiness or resource heterogeneity, or reduced interspecific competition due to disturbance (e.g. flood scouring, water level fluctuation, management, or grazing) (Grime, 1979; Kautsky, 1988; Townsend, 1989; Grime, 1998). When there are selective declines in species of fertile habitats the logical deterministic explanation is that one or more mechanisms that promote coexistence have, in some way, been compromised.

Having restricted the analysis to species associated with fertile conditions (LMNI>6), in the broads there was found to be a correlation between the change index and the water depth niche of different species, with those species preferring shallower water (<0.5 m) declining, and species with depth preferences of 2-4 m, stable or increasing. At first sight this seems counterintuitive, as the broads have been getting steadily shallower, especially in the last century when levels of eutrophication have led to increased sedimentation rates (Osborne and Moss, 1977; George, 1992). However, the physical structure of the broads has changed considerably over the last century due to the loss of fringing and within-lake reedswamp. This occurred quite dramatically in the 1940 & 50s (Boorman and Fuller, 1981), seemingly due to a combination of factors such as feral coypu (Ellis, 1963) and increases in nitrogen loading (Boar *et al.*, 1989). The reedswamp, consisting of emergent species such as *Phragmites australis*, *Typha angustifolia* and *Schoenoplectus lacustris*, that are able to establish in relatively deep water (1-1.5 m) would have lent complex structure to the broads, sheltering both the margins and patches of open water from wind or boat-induced wave action, and encouraging sedimentation. In fact, until the reedswamp disappeared, it had been steadily encroaching on the open water of many of the broads (Boorman and Fuller, 1981; George, 1992). This structure allowed submerged, or free-floating species characteristic of shallow, low energy conditions, such as *Utricularia vulgaris*, *Potamogeton compressus*, *Stratiotes aloides* and *Hottonia palustris* to grow in the central parts of the broads in close association with the reedswamp, as is described by Pallis (1911). When the reedswamp disappeared, so too did the associated aquatic vegetation, and the underlying propagule- rich sediment was presumably dispersed by wind action, accumulating in areas of inhospitable deeper water. Thus, shallow water species of low energy habitats were replaced by a suite of species better adapted to slightly deeper (or perhaps less transparent) water, and more turbulent conditions, such as *Elodea canadensis*, *Potamogeton crispus* and *Nuphar lutea*. Shallow water species are also likely to be more light-demanding, and their decline is therefore consistent with reduced water transparency associated with increased phytoplankton densities, mineral turbidity caused by bed re-suspension, and, in some broads, water coloration by iron ochre.

As well as promoting coexistence through physical patchiness, rhizosphere oxygenation by reedswamp should also introduce heterogeneity in carbon and nutrient supplies (Mitsch and Gosselink, 2000). This can facilitate coexistence of submerged macrophytes (Espinar *et al.*, 2002). In naturally infertile habitats reedswamp creates patches with elevated fertility, as reported by Espinar *et al.*, (2002) enabling the growth of several species excluded from bare sediment. In more fertile habitats it seems possible that radial oxygen release by the rhizomes of emergent plants may generate localized pockets of reduced fertility, due to increased iron-phosphorus binding. Potentially this could have facilitated the coexistence of various shallow, still water plants within a more generally fertile, open water environment.

In contrast to the broads, in the meres the correlation between the change index and species trophic preference (LMNI) was strongly significant, suggesting that many of the species that have declined, such as *Lobelia dortmanna*, *Eleocharis multicaulis*, *Subularia aquatica*, *Isoetes lacustris* and *Myriophyllum alterniflorum*, were more exclusively characteristic of low nutrient lakes, than in the broads. There were still, however additional plant characteristics which correlated to the change index and hence may also have affected declined or survival of species. There was a specific loss of species of more acidic conditions, such as *Scheuchzeria palustris*, *Pilularia globulifera*, *Isoetes lacustris, Eleocharis multicaulis* and *Myriophyllum alterniflorum*, and persistence or increase in species characteristic of higher alkalinity (Ellenberg R), such as *Zannichellia palustris, Ceratophyllum demersum, Lemna minor* and *Carex elata*. There is a certain extent to which Ellenberg's acidity values are linked to trophic (LMNI) values (these factors are highly correlated; $p > 0.005$), but the fact that Ellenberg's R was correlated to the change index in the meres, but not in the broads, indicates that some of the naturally less alkaline of the meres may have been particularly susceptible to species loss during eutrophication. It is also possible that some of the species to have declined may have been growing in marginal, sandy or peaty 'mosses' associated with the meres but that these habitats were lost as water levels became increasingly stabilised and low growing marginal or shoreline vegetation was replaced by luxuriant reedswamp or riparian woodland. A negative correlation of the change index to species which grow in sluggish/standing water conditions (e.g. *Utricularia spp., Lythrum portula* and *Pilularia globulifera*) suggests that there was also a decline in the availability of still water environments associated with water level rise and stabilization and the consequent loss of the marginal bog habitats. Some contemporary accounts actually describe these habitat features as "ditches" or "swamps" at the margins of meres (Leighton, 1841; Warren, 1899).

Change in species distributions within the broads and meres appears to predominantly reflect trophic associations, as would be expected in two sets of lowland lakes which have experienced chronic increases in nutrient inputs over much of the last century (George, 1992; EN, 1998; Fisher *et al.*, 2009). However, there are other directly contributing environmental factors, often themselves linked to eutrophication, which can determine whether individual species are able to persist or not. These might be general, e.g. reed dieback or increased alkalinity, or lake-specific, e.g. presence of non-native invasive species, increased densities of benthivorous cyprinid fish, or increased growth of marginal vegetation, but all are part of the overall syndrome of eutrophic lakes. There are also less well documented ecological traits which it was not possible to consider here that have probably contributed to species declines, such as sediment structure and hydraulic forces (Schutten and Davy, 2000; Schutten *et al.*, 2005) that are likely to change in parallel with increased nutrient supply.

In summary, the change index offers an ecologically relevant measure of species change which can be applied in future to current ecological status assessments of lowland lakes. Macrophyte surveys could therefore offer information both on current nutrient status of a lake, inferred from aquatic vegetation, as found in many ecological assessment methods (Moss *et al.*, 2003; Penning *et al.*, 2008a; Willby *et al.*, 2009), but could also provide an indication of the extent of likely change over the last 100 years that reflects both generic effects of eutrophication, but also more local factors. Restoration of aquatic vegetation in shallow productive lakes may depend crucially on restoring aspects of characteristic structure that contribute to resource heterogeneity, but this in itself is fundamentally reliant on nutrient reduction.

CHAPTER 5 Combining historical records and palaeolimnology to reconstruct changes in the aquatic vegetation of a shallow eutrophic lake, Barton Broad, Norfolk

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5.1 Abstract

This study investigates recent and historical changes to macrophyte community composition and architecture in a shallow, eutrophic lake, Barton Broad, Norfolk, England, utilising a combination of historical records and palaeolimnology. This included a survey of all literature referring to aquatic plants in the broad, as well as herbarium specimens, old photographs and the notebooks and comments made by local naturalists. Additionally, sediment samples were extracted from the bottom of the broad and analysed for sub-fossil remains and pollen of macrophytes. Two types of sediment samples were taken: large bulk samples from the bottom of cores, analysed to give a picture of pre-1850 communities found in the lake and complete cores, analysed in order to provide a chronology of macrophyte community change throughout the history of the lake. The study found that early communities did not consist entirely of low growing, oligotrophic and mesotrophic species, but in fact comprised a mixture of these and other more characteristically high nutrient species associated with taller, or free-floating growth habit. As eutrophication progressed throughout the last century, the community was increasingly dominated by these latter growth forms. Diversity was maintained, however, since encroaching reedswamp generated a mosaic of low energy habitats which supported a range of species unable to withstand the hydraulic forces associated with more open water habitat. When the reedswamp disappeared in the 1950s, many of the dependent aquatic macrophytes also declined. Today only species more resilient both to eutrophication and the hydraulic forces associated with open water are able to persist, and then usually only erratically and in small numbers. This

study demonstrates the benefit of a combined approach to palaeolimnology which incorporates other available historic information.

5.2 Introduction

The eutrophication of freshwater lakes remains one of the primary challenges facing lake managers, both in the UK and worldwide (Rast and Holland, 1988; Carvalho and Moss, 1995; Moss, 1999; Gulati and van Donk, 2002; Hilt *et al.*, 2006; Schindler, 2006; Jeppesen *et al.*, 2007). Macrophytes play an important part in the functioning of lakes, particularly shallow lakes where they can colonise the entire extent of open water (Jeppesen *et al.*, 1998; Moss, 1998). Eutrophication results in macrophytes being increasingly unable to compete for light against faster growing phytoplankton. At high nutrient concentrations these can dominate the water column to the eventual exclusion of other plants. The effects of eutrophication have been well documented in the Norfolk Broads, a series of shallow eutrophic lakes in eastern England (George, 1992; Moss, 2001). These former medieval peat diggings were once famed for their species rich communities of aquatic plants and clear waters. Over the last 100 years, however, they have suffered the effects of eutrophication; decreased water transparency, increased phytoplankton density, decreased in macrophyte diversity, and ultimately in some lakes, a complete loss of aquatic plants.

The generally accepted model of macrophyte community change in the Norfolk Broads as postulated by various authors based on historic records and diatom cores (Osborne and Moss, 1977; Moss, 1978; Moss, 1979, 1980, 1988; George, 1992; Phillips, 1992) is that there are three phases: Phase 1 is the pristine, clear water state that existed prior to 1800. In this phase the broads were thought to be dominated by charophytes and 'low growing' plants such as *Potamogeton alpinus, Utricularia intermedia* and *Najas marina*. Phase 2 occurred with increased nutrient concentrations and was characterised by taller growing 'rank' species such as *Zannichellia palustris, Potamogeton pectinatus, Ceratophyllum demersum, Stratiotes aloides* and *Myriophyllum spicatum*. These species could potentially out-compete Phase 1 species at higher nutrient concentrations, because they are canopy forming, and could therefore also compete effectively for light with epiphytes and phytoplankton. Phase 3 occurred at yet higher nutrient concentrations when macrophytes became sparse or absent, and the water column became dominated by phytoplankton, resulting in the phytoplankton dominated conditions which continue to prevail in many of the broads to the present day. Whilst this model has been used to inform lake management and restoration efforts (Phillips, 1992; Phillips *et al.*, 1999), there is little actually known about the macrophyte species and structure of Phase 1. This first pre-disturbance phase often occurred prior to the first historical records, and whilst diatom analysis of sediment cores can show some changes in ecosystem functioning, the Phase model has never been tested against actual plant data as can be done through macrofossil analysis of sediments.

Barton Broad is the second largest (70 ha.) of the Norfolk Broads and is very shallow throughout (mean depth 1.4 m). Situated on the River Ant (Figure 5.1), it originated from the flooding of peat cuttings around the 13th century (Lambert *et al.*, 1960).

Accounts of Barton Broad from the early 19th century describe it as rich in aquatic vegetation, including charophytes (Gurney, 1904; Nicholson, 1906; Pallis, 1911). After the second world war, there were increasing concerns that the lake was in fact too densely vegetated by aquatic plants, with reedswamp and macrophytes encroaching well into the broad and threatening a developing interest in leisure boating (George, 1992). Between the late 1950s and early 1960s the macrophytes and reedswamp declined strongly, such that, by 1970, no plants at all were found in the lake (Mason and Bryant, 1975). This instigated a series of early investigations into the effects of eutrophication on the ecology of the broads, including Barton Broad (Mason and Bryant, 1975; George, 1977; Osborne and Moss, 1977). Subsequently, Barton Broad became the first of several broads to form the subject of a nutrient reduction and restoration program which started in the late 1970s and continues today (Madgwick, 1999; Phillips *et al.*, 2005).

The changes in aquatic vegetation in Barton Broad, as inferred from historic accounts, is well documented (Jackson, 1978, 1981a, b; George, 1992). Using palaeolimnological techniques, these changes have been placed in the context of increased phosphorus concentrations and a shift in dominance from epi-benthic to planktonic diatoms (Osborne and Moss, 1977; Moss, 1980; Bennion *et al.*, 2001). Despite these studies, little is known about the pre-disturbance macrophyte communities of the broad. Study of the pollen and macrofossil remains of aquatic plants in sediment cores can give a more direct insight into the dynamics of macrophyte communities. This study uses macrofossils and pollen based palaeolimnological analyses in combination with historic and contemporary records of plants growing in Barton Broad to construct a unique insight into the composition, architecture and functioning of previous macrophyte communities in the lake, as well as the changes which culminated in plant loss in the 1960s.

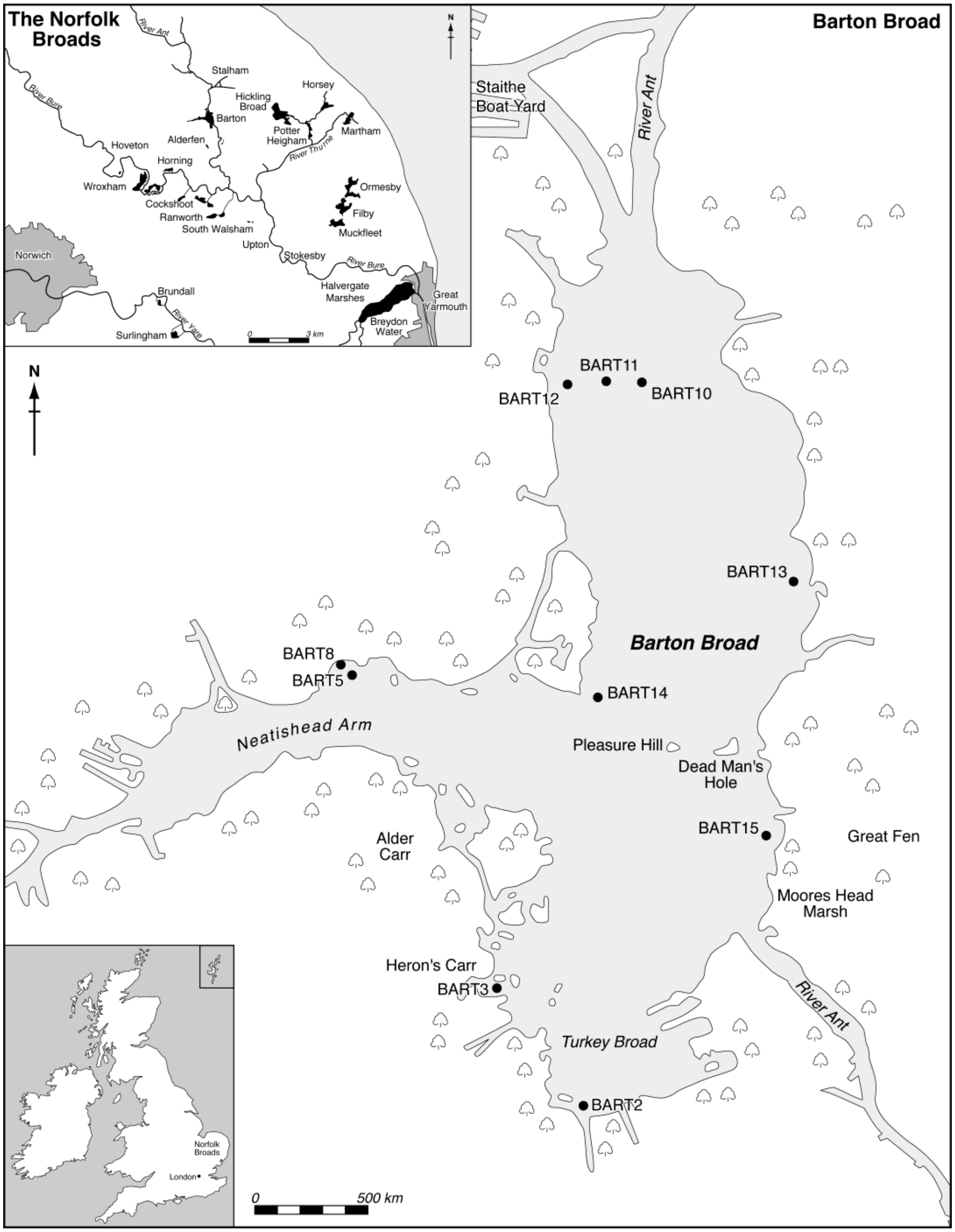

Figure 5.1. Map of Barton Broad showing the core locations.

5.3 Method

5.3.1 Core sampling

Ten sediment cores were taken from a variety of locations across the lake in November 1998 (BART2 & BART3), February 1999 (BART5), October 2000 (BART8) and March 2008 (BART10-15) (Figure 5.1), using a standard diameter (7.4 cm) Livingstone type piston corer (Livingstone, 1955). Sampling locations were chosen to cover a broad range of open water habitats in an attempt to capture as much of the macrophyte diversity in the broad as possible. Core locations were recorded using a handheld GPS and visible changes in sediment colour and texture were noted and photographed in the field. BART5 (96 cm length) and BART3 (99 cm length) from the Neatishead Arm and Heron's Carr area of the broad respectively, were extruded and sliced on site at 1 cm intervals. In order to gain a more comprehensive picture of the macrophyte species growing in the broad prior to 1850, additional macrofossil analysis was carried out on bulk sampled cores from the bottom of the sediment profile (i.e. constituting early, pre-1850 sediment). This was necessary to provide a more complete species list as macrofossils were relatively scarce in the 1 cm sections of the chronological cores. All other cores were therefore divided into 10 cm sections of which the 10 cm section closest to the bottom of the lake sediment was chosen for macrofossil analysis. This was identified by observing the level of the peat (which constitutes the lake bottom prior to sediment deposition) and choosing the first 10 cm slice above this which was comprised entirely of lake sediments (i.e. was sure not to contain peat).

