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Changes in aquatic macrophyte communities in Loch Leven – evidence of recovery from eutrophication?

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Keywords

Lake, plant, diversity, phosphorus, growing depth, charophyte, Potamogeton

This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiologia.

Abstract

This paper assesses changes in the macrophyte community of Loch Leven over a period of 100 years. Evidence is presented that shows that these changes are associated with both eutrophication, and subsequent recovery from eutrophication following reductions in anthropogenic nutrient inputs to the loch. This study uses macrophyte survey data from 1907, 1966, 1972, 1975, 1986, 1993, 1999 and 2008. In each of these surveys, except for that conducted in 1907, the loch was divided into 19 sectors, each with at least one transect, ranging from the shallowest to the deepest occurrence of macrophytes. From these data, a range of indicators of recovery were considered at a whole lake scale: the relative abundance of taxa, taxa richness and evenness and maximum growing depth. All of these metrics showed an improvement since 1972. Species richness, measured at the scale of survey sector and individual samples also appears to have increased in recent years. All of these measures, coupled with ordination of presence/absence composition data from all survey years, indicate that the macrophyte community in the loch is recovering towards the state recorded in 1907.

Introduction

Loch Leven has been a focus for ecological and water quality research since the late 1960s. During this period there have been problems with eutrophication caused by industrial, agricultural, and sewage effluent, with nutrient inputs reaching a peak in the 1980s (May et al., submitted). A decline in the abundance, diversity and maximum growing depth of macrophytes reflected the resultant deterioration in water quality (Jupp et al., 1974). Since then, external inputs of phosphorus to the loch have been reduced (May et al., submitted) and, over the past decade, there appears to have been a significant reduction in phosphorus concentration in the loch water (Carvalho et al., submitted; Ferguson et al., 2008).

Macrophytes are generally considered good indicators of water quality, particularly in relation to eutrophication pressures (Penning et al., 2008a; Penning et al., 2008b; Schaumburg et al., 2004; Søndergaard et al., 2005). They play a key physical structuring role in shallow lakes providing important habitat for invertebrates, fish and birds (Jeppesen et al., 1998; Warfe & Barmuta, 2006). The US EPA Lake and Reservoir Bioassessment and Biocriteria protocols comment: "Macrophytes respond more slowly to environmental changes than do phytoplankton or zooplankton and might be better integrators of overall environmental conditions. This would allow a single sampling event per year, during the time of maximum abundance of macrophytes." (US Environmental Protection Agency, 1998). It is, therefore, timely to examine the changes in the macrophyte community of Loch Leven, over both the eutrophication and recovery period, and to put these changes into context of the historical past (West, 1910).

Although earlier records exist for individual species, aquatic macrophytes were first surveyed systematically at Loch Leven by West in 1907 (West, 1910), as part of the bathymetric survey of Scottish Lochs (Murray & Pullar, 1910). Data from the 1907 survey form a historical baseline against which more recent data can be compared, including surveys of Jupp et al. (1974), Britton (1975), Robson (1986), Murphy and Milligan (1993), and Griffin and Milligan (1999). This paper compares these data with macrophyte data collected in 2008 to examine whether changes in macrophyte communities provide evidence for a continuing recovery of Loch Leven from eutrophication. This paper examines the following specific questions; (1) do long-term changes in the species composition of aquatic plants reflect the well documented eutrophication and subsequent recovery from eutrophication in Loch Leven, and (2) has the aquatic plant community returned to a state comparable with that observed in 1907?

Methods

Site description

Loch Leven is a shallow lake (mean depth of 3.9 m and maximum depth about 25 m), with a surface area of 13.3 km^2. It is located near the town of Kinross, in the central lowlands of Scotland, UK. The structure and physical environment of the loch are described in detail by Smith (1974). Further details about the catchment, nutrient inputs, and historical alterations can be found in May & Spears (submitted) and May et al. (submitted).