5.3.2 Core chronology and lithostratigraphy

Percentage organic matter and $CaCO_3$ were estimated for each of the 1 cm levels of BART5 and BART3 using standard loss on ignition (LOI) procedures (Dean, 1974).

Both radiometric dating and spheroidal carbonaceous particle (SCP) analysis were used to provide a chronology for core BART5. An approximate date was assigned to BART3 by comparing the lithostratigraphic profile of the two cores and assuming that the observed change from light marl to dark silt found in both cores occurred at roughly the same date. Additional SCP counts were conducted on the bulk samples from the other cores to check that these were deposited prior to 1850, the time of first SCP depositions in the area.

Sediment samples were analysed for ^{210}Pb, ^{226}Ra and ^{137}Cs by direct gamma assay in the Liverpool University Environmental Radioactivity Laboratory, using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby *et al.*, 1986). ^{210}Pb was determined via its gamma emissions at 46.5keV, and ^{226}Ra by the 295keV and 352keV γ-rays emitted by its daughter isotope ^{214}Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. ^{137}Cs was measured by its emissions at 662keV. The absolute efficiencies of the detectors were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self absorption of low energy γ -rays within the sample (Appleby *et al.*, 1992).

SCP analysis followed the method described in Rose (1994). Dried sediment was subjected to sequential chemical attack by mineral acids to remove unwanted fractions leaving a suspension of mainly carbonaceous material and a few persistent minerals in water. A known fraction of the resulting suspension was evaporated onto a coverslip and mounted onto a microscope slide. The number of SCPs on the coverslip was counted using a light microscope at x450 magnification and the sediment concentration calculated in units of 'number of particles per gram dry mass of sediment' (gDM^{-1}). The criteria for SCP identification under the light microscope followed Rose (2008). The detection limit for the technique is c. 100 gDM^{-1} and concentrations have an accuracy of c. ± 45 gDM^{-1}.

The dating of the BART5 core followed the method described in Rose *et al.* (1995) whereby three main features of the SCP profile are used to provide dates: the start of the record, the rapid increase in SCP concentration and the peak in SCP concentration.

5.3.3 Macrofossil analysis

A total of 17 (BART5) and 16 (BART3), 1 cm levels from c. 5 cm intervals along the length of the BART5 and BART3 cores were analysed for macrofossils respectively.

Volumetrically measured subsamples of c. 20 cm^3 were washed through a 125 µm sieve using a gentle jet of tap water, and the entire residue was examined under a stereo-microscope at 30x magnification. The macrofossils were enumerated and identified using a reference collection of plant seeds and vegetative parts. For the pre-1850 bulk sediment, subsamples of around 300 cm^3 were washed through a 355 µm sieve and examined for macrofossils. If fossil species were uncommon, these were counted throughout the 300 cm^3 sample, but if they were too numerous to count in this manner, they were counted in a 30 cm^3 subsample. For the bulk sampling of BART3, which had already been divided into 1 cm levels, a 10 cm section was chosen at the bottom of the core (64-74 cm) and the remainder of the sediment (230 cm^3) counted for macrofossils using the same procedure.

5.3.4 Pollen analysis

Subsamples for pollen analysis were taken from each of the eight 10 cm bottom sediment cores used for macrofossil analysis. These were prepared for pollen analysis by a standard chemical procedure, using HCl, NaOH, sieving, HF, and Erdtman's acetolysis to remove carbonates, humic acids, particles >170 µm, silicates, and cellulose, respectively. The samples were then stained with safranin, dehydrated in tertiary butyl alcohol, and the residues mounted in 2000 cs silicone oil (method B of Berglund and Ralska-Jasiewicsowa, 1986). Slides were examined at a magnification of 400x (1000x for critical examination) by equally-spaced traverses across slides to reduce the possible effects of differential dispersal on the slides (Brookes and Thomas, 1967). The aim was to achieve a count of 500 grains of land pollen and spores. Pollen identification, where necessary, was aided using the keys of Moore *et al.* (1991), Faegri & Iversen (1989), and a small modern pollen reference collection.

5.3.5 Historical macrophyte data

Historical macrophyte records and descriptions of macrophyte growth in Barton Broad were compiled from a variety of sources including journal articles (Geldart, 1889; Salmon and Bennett, 1902; Bennett and Salmon, 1903; Nicholson, 1906; Boardman, 1939; Morgan, 1972; Mason and Bryant, 1975), books (Christopher Davies, 1882; Emerson, 1893; Dutt, 1903; Ready, 1910; Pallis, 1911; Buxton, 1950; George, 1992; Moss, 2001), Norfolk county floras (Trimmer, 1866; Nicholson, 1914), sketches and field notes of local naturalists, the Nature Conservancy Council files, old photographs and postcards, herbarium specimens from the Natural History Museum, London and Castle Museum, Norwich, as well as Broads Authority macrophyte surveys conducted on an annual basis from 1983 until the present (Jackson, 1983). The collection of over 230 records (i.e. taxa x unique date), covered a period from the 1870s to 2008 and included records and descriptions of 54 aquatic plant species.

5.3.6 Data manipulation and presentation

All macrofossil counts were standardised as numbers per 100 cm^3 of wet sediment and core diagrams of BART3 and BART5 were generated using C2 (Juggins, 2007). Bulk pre-1850 samples were plotted on a log scale as numbers of fossil remains varied considerably. Given the low numbers of aquatic pollen, data are presented alongside the macrofossil counts as presence/absence, rather than actual counts.

All plant nomenclature follows Stace (1997). Only species with Ellenberg moisture values of 9 or above were included in this study as the primary focus was on the dynamics of open water vegetation rather than the marginal fen.

5.4 Results

5.4.1 Core lithostratigraphy and chronology of BART5 and BART3

Both cores showed three distinctive lithostratigraphic layers (Figure 5.2 and Figure 5.3). In BART5 the base of the core constituted a mixture of peat and marl (70-75 cm), followed by a large light marl layer (29-70 cm), and nearest the surface, a dark silt layer (0-29 cm). BART3 had broadly comparable layering, but this core did not reach the basal peat layer so instead had a layering of dark marl (65-75 cm) followed by light marl (27-65 cm) and dark silt near the surface (0-27 cm). This is also evident from the

LOI data where the 80 % peak in organic matter at the base of BART5 represents the high organic content of the peat at this depth. BART3 does not have an LOI peak at this point despite organic content being higher here, confirming that the core had not reached the peat (Figure 5.2 and Figure 5.3). Both cores also showed a decrease in % sediment dry weight (from 19.8 to 8.2 in BART3 and from 21.6 to 8.8 in BART5) and an increase in % LOI (from 14.5 to 20.2 in BART3 and from 15.6 to 23 in BART5) from near the start of the dark silt layer, to the surface, indicating a gradual increase in organic matter in this layer, i.e. from the 1960s onwards.

Dating of the BART5 core by ^{210}Pb alone was not possible because of the very poor record of ^{210}Pb fallout. The ^{137}Cs activity has a relatively well-resolved peak at a depth of 25.5 ± 3.5 cm that can be assumed to record the maximum fallout of the radionuclide in 1963 from the atmospheric testing of nuclear weapons. The ^{137}Cs record implies a mean post-1963 sedimentation rate of 0.13 ± 0.04 g cm^{-2} y^{-1} (0.71 cm y^{-1}).

SCP concentrations for BART5 are given in Figure 5.4. The first presence of SCPs occurs at 44-45 cm and concentrations increase gradually, though irregularly, up to 17-18 cm. Between here and 15-16 cm there is then a major increase in concentration to more than 2600 gDM^{-1}. Concentrations then decline from 15-16 cm to the sediment surface. If it is assumed that the SCP concentration peak represents the period of maximum deposition then 15 – 16 cm may be ascribed the date 1978 (± 5) years. This is in reasonable agreement with the radiometric dating, although 15.5 cm would be given the slightly younger radiometric date of 1981 (± 5 years). The SCP 1978 date produces a mean sediment accumulation rate for the most recent 21 years of 0.738 cm yr^{-1} (0.596 – 0.938 cm yr^{-1}). If this rate is extrapolated below 16 cm, then 1950, usually indicated by a rapid increase in SCP concentration, would be expected to occur at c. 36 cm (29.5-47.5 cm). However, the rapid increase feature in BART5 is not very obvious. This may be because it occurs at the start of the SCP record, at the lower end of the depth range, where the SCP concentrations move from below to above the analytical limit of detection for the first time. Given this, and the shape of the profile, it seems likely that the 1950s would be at c. 39 cm with the profile below this truncated as a result of falling below the analytical detection limit.

Given the uncertainty in identifying the rapid increase feature in SCPs, and the poor record of ^{210}Pb fallout, all dates, especially those prior to 1963, should be treated with caution.

5.4.2 Macrofossil stratigraphy of BART3 and BART5

Both chronological cores, BART5 and BART3, showed a similar sequence of compositional change, although macrofossils were more abundant in BART5, which also had more species (9 rather than 7) (Figure 5.2 and Figure 5.3). Three main zones were observed for the macrofossils which corresponded well with the lithostratigraphic changes. In zone 1, in the lower half of the light marl (and into the dark marl in BART3), *Nitella* and *Chara* were abundant along with *Stratiotes aloides* and Nymphaeaceae. *Chara* in BART3 were only found in a fraction of the quantities found in BART5 and it is likely that the *Chara*-rich period is not well represented here because the core did not penetrate sufficiently deeply (i.e. not to the peat). In BART5 zone 1 also contained other species such as *Potamogeton friesii* and *Zannichellia palustris*. In zone 2, which stretched from half way up the light marl to the beginning of the dark silt, Nymphaeaceae and *Stratiotes aloides* were still common in both cores, and a few *Schoenoplectus lacustris* seeds were also found although the other species had declined. In BART5 *Nitella* oospores were also found in this period, as were evidence of *Najas marina* and *Ceratophyllum*. Interestingly these *Najas marina* fragments were not a new occurrence, but rather, a re-appearance, as fragments were also found towards the base of BART5. The dark silt layer of zone 3, which was the most recent sediment, contained *Stratiotes aloides* leaf spines and *Nymphaeaceae* leaf trichoschlereids in much lower numbers than the other zones, in both cores. Apart from small numbers of *Chara* oospores and *Schoenoplectus lacustris* seeds, the only other species found in this layer, was *Najas marina*.

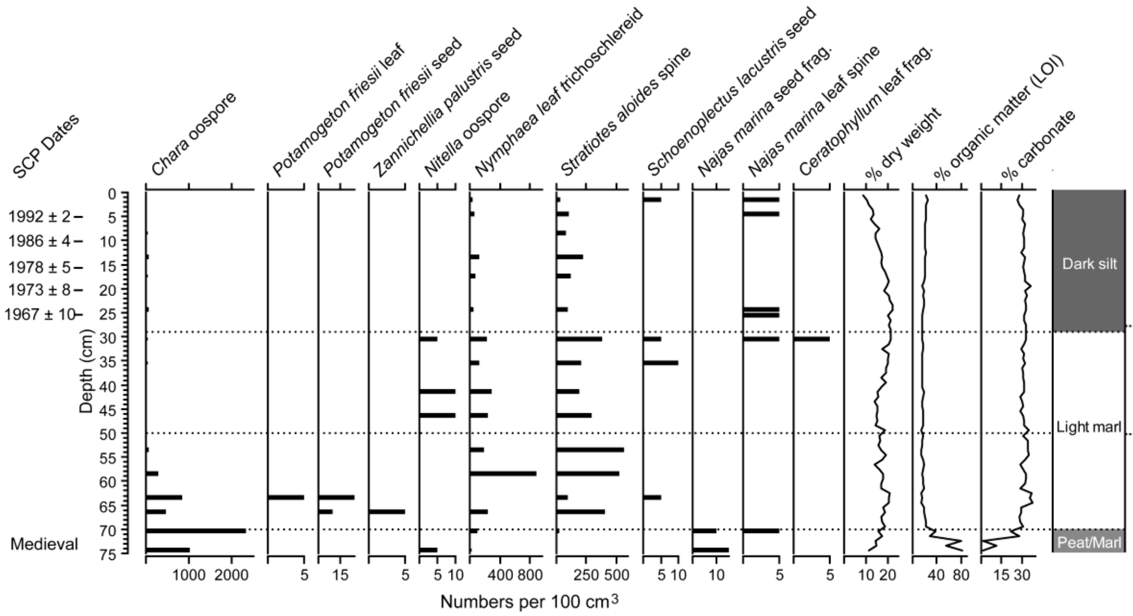

Figure 5.2 Macrofossils and lithostratigraphy of core BART5 including SCP ascribed dates.

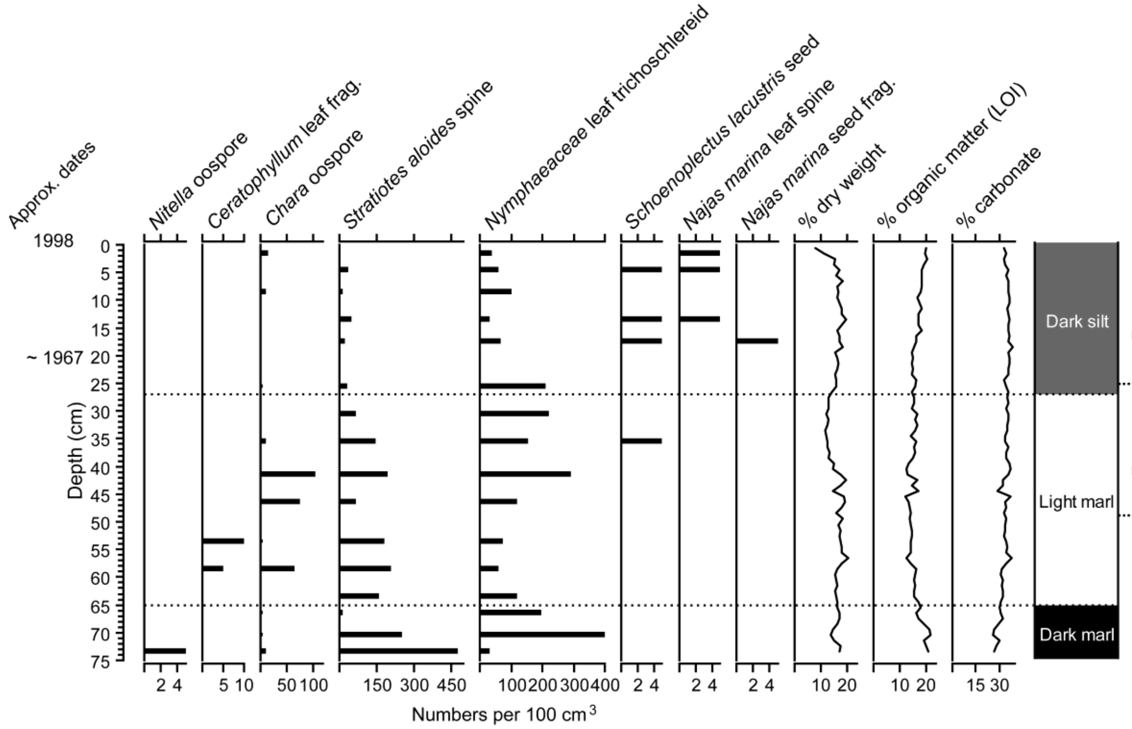

Figure 5.3 Macrofossils and lithostratigraphy of core BART3. The location of the 1967 date was approximated by comparing the lithostratigraphy of BART3 with BART5 which was dated.

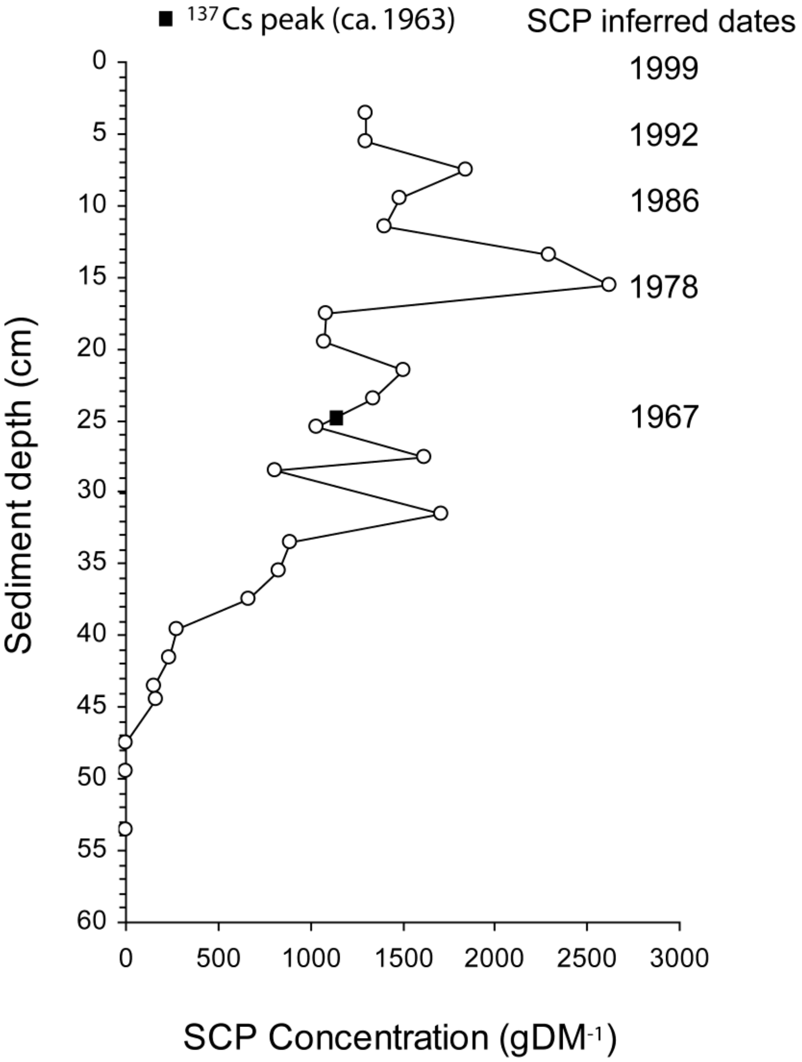

Figure 5.4 SCP concentrations down the length of core BART 5 with SCP and ^{137}Cs derived dates.