Data selection

To assess long-term, community-wide changes in the macrophyte community, datasets of taxonomic occurrence were selected on the basis of comparability and completeness. As a result, many historical records that did not form part of a comprehensive survey of the lake, including some of those described by Jupp et al. (1974), were excluded. Sources of the data used in this study are shown in Table 1. Apart from Jupp et al. (1974), most of these are unpublished reports. Palaeobotanical data were also available for Loch Leven (Salgado et al., 2010).

The survey conducted in 1907 (West, 1910) is the earliest comprehensive dataset for macrophytes at Loch Leven. Although the survey gives information on which plants were found, in contrast to the other studies, no measures of abundance were recorded and the sampling method is unknown. For this reason, these data were only suitable for use in assessing change in terms of presence/absence of species.

Sampling methods

Taxonomic occurrence data were used only from surveys for which the sampling methods were generally consistent. The main differences between surveys were the total number of samples taken (see Table 1), the length of drag when sampling, and the size and shape of sampling rake used.

All of the surveys (apart from 1907) were conducted along pre-determined transects using a boat. Since 1986, the lake has been divided into ‘sectors’ that have been sampled consistently in terms of transect and sampling locations. For all data collected since 1986, it has been possible to assign a sector to each sample, which has allowed analysis of diversity across a range of spatial scales.

Samples of the aquatic vegetation (post 1907) were obtained at intervals along these transects using a double headed rake. The rake was constructed from two garden rake heads joined back-to back with wire mesh attached to the faces of the rake heads. Although the basic design of the sampling rake remained constant in most of the surveys, some aspects of the design changed from survey to survey. For example, Jupp et al. (1974) explained that, in the 1972 survey, drag-rakes varied between transects in their weight (1240 to 1923 g), width (19 to 28.7 cm), prong length (14 to 19 cm), number of prongs per side (8 to 12), prong shape (straight to strongly curved), and screen mesh size (1 to 2.5 cm). These details are not always given in subsequent surveys.

In the earlier modern surveys (1966, 1972 and 1974), the boat was kept in constant motion and the sampling rake was allowed to drag along the bottom for between 50 and 100 m (Jupp et al., 1974). In 1986 sampling distances of between 5 and 129 m were used (Robson, 1990). In all the surveys since then, drag distances of only 2 m have been used (Griffin & Milligan, 1999; Murphy & Milligan, 1993; this study).

A bathyscope was also used to observe underwater plants in some of the surveys. The taxa seen through the bathyscope were given equal consideration to those sampled with the rake. In many of the surveys, a measure of abundance, either a weighting or some semi-quantitative measure, was given to either individual taxa or the sample as a whole. These measures of abundance have not been used as part of the analyses presented here because it was judged that these measured were not compatible between surveys. At the sample level (either bathyscope or rake), only presence/ absence data have been used for this study.

Taxa aggregation and exclusion

Occurrence records for some taxa were aggregated. This was either because they had been previously aggregated in some of the surveys used, or because it was judged that, in some surveys, these taxa may have been confused due to their similarity. These aggregates included *Potamogeton filiformis* / *P. pectinatus*, all *Chara* species, all *Tolypella* and *Nitella* species, *Potamogeton berchtoldii* / *P. pusillus*, all *Ranunculus* taxa, and *Myriophyllum alterniflorum* / *M. spicatum*.

Some taxa were excluded from the analyses because they did not seem to have been recorded in a consistent manner. This group includes all lemnids (free-floating plants), bryophytes, algae other than charophytes, the floating-leaved *Nymphaea alba*, and emergent vegetation. This left submerged vascular plants, with some aggregations, and charophytes. A total of 18 taxa were included in the analyses (Table 2).

Indicators of recovery

A number of measures were used to examine temporal and spatial changes within the macrophyte community. The simplest of these was loch-wide richness, which was calculated as the total number of taxa (as defined above) found in any single survey.