5.4.3 Pre-1850 macrofossils and pollen

A total of 28 aquatic macrophyte taxa were found in the macrofossil and pollen analysis of the pre-1850 samples (Figure 5.5). This is significantly more than the 9 taxa found in cores BART3 and BART5. *Chara,* Nymphaeaceae, Potamogetonaceae and *Schoenoplectus lacustris* were represented in all of the bulk samples. *Chara* oospores, *Ceratophyllum* leaf fragments, *Nymphaeaceae* leaf trichoschlereids, *Najas marina* seed fragments and *Stratiotes aloides* leaf spines were the most numerous macrofossil remains. *Potamogeton* leaves, seeds and pollen were well distributed in smaller quantities, but were not always identifiable to species level. In some instances however, whole seeds or diagnostic leaf structures were preserved, which allowed the identification of five different *Potamogeton* species, including *Potamogeton coloratus* in core BART10. Similar species were found in samples from the different locations in the broad, with numbers of taxa ranging from 11 (BART2) to 20 (BART11).

Overall pollen preservation in the slides was good but pollen of obligate aquatics, which were the subject of this study, was less well preserved. Their pollen can be very fragile as it is often released directly into the water or onto its surface so does not need to survive in air. Whilst the macrofossil analysis yielded more taxa (21), the pollen analysis, which identified 17 taxa, also added a number which were not represented at all by macrofossils, such as *Callitriche spp., Hippuris vulgaris, Hydrocharis morsus-ranae, Lemna spp., Littorella uniflora, Myriophyllum alterniflorum* and *Sagittaria sagittifolia*.

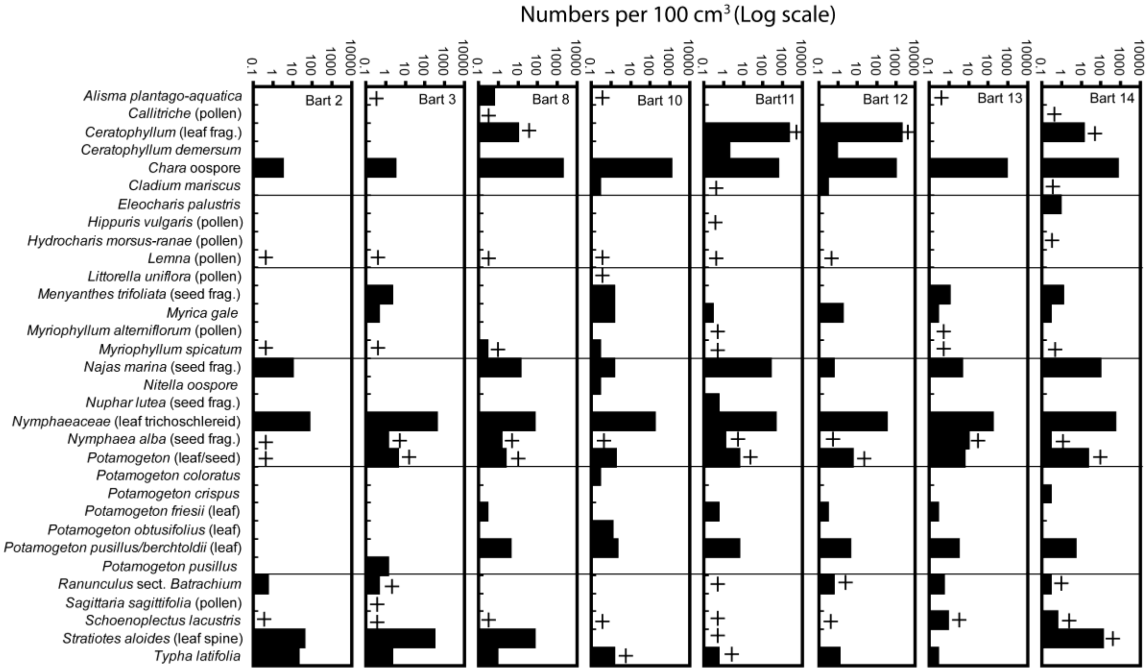

Figure 5.5 Macrofossil and pollen found in the pre-1850 bulk sediment samples. Macrofossils are shown as numbers per 100 cm^3 on a log scale. + represents remains/pollen found in pollen analysis. Remains found are seeds unless specified otherwise.

5.4.4 Historical macrophyte data

Of the 52 macrophyte taxa recorded in Barton Broad since the first record in 1884, including 40 species before 1960, only 27 have been recorded after 1960, despite detailed annual plant surveys by the Broads Authority since 1983 (Figure 5.6). Since these surveys started there have been eight survey years (1987, 1989-92 and 2001) where aquatic vegetation was absent from the broad, leading to no species records. In surveys where plants were found they were generally in low numbers, the commonest being *Ceratophyllum demersum, Elodea canadensis*, *Elodea nuttallii* and *Potamogeton pectinatus* (Broads Authority unpublished data). Other species which have persisted after 1960 in small numbers include *Najas marina, Potamogeton obtusifolius, Potamogeton perfoliatus*, a few charophyte species, *Nymphaea alba, Nuphar lutea*, *Potamogeton pusillus, Sagittaria sagittifolia*, *Schoenoplectus lacustris* and *Sparganium emersum*. Over the last twenty years a number of species have also been recorded for the first time in the broad, including *Potamogeton crispus, Potamogeton berchtoldii, Potamogeton trichoides, Elodea nuttallii*, *Elodea canadensis*, *Lemna trisulca*, *Nitella mucronata*, *Ranunculus circinatus, Chara virgata*, *Sparganium emersum, Spirodela polyrhiza* and *Zannichellia palustris*. Some of these are most likely due to misidentifications or under-recording of these species in earlier records, e.g. *Chara virgata* and *Potamogeton berchtoldii* have only been taxonomically resolved fairly recently (Moore, 1986; Preston, 1995), whereas others may have been present but were simply not recorded, either because they were not sufficiently noteworthy, or because there were no regular surveys prior to 1983 and they were therefore overlooked. This was evidently the case for *Potamogeton crispus* and *Zannichellia palustris* which were not recorded before 1960, but were found in BART14 (Figure 5.5) and BART5 (Figure 5.2) of the macrofossil samples respectively, at levels dated earlier than 1960. A few cases also represent recent invasions by non native species (e.g. *Elodea* spp).

Species recorded prior to 1960, but no longer found in the broad include a number of charophytes (*Nitella flexilis, Nitellopsis obtusa, Chara contraria* var. *contraria, Chara aspera* and *Chara hispida*), various *Potamogeton* species (*Potamogeton polygonifolius, Potamogeton natans, Potamogeton praelongus, Potamogeton compressus, Potamogeton friesii, Potamogeton lucens*), as well as *Hippuris vulgaris, Myriophyllum spicatum, Myriophyllum verticillatum, Utricularia intermedia, Utricularia vulgaris, Hottonia palustris, Butomus umbellatus, Hydrocharis morsus-ranae, Persicaria amphibia, Ranunculus aquatilis* and *Stratiotes aloides* (Figure 5.6). Species loss seems to have occurred in two obvious periods; just before 1920 when a large number of species including *Potamogeton lucens, Potamogeton compressus* and *Chara hispida* disappeared, and around 1950 when a handful of other species such as *Utricularia vulgaris* and *Stratiotes aloides* disappeared.

As well as the change in species over the period for which records exist, the structure and abundance of macrophytes has also changed dramatically. When old and new photographs of Barton Broad are compared (Figure 5.7), it is evident that there has been a dramatic change in vegetation since the 1950s, with the loss of extensive Nymphaeaceae and *Schoenoplectus* beds. *Schoenoplectus* stands formerly grew out into the open water of the broad, and together with *Typha angustifolia* dominated reedswamp on their landward edge, meant that little open water remained and total encroachment was considered a threat (Table 5.1). The change is well recorded in the literature (Table 5.1), which also documents the change from an open broad dominated by charophytes in the late 1800s, followed by increasing encroachment by reedswamp up to the 1950s, and finally in the late 1950s and early 1960s, the disappearance of macrophyte cover and contraction of reedswamp.

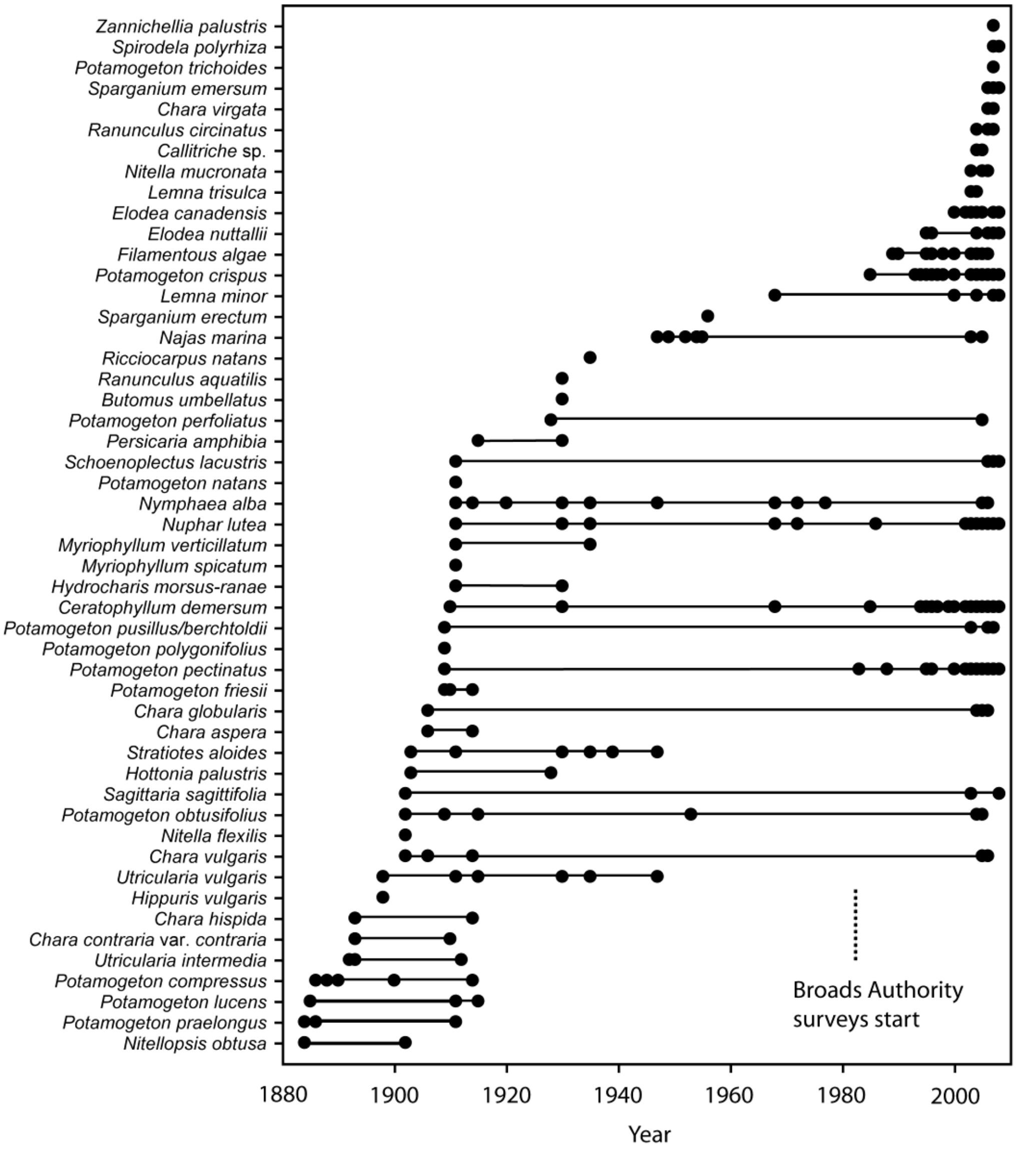

Figure 5.6 Macrophyte changes in Barton Broad as documented from historical records and modern surveys.

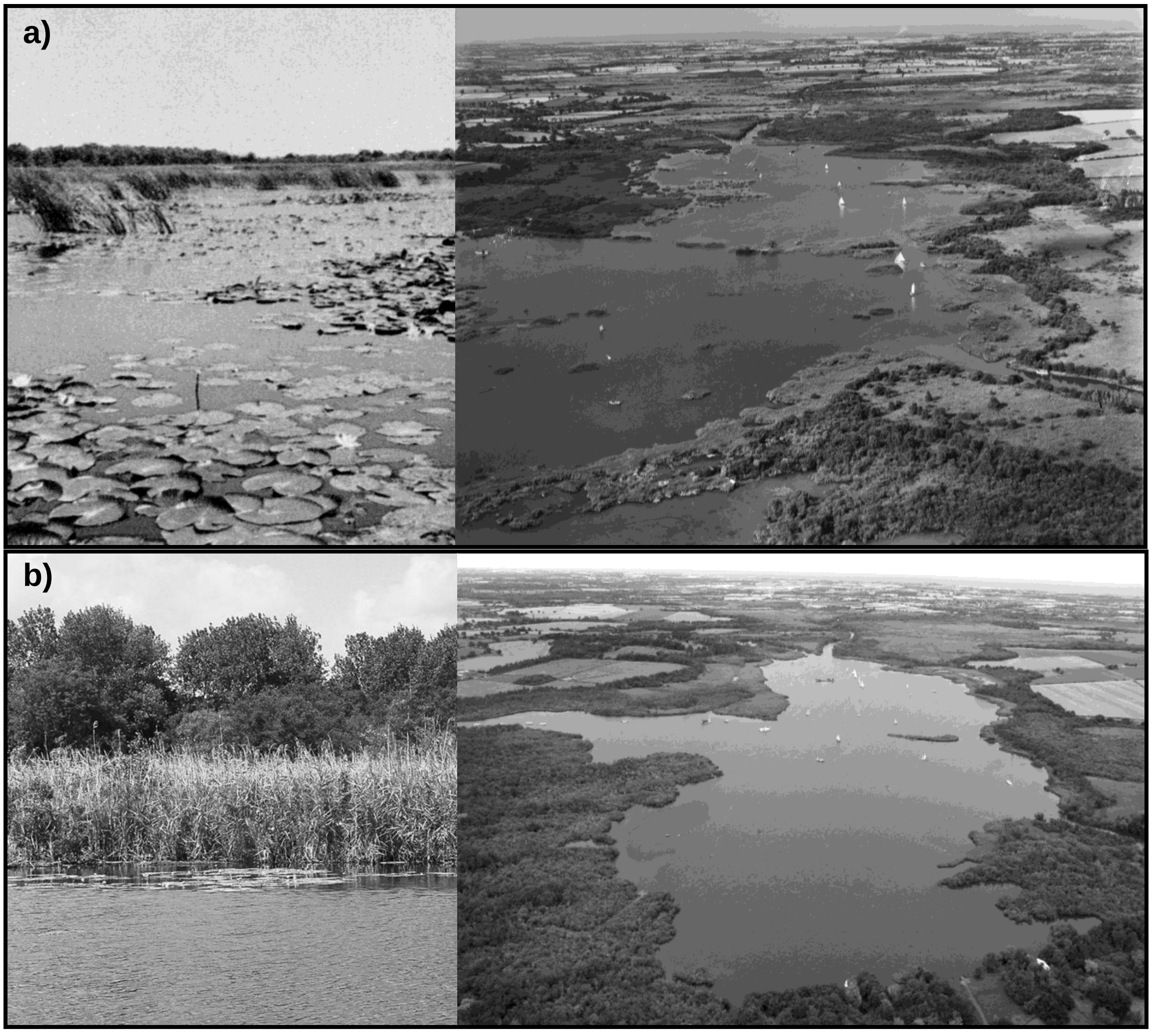

Figure 5.7 Barton Broad littoral and aerial view in a) summer 1951 and b) summer 2003 and 2008. Photos in a) reproduced from Mottram, 1951 and © English Heritage, NMR, Aerofilms Collection and b) Carl Sayer 2003 and © Mike Page 2008.

Table 5.1 Chronology of macrophyte growth in Barton Broad as detailed from literature sources.

1870s	"A fine sheet of water with good depth…"	(Ready, 1910)
1882	"…is full of mud; there being large "hills" where water is not more than 2 feet deep." "light yellow"	(Christopher Davies, 1882)
1889	"At our new anchorage on Barton Broad we could look through six feet of water, absolutely clear, down to a bottom of smooth yellow mud, with here and there a clump of dark green weed. Elsewhere acres of matted tangle grow densely under water, and even rise in summer to the surface. We lay in a deep curved bay, open towards the north, margined by walls of reeds and rushes, backed by rising land and trees, and islanded with clumps of giant rush."	(Doughty, 1889)
1893	"…we sailed through wastes of reed, gladden [*Typha*], and bolder [*Schoenoplectus*], until we reached the wide expanse of Barton, with its low-lying shores."	(Emerson, 1893)
Since early 1900s	Increasing reedswamp encroachment noticed	(Gurney, 1904; Ready, 1910)
1902	"A great deal of open water"	(Nicholson, 1902)
1903	"…Barton is very shallow except in the wherry [boat] channels…" "…and sailing close to the fringing reed-beds I often heard the water-weeds which cover the shallows brushing against the sides of my boat." "…shoal water was only distinguishable by its dark patches of weeds and sparse growth of rush and sedge." "…I turned into a little a inlet where the white water-crowfoot [*Ranunculus*] was in full bloom"	(Dutt, 1903)
1904	Relatively small area of open water rapidly growing up. Characterised by large beds of Chara. "characterised by the presence of large beds of *Chara*"	(Gurney, 1904)
1906	"In Barton Broad, there is an extensive growth of Characeae, consisting (probably with other species) of *Chara fragilis*, Desv. [*Chara globularis*], *Chara aspera*, Willd., var. *capillata* [*Chara aspera*], Braun., *Chara vulgaris*, L., and *Chara vulgaris* var. *papillata*, Wallr. [*Chara vulgaris*]. The great abundance of the genus Chara in these waters, is an indication of the presence of a considerable quantity of calcium carbonate held in suspension…" "…dark green carpet of Chara covering the bottom."	(Nicholson, 1906)
1910	"…was a fine sheet of water with good depth in those days, though latterly it has become much choked up by dense growths of weed."	(Ready, 1910)
1911	Marietta Pallis' vegetation transect through Barton Broad published, showing the progression from dry land, through reedswamp to open water. It clearly shows the structural heterogeneity of the vegetation and the association of submerged and floating leaved macrophytes with the reedswamp.	(Pallis, 1911)
1911	*Stratiotes aloides* occupying a large extent of the broad	(Boardman, 1939)
1915	*Persicaria amphibia* infrequent and leaves algae coated	Pallis 1915 herbarium specimen, NHM London

1920s	"The open water was enhanced by clumps and ronds of gladdens [*Typha angustifolia*] and and bolders [*Schoenoplectus lacustris]*, much sought after by the basket weaving industry. From the marshes, which now form the banks of the broad, deep banks of reed [*Phragmites australis*] spread out over the shallower water, bolders and gladdens taking over in the deeper pools. Beyond the navigation channels, kept clear by the Commissioners, lay masses of weeds with the occasional clear pool, arresting the passage of boats and making rowing very difficult. Large areas of yellow [*Nuphar lutea*] and white water lilies [*Nymphaea alba*] and water soldier [*Stratiotes aloides*] abounded. The mass of underwater weeds consisted mainly of hornwort [*Ceratophyllum*], milfoil [*Myriophyllum*], bladderwort [*Utricularia*], and pond-weeds [*Potamogeton* species]. In sheltered shallow corners, the beautiful water-crowfoot [*Ranunculus* subgenus *Batrachium*], frog-bit [*Hydrocharis morsus-ranae*], amphibious persicaria [*Persicaria amphibia*] and the greater spearwort [*Ranunculus lingua*] flourished."	(Gane, 1976)
1924	Sewage effluent starts being discharged into the Ant upstream of Barton from North Walsham Sewage Treatment Works (STW)	
1910s-40s	The broad decreased in size but the percentage of open water increased in relation to the percentage of reedswamp	(Boorman and Fuller, 1981)
Late 1940s	The broad stopped shrinking in size and the percentage of open water increased	(Boorman and Fuller, 1981)
1943	"Some broads decreased in size through the encroachment of reeds till they almost disappeared, as for instance Sutton Broad. …Barton is in a transitional stage, the reed beds covering about a third of the water, but here they have been encouraged and have been planted" "Shallow broads such as Barton and Hickling, where light can penetrate to the bottom, are richer in weed and consequently clearer; they have, moreover, a higher phosphate content than the Bure Broads"	(Rudd, 1943)
1947	*Utricularia vulgaris* in peatier more sheltered parts	(Ellis, 1947)
1949	Mechanical cutting of the macrophytes started opening up 50 acres of water not open since 1900	(Buxton, 1950)
1950s	*Najas marina* generally on naked mud in scattered clumps which often have hollow centres (Heron's Car and near pleasure island)	(Crompton, 1977)
Early 1950s	Stalham STW opened and capacity of North Walsham STW increased	(George, 1992)
1950s	Coypu escaped into the wild	(George, 1992)
1952	"The bulrush (*Schoenoplectus lacustris*) forms a rather open community, associated with white water lily (*Nymphaea alba*). It is later invaded by the lesser reedmace (*Typha angustifolia*). (…) the task of restoring overgrown open water is now of major importance. The increase of power-driven water traffic has had some effect in this direction itself."	(Lambert, 1953)
1960s	Macrophytes declined	(George, 1992)
1963	Sharp winter and around this time; loss of *Schoenoplectus lacustris* and water lilies	Yaxley pers. comm.
1963	Loss of reedswamp noted linked to coypu grazing	(Ellis, 1963)
1977	Phosphorus stripping introduced in STW upstream of broad	(George, 1992)
by 1980	All significant discharges upstream of lake had phosphorus removal	(George, 1992)
1981/82	15000 *Stratiotes aloides* and *Nupha lutea* introduced to NE of the broad by Norfolk Naturalists' Trust, but unsuccessfully	(George, 1992)
1987	Coypu eradicated	(George, 1992)

1989	Broads Authority set up with jurisdiction to protect the environmental, leisure and navigational interests of the Broads	Broads Authority
1995	Broads Authority mud pumping started	“
1997	Improved phosphorus removal techniques at STWs	“
1997-2000	Surface sediment removal by the Broads Authority	“
2000	Mud pumping of main broad finished	“
2000	First fish-proof enclosures installed	“
2003	Macrophytes begin to recolonise within enclosures	“
2005	Plants growing outside of enclosures. Extensive plant growth was observed chiefly along the western edge of the main broad	“
2008	*Schoenoplectus lacustris* found growing in the north west bay of the broad	“

5.5 Discussion

5.5.1 A combined approach

Macrofossils remains are not particularly numerous in the sediment of Barton Broad. This means that while sediment cores analysed at 1 cm intervals for macrofossil remains are useful in showing overall changes to macrophyte communities over the last 200 years, this level of resolution underestimates past species richness. In this study the high resolution sampling was complemented with bulk sampling of pre-1850 core material increasing the representation of rarer remains to get a more comprehensive insight into pre-1850 macrophyte communities. By analysing 10 cm blocks from the bottom of 8 cores it was possible to add 15 species to the list compiled from the 2 conventional cores. Ayres *et al.* (2008) also used a similar bulk sampling approach to complement their higher resolution macrofossil cores, and also found that it added species to their total. The species added in this study using this bulk approach were primarily those which leave remains which are large but less numerous, such as *Potamogeton coloratus* or *Nuphar lutea* seeds.

Although pollen analysis of the bottom sediments identified fewer species than the macrofossil analysis, it did add a further 7 species, including taxa which rarely leave remains, such as *Lemna* and *Callitriche* species. Of the 29 species recorded in historical records prior to 1912, half were also recorded in the macrofossil and pollen analysis.

Those which the historical records added were mainly species which are often hard to resolve taxonomically from sub-fossil remains, such as *Chara* and *Potamogeton* species. The early historical records were, however, most probably not coincident with the bulk macrofossil and pollen counts, which probably represented an earlier community. Of the 29 species in the historical records prior to 1912, only 9 of these were actually recorded prior to 1900. The different methods used here to reconstruct past macrophyte communities each have their strengths and weaknesses (Chapter 2), but by using this combined approach this study was able to illuminate on a complex history of macrophyte community change over the last two centuries.

5.5.2 Pre-disturbance macrophyte communities

In Barton Broad, the earliest descriptions of macrophyte growth suggest that the lake was characterised by large beds of *Chara* (Gurney, 1904; Nicholson, 1906) (Table 5.1). Several species of charophyte were recorded prior to 1900, as well as *Potamogeton compressus, Potamogeton lucens, Potamogeton praelongus, Utricularia intermedia* and *Utricularia vulgaris* (Figure 5.7). Moreover the broad is described as being open and good for sailing, although it was also noted to be prone to encroachment by reedswamp at this time (Table 5.1). Besides this information, and charophyte oospores which have been found in sediment cores analysed for diatoms (Moss, 1980), there is no further evidence supporting the traditional description of Phase 1.

Whilst historic records are useful in helping illuminate this early vegetation in the broad, they may be insufficient to give a detailed picture, not least because the earliest records do not start until 1884. The findings from macrofossil analysis of the bottom of sediment cores from Barton Broad, provide the only direct insight into pre-disturbance macrophyte communities in the lake. The range of species found in the pre-1850 sediment suggest that the community was more structurally diverse than previously thought, also including a range of taller growing species such as, *Myriophyllum spicatum* and *Zannichellia palustris*, and a variety of different architectures including floating leaved or floating species *(Nuphar lutea* and *Stratiotes aloides*), broad and fine leaved Potamogeton species and dissected leaved taxa such as *Ceratophyllum* and *Myriophyllum.*

Alongside these species, it was particularly surprising to find evidence of *Littorella uniflora* and *Myriophyllum alterniflorum* growing in the broad in the same period. These species are typical of low alkalinity, nutrient poor lakes, although they can be found in high alkalinity situations, particularly where nutrient concentrations are low (Preston and Croft, 1997). *Littorella uniflora,* is a low growing plant of isoetid growth habit often growing in shallow margins as it tolerates emersion. Although normally associated with mesotrophic or oligotrophic conditions, it can grow in eutrophic waters (Preston and Croft, 1997; Vestergaard and Sand-Jensen, 2000a; Pedersen *et al.*, 2006), but has declined in south-east England partly due to its sites becoming overgrown with rank vegetation (Preston and Croft, 1997). Records from 1840 and earlier show that *Littorella* was growing in the nearby Filby Broad (Trimmer, 1866; Nicholson, 1914), so it is possible that it previously grew in several of the broads. Although it is traditionally associated with gravel substrate it can also be found on peat (Preston and Croft, 1997) and could well have populated some of the shallow peat bulks (raised ridges of peat) which used to be dispersed throughout Barton Broad.

Chara oospores were abundant in the bottom sediments of Barton Broad suggesting that *Chara* were dominant and probably formed meadows throughout the open water of the lake (Figure 5.5 and Fig. 8 a). Early accounts of the variety of *Chara* species found in the broad (Nicholson, 1906) further support the idea of a structurally diverse community, with *Chara aspera*, a shallow water species, growing towards the shallower margins or on peat bulks, and *Chara vulgaris* and *Chara globularis* occupying the deeper open water. *Potamogeton coloratus*, a species typical of nutrient poor, calcium-rich conditions and often associated with *Chara* (Preston and Croft, 1997), was represented by a sub-fossil seed in BART 10. This species may also have been more widespread in many of the broads, having been found historically in Hickling Broad, Calthorpe Broad and Ormesby Great Broad (Madgwick unpublished data, Jackson, 1981b).

Najas marina seed fragments were also found abundantly in the pre-1850 samples. The chronological cores, BART3 and BART5, suggest however, that *Najas marina* was not continuously present, but rather occurred early on in the history of the lake, then disappeared before re-appearing again some time before the late 1930s.

The suggestion is that rather than there being an assemblage of low growing plants in the early phase, there was in fact a very diverse community which included both low and tall growing species, alongside a dominant and diverse charophyte flora. Perhaps the lower nutrient concentrations were instrumental in maintaining the coexistence of a wide range of species, as can be found elsewhere in contemporary naturally mesotrophic lakes (Murphy, 2002), preventing competitive displacement of charophytes and low growing species by taller, faster growing species.

There are a number of spatial analogues that either support descriptions of the classic Phase 1 assemblage, or which match the more diverse version of Phase 1 that was observed. For example the Loch of Strathbeg, a shallow, high alkalinity lake in NE Scotland, which was formed in the late 1700s by the evolution of a coastal sand bar, historically had an aquatic vegetation dominated by *Chara aspera, Littorella uniflora* and *Myriophyllum alterniflorum,* with few other species (Pritchard, 1990). Though reminiscent of the classic Phase 1 assemblage, this may not, however, be fully representative of the Norfolk Broads, which are more sheltered, and potentially more fertile naturally, and have a strong continental influence on their flora. Elsewhere, several authors (e.g. Small, 1931; Forbes, 2000) have commented on the close similarities between the aquatic flora of East Anglia and that found in the Lough Neagh fenlands or in County Fermanagh, Northern Ireland. Unpublished data from the Northern Ireland Lake Survey of 1991 reveals that shallow, high alkalinity, non-marl lakes with low levels of enrichment (growing season TP <50ug/L) have an aquatic flora including both *Littorella uniflora* and *Chara globularis* growing alongside species such as *Stratiotes aloides, Nymphaea alba, Hydrocharis morsus ranae, Ranunculus circinatus* and a wide range of pondweeds, or alternatively, *Chara hispida* growing with *Hippuris, Utricularia vulgaris, Nuphar lutea, Nymphaea alba, Potamogeton coloratus, Potamogeton lucens* and other pondweeds (Willby *et al.*, 2009). Both of these combinations share many of the attributes of the Barton pre-1850 flora that was observed.

5.5.3 Early eutrophication 1900-1950

Littorella uniflora and *Myriophyllum alterniflorum* were never historically recorded suggesting that these species disappeared before 1900, possibly due to a change in sediment structure caused by eutrophication, or an increased competitive pressure on their habitat (Pedersen *et al.*, 2006). Other species lost before the 1920s include *Potamogeton lucens*, *Potamogeton compressus, Chara hispida* and *Nitellopsis obtusa*. There is also a suggestion that the *Chara* meadows described by Gurney and Nicholson prior to 1906 (Gurney, 1904; Nicholson, 1906), may have disappeared. By the time Marietta Pallis drew a detailed transect of the broad's aquatic flora in 1911, *Chara* did not feature in the drawing and she only mentions *Chara hispida* as "less abundant" in the Ant Broads (Pallis, 1911). This decline in *Chara* is also seen clearly in zone 1 of BART5 (Figure 5.2).

In contrast to the late 19th century descriptions of Barton Broad, accounts from as early as 1904 describe a lake increasingly encroached upon by emergent vegetation (Table

5.1). By examining maps and aerial photographs, Boorman and Fuller (1981) showed that reedswamp increased in the broads from 1880 to 1905 by colonising open water. After 1905 the rate of colonisation was slower and much was lost through succession to fen. From 1946 onwards there was a dramatic loss of reedswamp and reversion back to open water. Barton Broad typified this trend: the transect drawing by Pallis in 1911 (Pallis, 1911) clearly shows a broad with extensive reedswamp interspersed with rich aquatic vegetation. The reedswamp was a prominent feature of the broad up to the 1950s as can be seen most dramatically from contemporary photographs (Figure 5.7) and accounts (Table 5.1). It consisted of *Schoenoplectus lacustris* at the open water end, followed by *Typha angustifolia* then *Phragmites australis* going inland (Pallis, 1911; Lambert, 1953). *Schoenoplectus lacustris* also formed islets of vegetation interspersed with beds of *Nymphaea alba*. Many aquatic species, particularly those favouring relatively still water, were probably able to thrive in the quiescent zones created by the shelter afforded by the stands of *Schoenoplectus lacustris* (Figure 5.7 a), such as *Stratiotes aloides, Hottonia palustris, Utricularia vulgaris and Myriophyllum verticillatum*, which were found in the broad in this era (Figure 5.6). Pallis herself noted the strong affinity the underwater plants had with the reedswamp and that they did not colonise the open water beyond it (Pallis, 1911). As the reedswamp continued to invade the open water up to the 1950s, there was increasing concern that weed cutting was required to stop the broad disappearing altogether (Rudd, 1943; Buxton, 1950; Lambert, 1953, Table 5.1). In 1952, it was noted that this trend was beginning to reverse (Lambert, 1953) and by 1963 there was recognition of the dramatic loss of reedswamp in Barton and throughout the Broads in general. This was linked to pressures of feral coypu grazing and eutrophication (Lambert, 1965; Boorman and Fuller, 1981; Boar *et al.*, 1989).

5.5.4 Plant loss

At around the same time as the reedswamp disappeared, many of the associated aquatic macrophytes also vanished causing a notable gap in macrophyte records between the mid 1950 and 1960s (Figure 5.6). This transition is also visible in the chronological macrofossil cores BART3 and BART5, as *Chara*, *Stratiotes aloides*, *Nymphaeaceae* and *Nitella* remains decline just before 1967 (Figure 5.2 and Figure 5.3). This loss may have been caused by the huge structural change which will have occurred when the in-lake swamp and reedswamp declined in the early 1960s. The scale of this structural change can be appreciated by comparing the photographs in Figure 5.7 which show how the reedswamp and in-lake swamp covered nearly all of the broad in the 1950s. Hydraulic forces acting on submerged plants will have increased once this disappeared, uprooting or breaking the remaining plants which had been persisting in the shelter afforded by the in-lake swamp community. The increased hydraulic forces, or perhaps increased dredging, may have eroded the peat bulks which also may have been providing additional in-lake structure.