Evenness was calculated using Simpson's index ($E_{1/D}$), calculated according to Magurran (2004, pp. 115-116). This measure can take values of between 0 and 1, where an evenness of 1 implies equal numbers of individuals of all taxa in the population, and an evenness of 0 implies only one taxon. Evenness was calculated for all survey years except 1907, for which no quantitative data were available.

Species counts at smaller spatial scales were examined by comparing the means, medians, and 10^{th}, 25^{th}, 75^{th} and 90^{th} percentiles of the number of taxa found in a single sample for years when the sampling method was considered to be equivalent, i.e. when there had been equal sampling effort per sample. These were the years 1993, 1999 and 2008. Similarly, the same statistics were compared for the number of taxa found in a survey sector for years when it was considered that the likelihood of finding all taxa in a sector was equivalent, i.e. there had been equal sampling effort per sector. These were the years 1986, 1993, 1999 and 2008.

A Euclidean multi-dimensional scaling (MDS) analysis was conducted using the R software package (R Development Core Team, 2008). This indirect gradient analysis produces a two-dimensional ordination of compositional change over the survey period. Presence/absence data from all surveys were used for this analysis.

Maximum growing depth

The maximum depth to which macrophytes grow in Loch Leven is discussed in an historical context by May & Carvalho (submitted). Data from this paper were combined with the observation of deepest submerged plants from the 2008 survey, to examine the patterns of change in maximum growing depth over time.

Results

Long-term variation in macrophyte community composition

There has been considerable variation in both the taxa present and their relative abundances, as shown by the surveys presented in this paper. Of the 18 taxa studied, three *Potamogeton* species were found in 1907 and have not been recorded since (*P. gramineus*, *P. lucens*, and the hybrid of *P. gramineus* x *lucens*, also known as *P.* x *zizii*). Another *Potamogeton* species, *P. obtusifolius*, was recorded in 1907 and 1972, but has not been found since. *Potamogeton praelongus* and *Ranunculus* spp. were observed in 2008, but had not been seen since 1907. Similarly *Potamogeton berchtoldii*/*pusillus* was recorded in 1907, then seen rarely in 1975 and 1993, before returning in some abundance in 1999 and 2008. Only two of the 18 taxa were not found in 1907. These were *Potamogeton crispus*, which was observed consistently from 1966 to 1993, but not since, and *Zannichellia palustris*, which has been found in every survey since 1966, but appears to be declining in the last two surveys.

Long-term variation in indices of diversity

At the whole lake scale, the values of all of the indicators of diversity examined were greater in 2008 than in any of the previous years, apart from 1907. Taxon richness was highest in 1907 (16 taxa), and lowest in 1966 (7 taxa) (Figure 1a). Taxa richness was 11 in 1972 and 1975, then 8, 10 and 9 in 1986, 1993 and 1999 respectively, and 13 in 2008. Evenness was lowest in 1966 (0.15) and highest in 2008 (0.53), and was generally constant between 1972 (0.37) and 1999 (0.34) (Figure 1b).

At the more local scale, there appeared to be some increases in taxon richness. The taxa count per sample increased from a mean of ~1.5 in 1993 to ~2.2 in 2008 (Figure 2). Similarly, mean taxa count per survey sector increased from ~3.5 in 1993 to ~6 in 2008 (Figure 3).

In the multi-dimensional scaling analysis (Figure 4), 69% of variability in species composition was explained by the first two ordination axes with the first (E = 9.7, variability = 46%) explaining twice as much as the second (E = 4.8, variability = 23%). The first axis appears to be consistent with the diversity indicators generally representing a recovery from degradation, as suggested by the fact that the earliest modern samples are furthest away from the 1907 point, and the 2008 survey was closest to it.

Maximum growing depth

Maximum depth of colonisation, as reported by May & Carvalho (submitted), declined from 1907 (4.6 m) to the early 1970s (1.5 m), then exhibited some improvement in the late 1970s and 1980s (2.4 m in 1979), and a dramatic improvement between 1990 (1.8 m) and the present day (4.3 m in 2008). These data are shown in Figure 5.