This dramatic change in Barton's aquatic vegetation was also reflected in similar changes throughout the Broads around this time, prompting national awareness of their plight, eventually leading to extensive research into the causes of plant loss and methods of restoring the lakes and their aquatic flora (George, 1992; Phillips, 1992; Madgwick, 1999; Phillips *et al.*, 1999; Moss, 2001). A campaign to reduce nutrient inputs into the broad was started in the 1970s and annual plant surveys were instigated in 1983. It was not until the early 1990s that macrophytes were consistently to be found growing in the broad again, but most species are still found in very low abundance and comprise those which are generally regarded as being more characteristic of eutrophic conditions, such as *Zannichellia palustris, Elodea canadensis, Elodea nuttallii, Potamogeton berchtoldii, Potamogeton pectinatus, Ceratophyllum demersum* and *Nuphar lutea*. The species able to persist in the broad are also limited by physical conditions linked to eutrophication, such as loose sediment and the higher hydraulic pressures associated with open water (Schutten *et al.*, 2005). Many of the species still found in the broad are fine-leaved, such as *Potamogeton pectinatus* and *Zannichellia palustris*, and therefore either more resistant to hydraulic forces, or are able to survive breakage or uprooting, such as *Ceratophyllum demersum* and *Myriophyllum spicatum*, due to their ability to regenerate vegetatively from broken off stems (Preston and Croft, 1997).

Recent mud pumping activity to remove phosphorus-rich sediment, as well as thirty years of controlling surface water nutrient inputs to Barton Broad, have resulted in reduced nutrient loading and algal growth, with visible changes in the composition of phytoplankton communities (Phillips *et al.*, 1999; Phillips *et al.*, 2005, Table 5.1). Whilst more macrophyte species have also re-colonised in recent years, such as *Schoenoplectus lacustris, Chara vulgaris* and *Sagittaria sagittifolia*, macrophyte growth has generally been restricted in quantity and often confined to fish-proof enclosures where conditions are more sheltered and plants less vulnerable to uprooting by benthivorous fish (Madgwick, 1999, Hoare pers. comm.). In 2005, macrophytes began to colonise in larger numbers outside of the fish-proof barriers, yet it seems unlikely that they will form a stable vegetation, or that some of the historic species characteristic of sheltered conditions will return, unless some of the physical structure previously offered by the reedswamp is also restored. The establishment of *Schoenoplectus lacustris* in the North West bay of the broad in recent years (D. Hoare pers. comm.) is an encouraging step in this direction

5.5.5 Conclusion

This investigation into the macrophyte history of Barton Broad using literature, herbarium and palaeo-sources has provided a more detailed picture of the communities that existed prior to 1850 and the onset of significant anthropogenic eutrophication. It indicates that the distinction between phase 1 and 2 is less clear cut than previously thought, with both low- and tall-growing species, or those more characteristic of low nutrient levels, and those characteristic of higher levels, able to coexist in a structurally diverse community. As nutrient concentrations gradually increased, the taller more prolific species appear to have out-competed the low-growing species, such as *Littorella uniflora* and *Chara aspera*. This change occurred progressively from 1900 or earlier, until the early 1950s. Despite this, macrophytes were abundant and diverse in this period, as the extensive reedswamp offered a mosaic of still water habitats similar to those conditions now found in some Broadland ditches where many of these species still persist (George, 1992). Once the reedswamp disappeared, the physical structure of the habitat was lost thus inhibiting macrophyte re-colonisation, despite subsequent reductions in nutrient loading (Phillips *et al.*, 2005).

This approach, which combines evidence from historical accounts, historic plant records, macrofossil and pollen palaeolimnological analysis, give a much more comprehensive picture of vegetational change than each component data source independently. Barton Broad is particularly suited to this sort of analysis as it is rich in historical records as well as being easy to core. The macrofossil and pollen analysis was particularly helpful in investigating what macrophytes grew in the pre-disturbance period of the lake, prior to first historic records. The bulk sampling approach also added many species which would not have been found in conventional macrofossil cores. As well as adding a different range of species, the historic descriptions accompanying many of the plant records were also invaluable as they helped build a picture of how the historically recorded plants were organised spatially, enabling the visualisation of the old structure and architecture of the broad. In summary, this study shows the value of putting palaeolimnological analysis into context using complementary data sources.

CHAPTER 6 Conclusion

There is increasing interest within ecology in looking back and looking forward; using biological evidence as a clue to the causes of past changes, and as an indicator of the possible trajectories of future change. Historical records are a significant data resource in this respect. The need to understand biological structure in water bodies under un-impacted conditions, as a reference point for measuring ecosystem health or biotic integrity has been given added impetus by the Water Framework Directive. This not only stipulates that water bodies must be restored to a state equivalent to a low level of impact, but also endorses the use of historical data (among other techniques) as a means of identifying what this pre-impact state may be. Historical data may be a particularly important resource for reconstructing un-impacted biology in base-rich, eutrophic lakes, as in England at least, many of these have been subject to human impacts for so long that there is little remaining evidence of past functioning, and few un-impacted examples for comparison. Thus, while interest in the use of historical data to reconstruct changes in aquatic vegetation is not new in itself, there is a need to critically consider the potential of different types of historical data (e.g. records, surveys, specimens), its use in different water body types (e.g. lakes, rivers, wetlands), and at scales beyond the individual water body (e.g. lake district, lake type).

This study required the compilation of over 22,000 aquatic plant records from over 3,000 visits to 134 lakes in the Norfolk Broads and West Midland Meres, spanning a time period of over 200 years from the late 18th century until 2008. Once compiled, these records presented a significant challenge to interpret. The historical records came from hundreds of different sources and recorders, each with different priorities and sampling methodologies, with data quantity varying enormously between lakes and time periods. These factors, combined with uncertainties over species’ names and localities, introduced sufficient bias to render most methods of multivariate analysis commonly used in ecology, such as correspondence analysis, not only invalid, but also impossible to interpret.

Chapter 2 demonstrated some of the generic problems found in historical record data, through examples from the compiled macrophyte data for the Norfolk Broads and West Midland Meres. It showed that the number of visits made to lakes was highly variable throughout the time span of the datasets, as was the number of records made per visit, both of which were strongly related to the number of species recorded. This variation in recording effort could easily lead to false assumptions about species richness if not recognised. The study was also able to demonstrate that there was bias in species recording and site selection, particularly for earlier records. The change in recording methods largely reflects the change in recording ethos over the last 200 years, from mainly *ad hoc* collection of interesting species, to comprehensive whole lake surveys.

These biases, and others discussed in Chapter 2 are relevant to the broads and meres dataset presented here, but also have a wider relevance for any study using a combination of historical records derived from multiple sources. Historical records are currently not widely used in a direct form by ecologists and conservationists, but they will become an increasingly important source of ‘hard evidence’ for degree of impact as conservation bodies and environmental agencies attempt to restore lakes back to “good ecological status” as required by the newly adopted Water Framework Directive, or to favourable condition, as required under the Habitats Directive. It is therefore particularly important that historical record data are properly understood and analysed in ways which acknowledge and overcome the various sources of bias, leaving behind patterns that can be interpreted ecologically.

Once the various problems with the data had been considered, it was decided to analyse the macrophyte datasets of the Norfolk Broads and West Midland Meres by using a novel variation of a method used to assess amount of change in distribution of plants from historical records used for the UK flora (Preston *et al.*, 2002; Telfer *et al.*, 2002). The method demonstrated in Chapter 3 used the historical data for the broads and meres to develop a “change index” based on species persistence over the last 200 years, within individual lakes. Species persistence, measured as the proportion of those lakes which contained a species in the historic period, and which still contained that species in the modern period, was found to have a linear relationship with current day levels of occupancy (i.e. the number of lakes occupied as a proportion of all lakes). This relationship was used to derive change index scores for species with limited historical data. As expected, species with high index scores and thus large modern distribution and high levels of persistence in lakes, were those which are characteristic of lakes with high nutrient concentrations, such as *Myriophyllum spicatum*, *Zannichellia palustris* and *Nuphar lutea*. Conversely, species associated with low nutrient levels, such as

Littorella uniflora and *Potamogeton alpinus* in the broads, and *Myriophyllum alterniflorum* and *Apium inundatum* in the meres, had low index scores. There were, however, many species, such as *Hydrocharis morsus-ranae* and *Stratiotes aloides*, which are characteristic of lakes with relatively high nutrient concentrations, but which had low index scores. This implies that increasing fertility is not the sole driver for change in the composition of lake macrophyte communities, but rather a complex interaction of various chemical, physical and biological factors allied to eutrophication, but which have more immediate effects. These various supporting factors were explored more fully in Chapter 4.

The change index was used not only to show periods of decline in low change index species in both the broads and meres, but was also used alongside contemporary data to rank lakes into those most and least changed in their macrophyte communities, compared to the historical analogue for the overall district of lakes. This was done by taking the average change index of all the species currently found in each lake and comparing the values for different lakes. Whilst this does not take into account important attributes of the vegetation community, such as diversity and abundance, the results demonstrated that many of the lakes were classified as expected, such as the Martham Broads and Whitemere which had low average change index values and Rostherne Mere and Ranworth Broad which had high averages. The use of a change index in this way not only enables the robust interpretation of datasets based on a large variety of historic sources but also offers a potentially useful tool for lake managers. It cannot however, state how much any individual site has changed over time, since the baseline for each site is generally unknown (due to the incompleteness of the historical record) or would have varied naturally between sites within a region due to site-specific factors. The average change index therefore effectively reflects the relative importance at a site of species that have declined across a complex of lakes as a whole.

Chapter 4 investigated in more detail the ecological significance of the change index. When species were spilt into functional groups based on their morphological characteristics using an accepted macrophyte classification system which also relates to habitat use (Willby *et al.*, 2000), there was found to be a highly significant difference in the functional group mean index values for both the broads and meres. The functional groupings of (i) isoetids, (ii) hydrocharids and stratiotids, (iii) utricularids, and (iv) parvonymphaeids and magnopotamids, were the groups with the lowest average index scores, suggesting that these had declined most in both lake districts during the period of the datasets. While these functional groups cover a wide range of growth forms (isoetid, free-floating submerged, free-floating rooted, submerged rooted) they principally contain species characterised either by a) their occurrence in relatively mesotrophic or oligotrophic lakes, such as *Isoetes lacustris*, *Littorella uniflora, Lobelia dortmanna, Utricularia* species and pondweeds such as *Potamogeton alpinus* or *Potamogeton gramineus*, b) their occurrence in shallow, low energy habitats such, as *Utricularia* spp, *Stratiotes aloides* and *Hydrocharis morsus-ranae* or c) their occurrence in deeper water such *Isoetes lacustris* and *Potamogeton praelongus* (Preston and Croft, 1997). These species could have declined not only due to increases in nutrient concentrations which stimulated growth of more productive canopy-forming species, but also due to the role of nutrient loading in reedswamp loss in the broads (Boorman and Fuller, 1981), which contributed to the loss of shallow, low energy habitats, and an increase in light attenuation in the deeper, phytoplankton- rich meres.

In order to test which particular ecological traits of these plants resulted in their decline or survival, they were each assigned a score of 0-2 for a variety of habitat characteristics assembled from the literature, including water depth, water level fluctuation, water movement and trophic state, as well as Ellenberg's indicator values for acidity (R). Non-hierarchical clustering of the species based on their ecological traits resulted in groups with distinct change index values, suggesting that changes in species could be partly explained by their ecological preferences. As established in Chapter 3, species characteristic of low nutrient conditions had consistently low index values, reinforcing the role of eutrophication in species decline in the broads and meres, but the main factors controlling decline or survival of species characteristic of high nutrient lakes, were less clear. In order to ascertain what ecological preference traits controlled the change index score (and hence whether species declined or survived) for eutrophic species, correlations were carried out between their index scores and the traits used in the cluster analysis. Of these traits, trophic preference was still the most significant, but with others, particularly depth preferences in the broads, and preferences for still water and lower pH in the meres, also contributing. These results revealed that trophic condition was the overriding influence on the status of macrophytes in the broads and meres, but that other, often site-specific factors associated with eutrophication were also important in determining which species declined or persisted.

A complementary approach to using historical records is illustrated in Chapter 5. This looks at macrophyte community change over the last 200 years using a combination of historical records and palaeolimnology, in a key lake within the Norfolk Broads; Barton Broad. Sediment samples were taken from the broad and analysed for macrofossil remains and pollen. Two types of sediment samples were taken: large bulk samples from the bottom of cores, analysed to give a picture of pre-1850 communities found in the lake, and complete cores, analysed to provide a chronology of macrophyte community change throughout the history of the lake. This was then integrated with historic records of plants growing in the broad dating back to 1884. Additionally, descriptive references to the aquatic vegetation were also compiled from books, journal articles, naturalists' notes and newspaper articles.

This combined approach covering a range of data sources was able to give a more detailed picture of macrophyte community change than had previously been done, or by using any single data source in isolation. By complementing the historic records with palaeoanalysis it was possible to establish key aspects of the vegetation that pre-dated the first historic records. The method of bulk sampling bottom sediment also added many species which would not have been picked up or identified to species level in a small number of conventional, more finely sliced cores, e.g. *Potamogeton coloratus* and *Nuphar lutea*. Pollen analysis of the bottom sediments also added species, including those which rarely leave macrofossil remains, such as *Lemna* and *Callitriche*. Most surprisingly pollen of *Littorella uniflora* and *Myriophyllum alterniflorum* was also found. These are species not generally associated with alkaline eutrophic lakes, implying that nutrient levels must have been much lower than at the present time and the structure of the broad quite different to provide suitable habitat for these species. All these sources of data, combined with very early descriptions of the broad (Gurney, 1904; Nicholson, 1906), indicate that the communities that existed prior to 1850 were probably dominated by charophytes, but were not simply low growing *Chara* meadows as previously thought (Moss, 1979; George, 1992; Phillips, 1992). Instead, it appears that the vegetation structure was much more complex and varied, and, even at this time, contained many tall, fast growing species conventionally associated with quite nutrient rich conditions, such as *Myriophyllum spicatum*, *Zannichellia palustris*, *Nuphar lutea*, *Stratiotes aloides* and *Ceratophyllum demersum.*

Subsequent changes in the aquatic flora were well documented in the historic records, historic descriptions and photographs, as well as in the macrofossil cores. This started with the loss of species such as *Littorella uniflora* and *Myriophyllum alterniflorum* and *Potamogeton coloratus* which were never historically recorded in Barton Broad, so had probably disappeared before the first botanists started collecting records there in the late nineteenth century. By around 1910 the charophyte lawns had probably also already diminished. Species such as *Potamogeton lucens, Potamogeton compressus, Nitellopsis obtusa* and *Chara hispida* all disappear from the historic records prior to 1920, probably due to the effects of increasing nutrient concentrations. At the same time, there is an increasing encroachment into the broad of reedswamp (Gurney, 1904; Ready, 1910; Boorman and Fuller, 1981). Whist this may have invaded the habitat of some of the species which were lost prior to 1920, it also provided a heterogeneous physical structure to the previously open water areas of the broad which allowed still-water species, such as *Stratiotes aloides, Hottonia palustris* and *Utricularia vulgaris,* to continue to thrive in the mosaic of open water and in-lake reedswamp. The pressures of eutrophication and coypu grazing probably contributed to the dying back of the reedswamp, which occurred in the 1950s, after pumping of sewage effluent into the broad began (Lambert, 1965; Boorman and Fuller, 1981; Boar *et al.*, 1989). Once the reedswamp had died back and the in-lake swamp had gone, the hydraulic forces and change in sediment structure caused by remobilisation would have been too much for the remaining plants, and would have prevented further recruitment from the sediment propagule bank, causing these species to disappear around 1960.

Subsequent reductions in nutrient loading to Barton Broad have not yet lead to a recovery of its macrophyte community, which, although improving, remains sparse and species-poor. It is reasonable to speculate that this will not be possible until some of the structure, previously present in the form of the in-lake reedswamp, is re-established. The case study of Barton Broad demonstrates the added value of, not just historic records, but also historic descriptions, to palaeolimnological analysis.

This thesis has demonstrated that there is considerable potential for the use of historical records in ecological studies of macrophyte communities in lakes. It has illustrated some of the common problems associated with these records, but has also provided examples of robust ways in which to use them and overcome these problems. With the increased accessibility of historic records, and construction of databases of plant records, such as that run by the National Biodiversity Network gateway (data.nbn.org.uk), it is hoped that more studies into past macrophyte communities or ecological change, will exploit historic records, either as a data source in their own right, or to complement conventional palaeoecological research methods. The use of historical records is not a cheap alternative and will always require careful scrutiny and evaluation but, in return, it offers a more comprehensive insight into past lake environments and the factors resulting in diversity loss and reduction in ecosystem quality.

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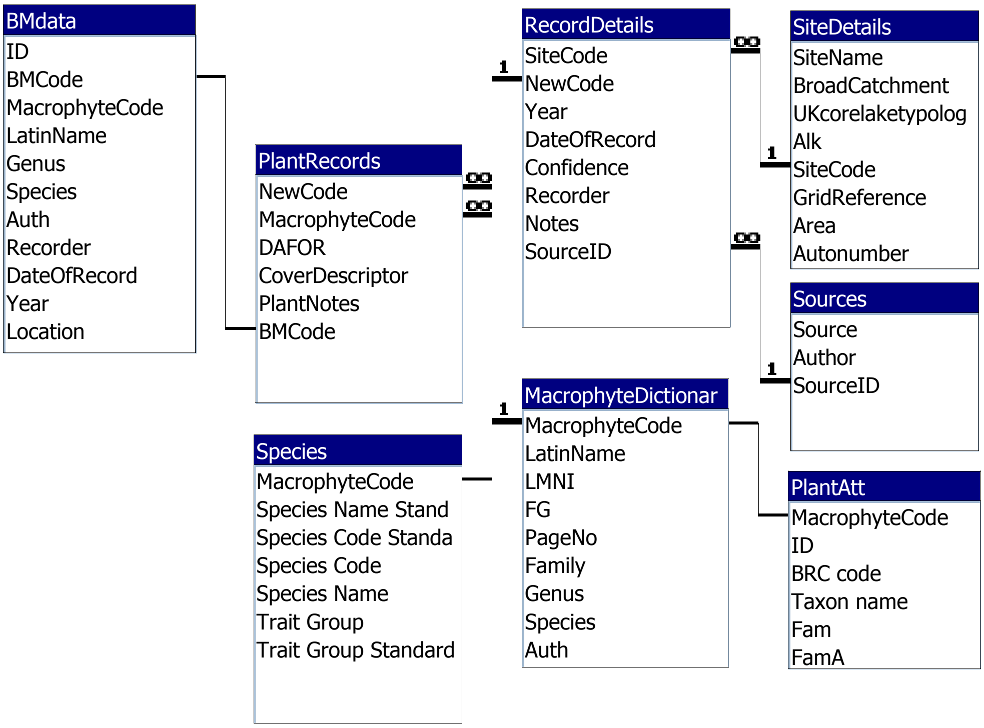
Appendices

Appendix 1. Microsoft Access 2003 database of historic plant records for the Norfolk Broads and West Midland meres……………………………………….(on enclosed CD)

Appendix 2. Database of historic plant records for the Norfolk Broads and West Midland meres saved as text (comma separated txt files)……………..(on enclosed CD)

Appendix 3: Graphical representation of the relationships between tables in the historic plant records database.



Appendix 4. An example of data held in the historic plants database; all records held for Barton Broad, Norfolk.

LatinName	CommonName	DateOfRecord	Year	Recorder	Source	Author	PlantNotes
Glyceria maxima	Reed sweet-grass	21.8.62	1862	Gould, S.	British Museum (Natural History) Herbarium.		Barton Broad, Barton Turf. Growing in shaded area near water. Common
Potamogeton praelongus	Long-stalked pondweed	4.8.1884	1884	Bennett, A.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Carex diandra	Lesser Tussock-sedge	1885	1885	Mennell, H. T.	Miscellaneous notes and observations. Trans. Norf. Nor. Nat. Soc. (1889) 4, 254-259.	Geldart, H. D.	
Oenanthe aquatica	Fine-leaved Water-dropwort	1885	1885	Mennell, H. T.	Miscellaneous notes and observations. Trans. Norf. Nor. Nat. Soc. (1889) 4, 254-259.	Geldart, H. D.	
Potamogeton lucens	Shining pondweed	8.8.1885	1885	Groves, H.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Carex curta	White sedge	June 1886	1886	Linton E. F.	Notes on a few Norfolk plants, including five newly found in the county. Trans. Norf. Nor. Nat. Soc. (1889) 4, 324.	Linton, E. F.	by the edge of Barton Broad, on the Barton turf side.
Carex elata	Tufted sedge	8.6.1886	1886	E.F.G	British Museum (Natural History) Herbarium.		
Potamogeton compressus	Grass-wrack pondweed	8.7.1886	1886	Linton, E. F.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton praelongus	Long-stalked pondweed	1886	1886	BSBI	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Potamogeton praelongus	Long-stalked pondweed	8.7.1886	1886	Linton, E. F.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton praelongus	Long-stalked pondweed	8.6.1886	1886	Linton, E. F.	Biological Centre, Monkswood. Herbarium.		
Potamogeton compressus	Grass-wrack pondweed	10.7.1888	1888	Bennett, A.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton compressus	Grass-wrack pondweed	18.7.1890	1890	Cotton, C.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Hippuris vulgaris	Mare's tail	20.7.1898	1898	Perring, F. H.	Biological Centre, Monkswood. Herbarium.		
Potamogeton compressus	Grass-wrack pondweed	1.8.1900	1900	Bennett, A. & Salmon, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton compressus	Grass-wrack pondweed	26.7.1900	1900	Bennett, J & Bennett, A.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Carex appropinquata	Fibrous Tussock-sedge	May 31. 1902	1902	Salmon, C.E.	British Museum (Natural History) Herbarium.		Great Fen, Barton Broad
Potamogeton obtusifolius	Blunt-leaved pondweed	1902	1902	Salmon, C. E.	Norfolk notes. J. Bot., (1902) 40, 94-101.	Salmon, C. E. & Bennett, A.	
Sagittaria sagittifolia	Arrowhead	September 1902	1902	Slater, Rev.H.H.	NBN Gateway		
Hottonia palustris	Water-violet	1903	1903	Bennett, A.	Norfolk Notes. J. Bot. (1903) 41, 202-204.	Bennett, A. & Salmon, C. E.	Barton turf
Stratiotes aloides	Water-soldier	1903	1903	Bennett, A.	Norfolk Notes. J. Bot. (1903) 41, 202-204.	Bennett, A. & Salmon, C. E.	
Potamogeton friesii	Flat-stalked pondweed	20.8.1909	1909	Moss, C. E.	Biological Centre, Monkswood. Herbarium.		
Potamogeton obtusifolius	Blunt-leaved pondweed	15.8.1909	1909	Moss, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton pectinatus	Fennel-leaved pondweed	26.8.1909	1909	Moss, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton polygonifolius	Bog pondweed	Aug 1909	1909	Moss, C. E.	Biological Centre, Monkswood. Herbarium.		
Potamogeton pusillus	Lesser pondweed	22.8.1909	1909	Moss, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton pusillus	Lesser pondweed	23.8.1909	1909	Moss, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton pusillus	Lesser pondweed	26.8.1909	1909	Moss, C. E.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Ceratophyllum demersum	Rigid Hornwort	28.8.1910	1910	Wilmot, A. J.	British Museum (Natural History) Herbarium.		
Potamogeton friesii	Flat-stalked pondweed	28.6.1910	1910	Adamson, R. S.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Hydrocharis morsus-ranae	Frogbit	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Myriophyllum spicatum	Spiked water-milfoil	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Myriophyllum verticillatum	Whorled water-milfoil	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nuphar lutea	Yellow Water-lily	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nymphaea alba	White Water-lily	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Potamogeton lucens	Shining pondweed	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Potamogeton natans	Broad-leaved pondweed	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Potamogeton praelongus	Long-stalked pondweed	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Schoenoplectus lacustris	Common Club-rush	Aug 1911	1911	Tansley, A. G.	The development of a Broadland estate at How Hill, Ludham, Norfolk. Trans. Norf. Nor. Nat. Soc. (1939) 15, 5-21.	Boardman, E. T.	
Stratiotes aloides	Water-soldier	1911	1911	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Stratiotes aloides	Water-soldier	Aug 1911	1911	Tansley, A. G.	The development of a Broadland estate at How Hill, Ludham, Norfolk. Trans. Norf. Nor. Nat. Soc. (1939) 15, 5-21.	Boardman, E. T.	"occupying a large extent of Barton Broad.
Nymphaea alba	White Water-lily	pre 1914	1914	Anon	A flora of Norfolk (1914).	Nicholson, W. A.	
Potamogeton compressus	Grass-wrack pondweed	pre 1914	1914	Anon	A flora of Norfolk (1914).	Nicholson, W. A.	
Potamogeton friesii	Flat-stalked pondweed	pre 1914	1914	Anon	A flora of Norfolk (1914).	Nicholson, W. A.	
Persicaria amphibia	Amphibious bistort	Aug 3rd 1915	1915	Pallis, M.	British Museum (Natural History) Herbarium.		Infrequent. Leaves nearly always algae coated. Typha angustifolia skeleton remain found amoung slime & dead roots.
Potamogeton lucens	Shining pondweed	2.8.1915	1915	Pallis, M.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Potamogeton obtusifolius	Blunt-leaved pondweed	5.8.1915	1915	Pallis, M.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Nymphaea alba	White Water-lily	1920's	1920	Ellis, E. A.	?EAE		in shallow peaty bays
Hottonia palustris	Water-violet	Sept. 1928	1928	Meinertzhagen, R.	British Museum (Natural History) Herbarium.		Submerged in deep water.
Potamogeton perfoliatus	Perfoliate pondweed	Sept. 1928	1928	Meinertzhagen, R.	British Museum (Natural History) Herbarium.		
Butomus umbellatus	Flowering rush	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		found near the banks and in dykes
Hydrocharis morsus-ranae	Frogbit	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		found in sheltered shallow corners
Nuphar lutea	Yellow Water-lily	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		
Nymphaea alba	White Water-lily	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		
Persicaria amphibia	Amphibious bistort	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		found in sheltered shallow corners
Ranunculus aquatilis	Common Water-crowfoot	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		found in sheltered shallow corners
Ranunculus reptans	Creeping Spearwort	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		found in sheltered shallow corners
Stratiotes aloides	Water-soldier	1930's	1930	Gane, G.	Barton Parish Magazine. 23.3.76		
Myriophyllum verticillatum	Whorled water-milfoil	29.8.35	1935	Ellis, E. A. & Geldart, A. M.	East Anglian Notebook. Norfolk and Suffolk Wild Life. Eastern Evening News. No. 1362. (1935).	Ellis, E. A. & Geldart, A. M.	numerous flowering spikes
Nuphar lutea	Yellow Water-lily	29.8.35	1935	Ellis, E. A. & Geldart, A. M.	East Anglian Notebook. Norfolk and Suffolk Wild Life. Eastern Evening News. No. 1362. (1935).	Ellis, E. A. & Geldart, A. M.	
Nymphaea alba	White Water-lily	29.8.35	1935	Ellis, E. A. & Geldart, A. M.	East Anglian Notebook. Norfolk and Suffolk Wild Life. Eastern Evening News. No. 1362. (1935).	Ellis, E. A. & Geldart, A. M.	
Stratiotes aloides	Water-soldier	29.8.35	1935	Ellis, E. A. & Geldart, A. M.	East Anglian Notebook. Norfolk and Suffolk Wild Life. Eastern Evening News. No. 1362. (1935).	Ellis, E. A. & Geldart, A. M.	
Stratiotes aloides	Water-soldier	pre 1939	1939	Gane, G.	Barton Parish Magazine. 23.3.76		absent but known to have occurred in the past
Najas marina	Holly-leaved naiad	c. 1947	1947	Ellis, E. A.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nymphaea alba	White Water-lily	c. 1947	1947	Ellis, E. A.	Notes on the natural history of the Broads area. (NCC files BG 9-10). (1947).	Ellis, E. A.	
Nymphaea alba	White Water-lily	c. 1947	1947	Ellis, E. A.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Stratiotes aloides	Water-soldier	c. 1947	1947	Ellis, E. A.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Najas marina	Holly-leaved naiad	Sept 1949	1949	Boardman, D. T.	Norfolk Rare Plant Survey. Vol VII. (Held at NCC, Norwich). (1977).	Crompton, G.	
Najas marina	Holly-leaved naiad	30.8.52	1952	Dunbar, R. E. C.	Norfolk Rare Plant Survey. Vol VII. (Held at NCC, Norwich). (1977).	Crompton, G.	found in bay near Heron's Carr. Also specimen in Norwich Castle Musuem.

LatinName	CommonName	DateOfRecord	Year	Recorder	Source	Author	PlantNotes
Potamogeton obtusifolius	Blunt-leaved pondweed	14.7.53	1953	Ryland, J. S.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Najas marina	Holly-leaved naiad	27.7.54	1954	Goodway, K. M.	Norfolk Rare Plant Survey. Vol VII. (Held at NCC, Norwich). (1977).	Crompton, G.	generally on naked mud in scattered clumps which often have hollow centres
Najas marina	Holly-leaved naiad	1951-1955	1955	Jermy, A. C.	Norfolk Rare Plant Survey. Vol VII. (Held at NCC, Norwich). (1977).	Crompton, G.	at Pleasure Hill btwn submerged peat cuttings and west side of north end
Sparganium erectum	Branched bur-reed	7.7.1956	1956		Norwich Castle Musuem (Natural History) Herbarium.		Barton turf
Ceratophyllum demersum	Rigid Hornwort	19.9.68	1968	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Lemna minor	Common duckweed	19.9.68	1968	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nuphar lutea	Yellow Water-lily	19.9.68	1968	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nymphaea alba	White Water-lily	19.9.68	1968	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Nuphar lutea	Yellow Water-lily	25.9.72	1972	Mason, C. F. & Bryant, R. J.	Changes in the ecology of the Norfolk Broads. Freshwater Biology, (1975) 5, 527-570.	Mason, C. F. & Bryant, R. J.	
Nymphaea alba	White Water-lily	25.9.72	1972	Mason, C. F. & Bryant, R. J.	Changes in the ecology of the Norfolk Broads. Freshwater Biology, (1975) 5, 527-570.	Mason, C. F. & Bryant, R. J.	
Nymphaea alba	White Water-lily	1977	1977	Tubbs, F. R.	Pers. comm. 15.12.77	Tubbs, F. R.	
Potamogeton pectinatus	Fennel-leaved pondweed	02/08/1983	1983	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	01/08/1985	1985	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	01/08/1985	1985	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	30/07/1986	1986	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	29/07/1988	1988	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	03/09/1993	1993	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	23/08/1994	1994	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	23/08/1994	1994	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	18/08/1995	1995	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	18/08/1995	1995	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	18/08/1995	1995	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	18/08/1995	1995	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	15/08/1996	1996	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	15/08/1996	1996	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	15/08/1996	1996	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	15/08/1996	1996	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	16/07/1997	1997	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	16/07/1997	1997	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	03/07/1998	1998	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	04/08/1999	1999	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	18/08/2000	2000	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	18/08/2000	2000	Broads Authority	Broads Authority		
Lemna minor	Common duckweed	18/08/2000	2000	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	18/08/2000	2000	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	18/08/2000	2000	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	13/08/2002	2002	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	13/08/2002	2002	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	13/08/2002	2002	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	13/08/2002	2002	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	25/07/2003	2003	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	25/07/2003	2003	Broads Authority	Broads Authority		
Lemna trisulca	Ivy-leaved duckweed	25/07/2003	2003	Broads Authority	Broads Authority		
Najas marina	Holly-leaved naiad	25/07/2003	2003	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	25/07/2003	2003	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	25/07/2003	2003	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	25/07/2003	2003	Broads Authority	Broads Authority		
Potamogeton pusillus	Lesser pondweed	25/07/2003	2003	Broads Authority	Broads Authority		
Sagittaria sagittifolia	Arrowhead	25/07/2003	2003	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	02/09/2004	2004	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	02/09/2004	2004	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	02/09/2004	2004	Broads Authority	Broads Authority		
Lemna minor	Common duckweed	02/09/2004	2004	Broads Authority	Broads Authority		
Lemna trisulca	Ivy-leaved duckweed	02/09/2004	2004	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	02/09/2004	2004	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	02/09/2004	2004	Broads Authority	Broads Authority		
Potamogeton obtusifolius	Blunt-leaved pondweed	02/09/2004	2004	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	02/09/2004	2004	Broads Authority	Broads Authority		
Ranunculus circinatus	Fan-leaved Water-crowfoot	02/09/2004	2004	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	05/08/2005	2005	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	05/08/2005	2005	Broads Authority	Broads Authority		
Najas marina	Holly-leaved naiad	05/08/2005	2005	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	05/08/2005	2005	Broads Authority	Broads Authority		
Nymphaea alba	White Water-lily	05/08/2005	2005	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	05/08/2005	2005	Broads Authority	Broads Authority		
Potamogeton obtusifolius	Blunt-leaved pondweed	05/08/2005	2005	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	05/08/2005	2005	Broads Authority	Broads Authority		
Potamogeton perfoliatus	Perfoliate pondweed	05/08/2005	2005	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	26/07/2006	2006	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	26/07/2006	2006	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	26/07/2006	2006	Broads Authority	Broads Authority		
Nymphaea alba	White Water-lily	26/07/2006	2006	Broads Authority	Broads Authority		
Potamogeton berchtoldii	Small pondweed	26/07/2006	2006	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	26/07/2006	2006	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	26/07/2006	2006	Broads Authority	Broads Authority		
Ranunculus circinatus	Fan-leaved Water-crowfoot	26/07/2006	2006	Broads Authority	Broads Authority		
Schoenoplectus lacustris	Common Club-rush	26/07/2006	2006	Broads Authority	Broads Authority		
Sparganium emersum	Unbranched bur-reed	26/07/2006	2006	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	2007	2007	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	2007	2007	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	2007	2007	Broads Authority	Broads Authority		
Lemna minor	Common duckweed	2007	2007	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	2007	2007	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	2007	2007	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	2007	2007	Broads Authority	Broads Authority		
Potamogeton pusillus	Lesser pondweed	2007	2007	Broads Authority	Broads Authority		
Potamogeton trichoides	Hairlike pondweed	2007	2007	Broads Authority	Broads Authority		
Ranunculus circinatus	Fan-leaved Water-crowfoot	2007	2007	Broads Authority	Broads Authority		
Schoenoplectus lacustris	Common Club-rush	2007	2007	Broads Authority	Broads Authority		
Sparganium emersum	Unbranched bur-reed	2007	2007	Broads Authority	Broads Authority		
Spirodela polyrhiza	Greater Duckweed	2007	2007	Broads Authority	Broads Authority		
Zannichellia palustris	Horned pondweed	2007	2007	Broads Authority	Broads Authority		
Ceratophyllum demersum	Rigid Hornwort	2008	2008	Broads Authority	Broads Authority		
Elodea canadensis	Canadian pondweedwaterweed	2008	2008	Broads Authority	Broads Authority		
Elodea nuttallii	Nuttall's waterweed	2008	2008	Broads Authority	Broads Authority		
Lemna minor	Common duckweed	2008	2008	Broads Authority	Broads Authority		
Nuphar lutea	Yellow Water-lily	2008	2008	Broads Authority	Broads Authority		
Potamogeton crispus	Curled pondweed	2008	2008	Broads Authority	Broads Authority		
Potamogeton pectinatus	Fennel-leaved pondweed	2008	2008	Broads Authority	Broads Authority		
Sagittaria sagittifolia	Arrowhead	2008	2008	Broads Authority	Broads Authority		
Schoenoplectus lacustris	Common Club-rush	2008	2008	Broads Authority	Broads Authority		
Sparganium emersum	Unbranched bur-reed	2008	2008	Broads Authority	Broads Authority		
Spirodela polyrhiza	Greater Duckweed	2008	2008	Broads Authority	Broads Authority		

Appendix 5. An example of data held in the historic plants database; all records held for *Utricularia* in the Broads and Meres.

LatinName	DateOfRecord	Year	SiteName	GridReference	Recorder	Source	Author	PlantNotes
Utricularia	1911	1911	Barton	TG359214	Pallis, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	more than one species of utricularia
Utricularia	1930's	1930	Barton	TG359214	Gane, G.	Barton Parish Magazine. 23.3.76		
Utricularia	18.4.39	1939	Crome's	TG374196	Geldart, A. M.	The development of a Broadland estate at How Hill, Ludham, Norfolk. Trans. Norf. Nor. Nat. Soc. (1939) 15, 5-21.	Boardman, E. T.	
Utricularia	pre-1953	1953	Sutton (Stalham)	TG375235	JM	The British Isles and their vegetation. (1953).	Tansley, A. G.	
Utricularia	1968	1968	Hickling	TG419214	George, M.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	more than one species of utricularia
Utricularia	July 1968	1968	Hickling	TG419214	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	more than one species of utricularia
Utricularia	22.7.68	1968	Horsey Mere	TG449222	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	more than one species
Utricularia	1968	1968	Blackfleet	TG444213	George, M.	Aquatic macrophytes. (NNC files Subject files)		
Utricularia	18.10.68	1968	Heigham Sound and Whiteslea	TG433205	George, M.	Field Notes. (NNC files C 22). (1971).	George, M.	
Utricularia	1.6.69	1969	Hickling	TG419214	Morgan, N. C. & Britton, R. H.	Conservation Review. Interim Report on Open Water. (NCC files HG 9, HI 861, HO 26 and RC 28). (1969).	Morgan, N. C. & Britton, R. H.	
Utricularia	23.9.69	1969	Upton Great	TG389134	Morgan, N. C.	Problems of the conservation of freshwater ecosystems. In: Conservation and Productivity of Natural Waters. Symp. Zool. Soc. Lond. (R. V. Edwards & D. J. Garrod). (1972) 135-154.	Morgan, N. C.	
Utricularia	25.8.71	1971	Martham South	TG459201	Hornby, R. J. & Pigg, F.	Field Notes. (NNC files MA 13). (1971).	Hornby, R. J.	
Utricularia	18.8.71	1971	Martham South	TG459201	Cadbury, C.	Field Notes. (NNC files MA 3). (1971).	Cadbury, C.	
Utricularia	1.8.75	1975	Martham South	TG459201	Wright, P. A. & Stevens, P. M. C.	Field Notes. (NNC files MA 4). (1975).	Wright, P. A.	in area close to the boathouse and associated with najas
Utricularia	1977	1977	Martham Somerton	TG450200	Norfolk Naturalists Trust	Vegetation Survey of Nature Reserves. (NCC files MA 29-35). (1978).	Norfolk Naturalists Trust	
Utricularia	1977	1977	Martham South	TG459201	Norfolk Naturalists Trust	Vegetation Survey of Nature Reserves. (NCC files MA 29-35). (1978).	Norfolk Naturalists Trust	
Utricularia	15.8.79	1979	Calthorpe	TG409259	Dollmon, H. E.	Pers. comm. 29.3.78	Dollman, H.	
Utricularia	22.8.79	1979	Hickling	TG419214	Linsell, S.	Pers. comm. 22.8.79	Linsell, S.	at mouth of dyke leading into broad
Utricularia australis	28.7.1899	1899	Martham Somerton	TG450200	Bennett, J & A.	British Museum (Natural History) Herbarium.		Dike connecting the Thurne with Martham Broad
Utricularia australis	1937	1937	Wheatfen	TG328057	Ellis, E. A.	Flora of Norfolk (1968).	Petch, C. P. & Swann, E. L.	Recorded as U. neglecta
Utricularia intermedia	28.9.1892	1892	Barton	TG359214	Clarke, W. G.	Norwich Castle Musuem (Natural History) Herbarium.		
Utricularia intermedia	31 Aug. 1893	1893	Barton	TG359214	Groves, H.	British Museum (Natural History) Herbarium.		Fen on South of Barton Broad, E Norfolk
Utricularia intermedia	October 1912	1912	Barton	TG359214	Clarke, W.G.	British Museum (Natural History) Herbarium.		Barton Turf Fen, Norfolk
Utricularia intermedia	28.9.1912	1912	Barton	TG359214	AHB	British Museum (Natural History) Herbarium.		Barton turf Norfolk
Utricularia intermedia	Sept. 1915	1915	Sutton (Stalham)	TG375235	Pallis, M.	British Museum (Natural History) Herbarium.		Sutton Fen
Utricularia intermedia	1920	1920	Sutton (Stalham)	TG375235	Clarke, W.G. & Gurney, R.	Notes on the genus Utricularia and its distribution in Norfolk. Trans. Norf. Nor. Nat. Soc. (1921) 11, 128-161.	Clakre, W.G. & Gurney, R.	
Utricularia intermedia	24.6.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	All species recorded from lousy bay. Littorella uniflora and Utricularia neglecta previously present
Utricularia intermedia	20.7.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	Littorella uniflora previously present
Utricularia intermedia	23.6.1921	1921	Hoveton Little Broad	TG330175	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	
Utricularia intermedia	June 1921	1921	Hoveton Little Broad	TG330175	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	near boathouse on Pound end broad
Utricularia minor	1798	1798	Shomere Pool	SJ504079	Williams, Rev E.	Leighton, W.A. (1839)	Leighton, W.A. (1839)	Ditch on Shomere Moss, near Condover.
Utricularia minor	<1805	1805	Surlingham (Bargate)	TG318078	Turner, D.	Flora of Norfolk, (1866).	Trimmer, K.	"Bogs at Surlingham". From Botanist's Guide
Utricularia minor	1821	1821	Betley Mere	SJ748479	Purton, Dr T.	Purton, T. (1821)	Purton, T. (1821)	Near Betley.
Utricularia minor	AUG 1835	1835	Bomere Pool	SJ498080	Leighton, Rev W.A.	Bolton Museum (2006)	Bolton Museum (2006)	
Utricularia minor	13 SEP 1835	1835	Bomere Pool	SJ498080	Babington, Prof C.C.	A flora of Shropshire (1841)	Leighton, W. A.	Ditches on the north side of Bomere Pool.
Utricularia minor	<1841	1840	Bomere Pool	SJ498080	Leighton, W. A.	A flora of Shropshire (1841)	Leighton, W. A.	ditches on the north side
Utricularia minor	7/1862	1862	Oak Mere	SJ574677	Boswell-Syme, J.T.I.	British Museum (Natural History) Herbarium.		
Utricularia minor	1874	1874	Hatch Mere	SJ552721	Warren, Sir J.B.L.	Warren, J.B.L.(Lord de Tabley) (1899)	Warren, J.B.L.(Lord de Tabley) (1899)	Pit-holes in the north swamp at Hatchmere.
Utricularia minor	1874	1874	Abbot's Moss	SJ590689	Warren, Sir J.B.L.	Warren, J.B.L.(Lord de Tabley) (1899)	Warren, J.B.L.(Lord de Tabley) (1899)	Pits in the centre of the swamp on Newchurch Common, by the letter N" in Ordnance Map."
Utricularia minor	July, 1877	1877	Oak Mere	SJ574677	Whitelegge, T.	British Museum (Natural History) Herbarium.		
Utricularia minor	1878	1878	Bomere Pool	SJ498080	Phillips, Rev W.	Transactions of the Shropshire Archaeological & Natural History Society Vol 1, 1878	Phillips, William	Ditches on the north side of Bomere Pool.
Utricularia minor	23rd August 1879	1879	Oak Mere	SJ574677	Bailey, C.	British Museum (Natural History) Herbarium.		Edge of Oakmere, in the neighbourhood of Delamere
Utricularia minor	25th June 1890	1890	The Mere, Ellesmere	SJ406349	Wolley-Dod, A.H.	British Museum (Natural History) Herbarium.		
Utricularia minor	1901	1901	Betley Mere	SJ748479	Welch, D.	Bagnall, J.E. (1901)	Bagnall, J.E. (1901)	Betley.
Utricularia minor	1910	1910	Hatch Mere	SJ552721	Dunlop, Mr G.A.	Dunlop, G.A. (1910)	Dunlop, G.A. (1910)	In shallow, mossy pools near edges of mere.
Utricularia minor	27.6.1910	1910	Sutton (Stalham)	TG375235	Wilmott, A.J.	British Museum (Natural History) Herbarium.		Norfolk: in shallow water fen near mouth of Sutton Broad
Utricularia minor	1920	1920	Sutton (Stalham)	TG375235	Clarke, W.G. & Gurney, R.	Notes on the genus Utricularia and its distribution in Norfolk. Trans. Norf. Nor. Nat. Soc. (1921) 11, 128-161.	Clakre, W.G. & Gurney, R.	
Utricularia minor	24.6.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	All species recorded from lousy bay. Littorella uniflora and Utricularia neglecta previously present
Utricularia minor	20.7.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	Littorella uniflora previously present
Utricularia minor	1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Utricularia in Norfolk in 1921: The effects of drought and temperature. Norf. Nor. Nat. Soc. (1921) 11.	Gurney, R.	"[not in flower but] survived the summer in a thriving condition at the edge of the Broad."
Utricularia minor	1950	1950	Hatch Mere	SJ552721	Butcher, Dr R.W.	Biological Records Centre (1970-2005)	Biological Records Centre (1970-2005)	[No date. This is approximate.]
Utricularia minor	1964-1969	1966	Abbot's Moss	SJ590689	Newton, Mr A.L.	Flora of Cheshire (1971)	Newton, Alan	Two bog pools near Abbot's Moss. With Eleocharis multicaulis. Flowering regularly.
Utricularia minor	28-Jun-83	1983	Abbot's Moss	SJ590689	Newbold, Dr C.	English Nature (1946-2005)	English Nature (1946-2005)	
Utricularia minor	May-91	1991	Abbot's Moss	SJ590689	Hawksford, Mr J.E.	Biological Records Centre (1970-2005)	Biological Records Centre (1970-2005)	
Utricularia minor	12-Jul-01	2001	Abbot's Moss	SJ590689	Hodgetts, Mr N.G.	Whild Associates (1993-2006)	Whild Associates (1993-2006)	Rare in bog pools in the Lily Pond.
Utricularia vulgaris	1800	1800	Hencott Pool	SJ480160	Williams, Rev E.	Leighton, W.A. (1839)	Leighton, W.A. (1839)	Hencote pool.
Utricularia vulgaris	29 JUL 1836	1836	Crose Mere	SJ430305	Bowman, Mr J.E.	A flora of Shropshire (1841)	Leighton, W. A.	In a deep ditch on the north margin of Croesmere Mere.
Utricularia vulgaris	1840	1840	Crose Mere	SJ430305	Bowman, J. E.	A flora of Shropshire (1841)	Leighton, W. A.	In deep ditch on North margin of the mere
Utricularia vulgaris	1841	1841	Hencott Pool	SJ480160	Dickinson, Mr F.	A flora of Shropshire (1841)	Leighton, W. A.	
Utricularia vulgaris	1844	1844	Betley Mere	SJ748479	Garner, Dr R.	Garner, R. (1844)	Garner, R. (1844)	Betley.
Utricularia vulgaris	1844	1844	Aqualate Mere	SJ772204	Garner, Dr R.	Garner, R. (1844)	Garner, R. (1844)	Frequent in pools... Aqualate.
Utricularia vulgaris	1844	1844	Maer Pool	SJ789384	Garner, Dr R.	Garner, R. (1844)	Garner, R. (1844)	Maer.
Utricularia vulgaris	August 1846	1846	Hickling	TG419214	Mann, R.J.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	1847	1847	Hickling	TG419214	Mann, R. J.	Royal Botanical Gardens, Kew. Herbarium.		
Utricularia vulgaris	<1866	1866	Hickling	TG419214	Trimmer. K.	Flora of Norfolk, (1866).	Trimmer, K.	
Utricularia vulgaris	19.7.1881	1881	Ormesby Great	TG467161		Norwich Castle Musuem (Natural History) Herbarium.		
Utricularia vulgaris	23 SEP 1882	1882	Fenemere	SJ445229	Beckwith, Mr W.E.	Beckwith, W.E. (1882)	Beckwith, W.E. (1882)	In ditches near Fenemere.
Utricularia vulgaris	1882	1882	Hencott Pool	SJ480160	Beckwith, Mr W.E.	Beckwith, W.E. (1882)	Beckwith, W.E. (1882)	
Utricularia vulgaris	17th July 1883	1883	Sutton (Stalham)	TG375235	Hanbury, F.J.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	12th July 1883	1883	Martham Somerton	TG450200	Hanbury, F.J.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	12.7.1883	1883	Martham North	TG458204	Hanbury, F. J.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	9. 1884	1884	The Mere, Ellesmere	SJ406349	Beckwith, W.E.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	8.1885	1885	Sutton (Stalham)	TG375235	Mennell, H. T.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	16.7.1885	1885	Upton Great	TG389134	Southwell & Geldart, H. D.	Miscellaneous notes and observations. Trans. Norf. Nor. Nat. Soc. (1889) 4, 254-259.	Geldart, H. D.	
Utricularia vulgaris	July 1/1889	1889	Hickling	TG419214	Salmon, C.E & E.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	6.7.1897	1897	Sutton (Stalham)	TG375235		Norwich Castle Musuem (Natural History) Herbarium.		
Utricularia vulgaris	20.7.1898	1898	Barton	TG359214	Perring, F. H.	Biological Centre, Monkswood. Herbarium.		
Utricularia vulgaris	1901	1901	Hencott Pool	SJ480160	Hamilton, Mr W.P.	Record of Bare Facts 11: 1901 (1902)	Record of Bare Facts 11: 1901 (1902)	Abundantly in flower at its old habitat Hencote Pool, where it has been in some seasons apparently extinct.
Utricularia vulgaris	1903	1903	Hencott Pool	SJ480160	Hamilton, Mr W.P.	Record of Bare Facts 15: 1905 (1906)	Record of Bare Facts 15: 1905 (1906)	The hibernacula or winter buds were found at Christmas in a garden tank, into which plants from Hencote pool had been introduced a season or two ago.
Utricularia vulgaris	July 1905	1905	Sutton (Stalham)	TG375235	Nicholson, W. A.	A preliminary sketch of the bionomical botany of Sutton and the Ant district. Trans. Norf. Nor. Nat. Soc. (1906) 8, 265-289.	Nicholson, W. A.	

LatinName	DateOfRecord	Year	SiteName	GridReference	Recorder	Source	Author	PlantNotes
Utricularia vulgaris	1906	1906	Heigham Sound and Whiteslea	TG433205	Nicholson, W. A.	A preliminary sketch of the bionomical botany of Sutton and the Ant district. Trans. Norf. Nor. Nat. Soc. (1906) 8, 265-289.	Nicholson, W. A.	
Utricularia vulgaris	2.8.1915	1915	Sutton (Stalham)	TG375235	Pallis, M.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	6.8.1915	1915	Horsey Mere	TG449222	Pallis, M.	British Museum (Natural History) Herbarium.		Rare
Utricularia vulgaris	2.8.1915	1915	Barton	TG359214	Pallis, M.	British Museum (Natural History) Potamogetonaceae Card Index	Dandy, J. E.	
Utricularia vulgaris	July 2 1915	1915	Upton Great	TG389134	White, J.W.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	1920	1920	Sutton (Stalham)	TG375235	Clarke, W.G. & Gurney, R.	Notes on the genus Utricularia and its distribution in Norfolk. Trans. Norf. Nor. Nat. Soc. (1921) 11, 128-161.	Clakre, W.G. & Gurney, R.	
Utricularia vulgaris	1920	1920	Hickling	TG419214	Clarke, W.G. & Gurney, R.	Notes on the genus Utricularia and its distribution in Norfolk. Trans. Norf. Nor. Nat. Soc. (1921) 11, 128-161.	Clakre, W.G. & Gurney, R.	"grows freely on Hickling Broad" "but is there found on the bottom in about 4 feet of water and not floating"
Utricularia vulgaris	24.6.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	far from being as abundant as in the past. 'All species recorded from lousy bay. Littorella uniflora and Utricularia neglecta previously present
Utricularia vulgaris	15.7.1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	flowering in profusion
Utricularia vulgaris	1921	1921	Sutton (Stalham)	TG375235	Gurney, R.	Utricularia in Norfolk in 1921: The effects of drought and temperature. Norf. Nor. Nat. Soc. (1921) 11.	Gurney, R.	"plants were growing with conspicuos vigour"
Utricularia vulgaris	14.12.1921	1921	Hickling	TG419214	Bullock-Webster, G. R.	Diaries. (Held at NCC, Norwich). (1921-29).	Gurney, R.	
Utricularia vulgaris	9.8.1927	1927	Martham Somerton	TG450200		Norwich Castle Musuem (Natural History) Herbarium.		
Utricularia vulgaris	13.8.1927	1927	Hickling	TG419214	Frogitt, T. J.	Biological Centre, Monkswood. Herbarium.		
Utricularia vulgaris	13 Aug. 1927	1927	Hickling	TG419214	Foggitt, T.J.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	Sept. 1928	1928	Hickling	TG419214	Meinertzhagen, R.	British Museum (Natural History) Herbarium.		deep water 5ft and stagnant
Utricularia vulgaris	1934	1934	Hickling	TG419214	Ellis, E. A.	Species list from weedcutting operations. (NNC files HI 29-). (1934).	Ellis, E. A.	all species identified from weedcutting operations
Utricularia vulgaris	22.8.35	1935	Hickling	TG419214	Pugsley, H. W.	Biological Centre, Monkswood. Herbarium.		
Utricularia vulgaris	22nd August 1935	1935	Hickling	TG419214	Reynolds, B. & Pugsley, H. W.	British Museum (Natural History) Herbarium.		
Utricularia vulgaris	29.8.35	1935	Barton	TG359214	Ellis, E. A. & Geldart, A. M.	East Anglian Notebook. Norfolk and Suffolk Wild Life. Eastern Evening News. No. 1362. (1935).	Ellis, E. A. & Geldart, A. M.	U.vulg- spikes appeared here and there above water
Utricularia vulgaris	c.1947	1947	Sutton (Stalham)	TG375235	Ellis, E. A.	Notes on the natural history of the Broads area. (NCC files BG 9-10). (1947).	Ellis, E. A.	in the peatier and more sheltered parts
Utricularia vulgaris	c. 1947	1947	Barton	TG359214	Ellis, E. A.	Notes on the natural history of the Broads area. (NCC files BG 9-10). (1947).	Ellis, E. A.	in the peatier and more sheltered parts
Utricularia vulgaris	1947	1947	Alderfen Broad	TG354195	Ellis, E. A.	Notes on the natural history of the Broads area. (NCC files BG 9-10). (1947).	Ellis, E. A.	In peatier and more sheltered parts
Utricularia vulgaris	1949	1949	Upton Great	TG389134	Lambert, J. M. & Jennings, J. N.	Alluvial stratigraphy and vegetational succession in the region of the Bure Valley. J. Ecology, (1951) 39, 120-148.	Lambert, J. M. & Jennings, J. A.	
Utricularia vulgaris	July 1949	1949	Upton Great	TG389134	Lambert, J. M. & Jennings, J. N.	Complete results of vegetation survey. (NNC files U 15-20). (1954).	Lambert, J. M.	generally confined to reedswamp.
Utricularia vulgaris	Aug. 1949	1949	Upton Great	TG389134	Lambert, J. M. & Jennings, J. N.	Complete results of vegetation survey. (NNC files U 15-20). (1954).	Lambert, J. M.	
Utricularia vulgaris	1951	1951	Hoveton Little Broad	TG330175	Lambert, J. M. & Jennings, J. N.	Alluvial stratigraphy and vegetational succession in the region of the Bure Valley. J. Ecology, (1951) 39, 120-148.	Lambert, J. M. & Jennings, J. A.	all species in shelter of reedswamp
Utricularia vulgaris	1951	1951	Upton Great	TG389134	Lambert, J. M. & Jennings, J. N.	Alluvial stratigraphy and vegetational succession in the region of the Bure Valley. J. Ecology, (1951) 39, 120-148.	Lambert, J. M. & Jennings, J. A.	generally confined to the shelter of the reedswamp
Utricularia vulgaris	23.7.52	1952	Upton Great	TG389134	Jermy, A. C.	Field Notes. (NNC files U 50). (1952).	Jermy, A. C.	in phragmites and typha reedswamp.
Utricularia vulgaris	Aug. 1954	1954	Heigham Sound and Whiteslea	TG433205	Lambert, J. M.	Complete results of vegetation survey. (NNC files HI 8-18). (1954).	Lambert, J. M.	all species recorded from transect across Heigham Sound
Utricularia vulgaris	Aug. 1954	1954	Heigham Sound and Whiteslea	TG433205	Lambert, J. M.	Complete results of vegetation survey. (NNC files HI 8-18). (1954).	Lambert, J. M.	all species recorded from transect across Whiteslea
Utricularia vulgaris	Aug. 1954	1954	Hickling	TG419214	Lambert, J. M.	Complete results of vegetation survey. (NNC files HI 8-18). (1954).	Lambert, J. M.	
Utricularia vulgaris	1955	1955	Betley Mere	SJ748479	Edees, Mr E.S.	Edees, E.S. (1972)	Edees, E.S. (1972)	Drain near Betley Mere.
Utricularia vulgaris	1956	1956	Calthorpe	TG409259	Jermy, A. C.	Annotated List of Vascular Plants. (NNC files C 55-58). (1956).	Jermy, A. C.	
Utricularia vulgaris	11.9.58	1958	Calthorpe	TG409259	Marsh, A. R.	Vegetation Map of Calthorpe Broad. (NNC files C 7). (1958).	Marsh, A. R.	
Utricularia vulgaris	1959	1959	Alderfen Broad	TG354195	Jermy, A. C.	Report on the vegetation and its ecological status at Alderfen Broad. (NCC files A 1-19). (1959).	Jermy, A. C.	Found in shelter of Typha stools
Utricularia vulgaris	1965	1965	Hickling	TG419214	Cadbury, J.C.	The Norfolk Naturalist's trust 39th annual report. 31st December 1965.		
Utricularia vulgaris	1968	1968	Hickling	TG419214	Hornby, R. J.	Correspondence - Aquatic plants in Norfolk Broads. (NNC files HO 29). (1972).	Hornby, R. J.	all species recorded from Catfield dyke
Utricularia vulgaris	1968	1968	Hickling	TG419214	Hornby, R. J.	Correspondence - Aquatic plants in Norfolk Broads. (NNC files HO 29). (1972).	Hornby, R. J.	all species recorded from swim coots
Utricularia vulgaris	5.9.68	1968	Martham Somerton	TG450200	George, M.	Aquatic macrophytes. (NNC files Subject files)		
Utricularia vulgaris	22.7.68	1968	Hickling	TG419214	Morgan, N. C.	Field Notes. (NNC files HI 41). (1968).	Anon	
Utricularia vulgaris	1968	1968	Hickling	TG419214	Morgan, N. C.	The Aquatic Vegetation of the Thurne Broads. (NCC files HO 25 and MA 15). (1972).	Hornby, R. J.	
Utricularia vulgaris	23.11.70	1970	Hickling	TG419214	SANKEY	Distribution map of Najas marina in Hickling Broad. (NNC files HI 22-23). (1970).	Sankey	
Utricularia vulgaris	1971	1971	Martham Somerton	TG450200	Hornby, R. J.	The Aquatic Vegetation of the Thurne Broads. (NCC files HO 25 and MA 15). (1972).	Hornby, R. J.	
Utricularia vulgaris	25.8.71	1971	Martham Somerton	TG450200	Mann, R. J. & Pigg, F.	Field Notes. (NNC files MA 13). (1971).	Hornby, R. J.	
Utricularia vulgaris	1972	1972	Martham Somerton	TG450200	Hornby, R. J.	The Aquatic Vegetation of the Thurne Broads. (NCC files HO 25 and MA 15). (1972).	Hornby, R. J.	Ceratophyllum demersum, Najas marina & Myriophyllum sp. were previously present.
Utricularia vulgaris	1972	1972	Martham South	TG459201	Hornby, R. J.	The Aquatic Vegetation of the Thurne Broads. (NCC files HO 25 and MA 15). (1972).	Hornby, R. J.	
Utricularia vulgaris	Sept. 1973	1973	Martham Somerton	TG450200	Britton, R. H.	Submerged vegetation survey of Martham Broad (NCC Files MA 18-20). (1973)	Britton, R. H.	
Utricularia vulgaris	Sept. 1973	1973	Martham South	TG459201	Britton, R. H.	Submerged vegetation survey of Martham Broad (NCC Files MA 18-20). (1973)	Britton, R. H.	
Utricularia vulgaris	1973-74	1974	Upton Great	TG389134	Hornby, R. J.	Conservation in the Upton Broad area. (NCC files U 6 and U 21-24). (1974).	Hornby, R. J.	Myriophyllum verticillatum & Potamogeton obtusifolius recorded in 1949-52 but not in recent years. Hydrocharis morsus-ranae, Lemna minor, Lemna trisulca & Potamogeton friessi not specified as recorded from the broad.
Utricularia vulgaris	20.8.74	1974	Calthorpe	TG409259	Hornby, R. J.	Field Notes. (NNC files C 60). (1974).	Hornby, R. J.	found in boathouse dyke, found growing in the water but apparently only near the edges.
Utricularia vulgaris	14.10.75	1975	Heigham Sound and Whiteslea	TG433205	George, M.	Field Notes. (NNC files HI 32). (1975).	George, M.	all sp recorded from bays away from main boat channel
Utricularia vulgaris	June 1975	1975	Martham Somerton	TG450200	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	Sept. 1975	1975	Martham Somerton	TG450200	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1975	1975	Martham South	TG459201	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1976	1976	Martham Somerton	TG450200	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1976	1976	Martham South	TG459201	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1976	1976	Heigham Sound and Whiteslea	TG433205	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1977	1977	Martham Somerton	TG450200	Phillips, G. L.	The distribution, biomass and productivity of submerged aquatic macrophytes in the Thurne Broads, Norfolk, 1975-1977. (Held at the NCC, Norwich). (1978).	Phillips, G. L. & Moss, B.	
Utricularia vulgaris	1977	1977	Hickling	TG419214	Norfolk Naturalists Trust	Vegetation Survey of Nature Reserves. (NCC files MA 29-35). (1978).	Norfolk Naturalists Trust	
Utricularia vulgaris	5.9.77	1977	Martham South	TG459201	Jackson, M. J. & Pigg, F.	The Changing Status of Aquatic Macrophytes in the Norfolk Broads. Trans. Norf. Nor. Nat. Soc. (1978) 24, 137-152.	Jackson, M. J.	
Utricularia vulgaris	14/08/1984	1984	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	14/08/1985	1985	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	08/08/1986	1986	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	17/08/1987	1987	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	17/08/1988	1988	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	01/09/1988	1988	Crome's South	TG374196	Broads Authority	Broads Authority		
Utricularia vulgaris	07/08/1989	1989	Cockshoot dyke	TG346160	Broads Authority	Broads Authority		
Utricularia vulgaris	13/08/1990	1990	Crome's South	TG374196	Broads Authority	Broads Authority		
Utricularia vulgaris	30/07/1998	1998	Strumpshaw	TG339067	Broads Authority	Broads Authority		
Utricularia vulgaris	23/06/1999	1999	Strumpshaw	TG339067	CSR	Carl Sayer's notes		
Utricularia vulgaris	21/08/1999	1999	Strumpshaw	TG339067	CSR	Carl Sayer's notes		
Utricularia vulgaris	01/09/2004	2004	Catfield Broad	TG376208	Broads Authority	Broads Authority		
Utricularia vulgaris	25/08/2005	2005	Strumpshaw	TG339067	Broads Authority	Broads Authority		
Utricularia vulgaris	18/07/2006	2006	Strumpshaw	TG339067	Broads Authority	Broads Authority		

Appendix 6. Counts of macrofossil remains (numbers per 100 cm^3) in the Barton bulk bottom sediment samples. Species were represented by seeds unless stated otherwise.

	Bart 2	Bart 3	Bart 8	Bart 10	Bart 11	Bart 12	Bart 13	Bart 14
Alisma plantago-aquatica			0.61					
Callitriche								
Ceratophyllum (leaf frag.)			10.00		2200.00	2103.33		13.33
Ceratophyllum demersum					2.07	0.91		
Chara oospore	3.33	3.13	1960.00	1203.33	576.67	1063.33	860.00	733.33
Cladium mariscus				0.30		0.30		
Eleocharis palustris								0.91
Hippuris vulgaris								
Hydrocharis morsus-ranae								
Lemna								
Littorella uniflora								
Menyanthes trifoliata (seed frag.)		2.30		1.52			1.18	1.21
Myrica gale		0.46		1.52	0.30	1.82	0.29	0.30
Myriophyllum alterniflorum								
Myriophyllum spicatum			0.30	0.30				
Najas marina (seed frag.)	10.56		13.94	1.52	248.93	0.61	4.71	97.88
Nitella oospore				0.30				
Nuphar lutea (seed frag.)					0.59			
Nymphaea (leaf trichoschlerid)	70.00	400.00	70.00	176.67	440.30	340.00	180.00	570.00
Nymphaea alba (seed frag.)		1.38	1.52		1.18		10.88	0.30
Potamogeton		4.15	2.42	1.82	6.21	5.76	6.47	22.42
Potamogeton coloratus				0.30				
Potamogeton crispus								0.30
Potamogeton friesii (leaf)			0.30		0.59	0.30	0.29	
Potamogeton obtusifolius (leaf)				1.21				
Potamogeton pusillus (leaf)			4.55	2.12	6.51	4.55	3.24	5.15
Potamogeton pusillus		1.38						
Ranunculus Batrachium	0.56	0.46				0.61	0.59	0.30
Sagittaria sagittifolia								
Schoenoplectus lacustris							0.88	0.61
Stratiotes aloides (leaf spine)	41.11	292.90	74.55					127.88
Typha latifolia	20.00	2.30	0.91	1.52	0.59	1.21	0.29	

Appendix 7. Counts of macrofossil remains (numbers per 100 cm^3) in the Barton sediment cores, a) BART5 and b) BART3.

a)

Depth (cm)	*Chara* spp. oospore	*Nitella* spp. oospore	*Carex* spp. seed	*Ceratophyllum* leaf frag.	*Juncus* spp. seed	*Najas marina* leaf spine	*Najas marina* seed frag.	*Nymphaea* leaf trichoschlerid	*Potamogeton friesii* leaf	*Potamogeton friesii* seed	*Schoenoplectus lacustris* seed	*Stratiotes aloides* spine	*Typha latifolia* seed
1.5	25	0	0	0	5	5	0	40	0	0	5	35	0
4.5	25	0	0	0	15	5	0	60	0	0	0	105	5
8.5	40	0	0	0	25	0	0	0	0	0	0	80	0
13.5	75	0	0	0	25	0	0	130	0	0	0	225	0
17.5	45	0	0	0	5	0	0	75	0	0	0	120	0
24.5	60	0	5	0	0	5	0	45	0	0	0	95	5
25.5	5	0	0	0	10	5	0	0	0	0	0	0	0
30.5	55	5	0	5	10	5	0	230	0	0	5	380	0
35.5	45	0	0	0	5	0	0	125	0	0	10	205	0
41.5	25	10	0	0	0	0	0	290	0	0	0	195	0
46.5	15	10	0	0	10	0	0	235	0	0	0	295	10
53.5	60	0	0	0	10	0	0	195	0	0	0	565	0
58.5	285	0	0	0	0	0	0	885	0	0	0	530	0
63.5	850	0	0	0	5	0	0	0	5	25	5	95	0
66.5	465	0	0	0	15	0	0	235	0	10	0	410	5
70.5	2325	0	10	0	20	5	10	95	0	0	0	20	0
74.5	1020	5	0	0	30	0	15	30	0	0	0	5	0

b)

Depth (cm)	*Chara* spp. oospore	*Nitella* spp. oospore	*Carex* spp. seed	*Ceratophyllum* leaf frag.	*Juncus* spp. seed	*Najas marina* leaf spine	*Najas marina* seed frag.	*Nymphaea* leaf trichoschlerid	*Schoenoplectus lacustris* seed	*Stratiotes aloides* spine	*Typha latifolia* seed
1.5	15	0	0	0	15	5	0	40	0	5	5
4.5	0	0	0	0	20	5	0	60	5	35	5
8.5	10	0	0	0	25	0	0	100	0	15	0
13.5	0	0	0	0	35	5	0	30	5	50	5
17.5	0	0	5	0	10	0	5	65	5	20	0
25.5	5	0	10	0	20	0	0	210	0	30	5
30.5	0	0	0	0	10	0	0	220	0	65	5
35.5	10	0	0	0	0	0	0	155	5	145	5
41.5	105	0	0	0	15	0	0	290	0	195	0
46.5	75	0	5	0	25	0	0	120	0	65	0
53.5	5	0	0	10	50	0	0	75	0	180	0
58.5	65	0	0	5	280	0	0	60	0	210	0
63.5	0	0	0	0	0	0	0	120	0	160	0
66.5	5	0	5	0	95	0	0	195	0	15	0
70.5	5	0	0	0	105	0	0	400	0	250	0
73.5	10	5	0	0	105	0	0	30	0	480	0