Discussion

The aquatic plant community at Loch Leven has clearly undergone large changes since 1907. By all measures presented in this study, there has been a decline between the early 1900s, and the 1970s and 1980s, followed by a recovery which appeared to be continuing in 2008. This is consistent with similar patterns observed in water quality and other biota, as reported by Carvalho et al., submitted; Gunn et al., submitted; May et al., submitted; Spears et al., submitted). Changes in species richness over time show this pattern most simply; of the 18 taxa considered in this study, the highest number (16) were found in 1907, while eight or less were found in the 1966, 1986 and 1993 surveys. In the most recent survey, in 2008, the situation improved, with 13 taxa being recorded.

The increases in taxonomic evenness, richness per sample and richness per sector recorded over the last three comparable surveys seem to indicate that smaller-scale diversity (i.e. at the sector and sample scales) has increased, at least since the early 1990s. This supports the interpretation of increasing richness at a whole lake scale and is consistent with improving water quality conditions. In particular, improvements in the late spring/early summer light climate (Carvalho et al., submitted) are likely to open up a much wider range of ecological niches within a transect or sector, in terms of both light requirements and substrate available for growth (Sand-Jensen et al., 2008; Vestergaard & Sand-Jensen, 2000). Increasing light availability may also protect plants from the limitations imposed by both wave action and grazing by waterfowl (Jupp & Spence, 1977).

These improvements in community measures are supported by recent increases in the maximum depth colonised by macrophytes. This measure was used as a target indicator by the Loch Leven Catchment Management Plan (LLCMP, 1999), with the target set at 4.5 m, close to the value found in 1907. This target appears to be nearly realised. Growing depths of 1.5 m in the early 1970s would have restricted substrate availability to predominantly more wave-disturbed and sandier sediments (Jupp & Spence, 1977; Spears & Jones, in preparation), whereas growing depths down to 4.5 m allow additional species that are more usually associated with more stable, finer sediments. Additionally, the reductions in nutrient concentrations recorded (Carvalho et al., submitted), specifically the reduced SRP concentrations for most months of the year and enhanced nitrogen limitation in summer, may reduce epiphyte burdens on macrophyte leaves and allow slower growing, deep water macrophytes, such as *P. praelongus*, to compete alongside species such as *P. berchtoldii* / *P. pusillus* and *Chara globularis*, which can quickly develop large dense stands.

In the absence of comparable quantitative data, changes in survey methodologies can be used to infer a general increase in total aquatic plant biomass since 1966. Specifically, longer rake drags would have been used when submerged macrophytes were less abundant. In the earlier modern surveys (1966, 1972 and 1974), the boat was kept in constant motion and the sampling rake was allowed to drag along the bottom for between 50 and 100 m (Jupp et al., 1974). This strategy would have been impossible in dense vegetation. In 1986 sampling distances of between 5 m and 129 m were used (Robson, 1990). In all of the surveys since then, drag distances of only 2 m have been used (Griffin & Milligan, 1999; Murphy & Milligan, 1993; this study). In the most recent survey (2008), rake drags of longer than 5m would have been a very ineffective means of retrieving a representative sample, as the rake was often full after a 2 m drag, and additional plant material would simply fall off.

It should also be noted that taxa richness and other measures of diversity used in this study are sensitive to sampling effort (Garrard et al., 2008; Wintle et al., 2004). This is of particular concern for rare taxa. It is unfortunate that sampling effort cannot be defined precisely here, due to the lack of information about methodologies for most of the survey data. However, it is clear that if there is a bias, then it is generally in favour of the earlier modern surveys, because in these surveys both the number of samples (Table 1), and the effort per sample (length of rake drag) were generally greater. This bias can only strengthen the conclusions made above regarding improvements in measures of aquatic plant diversity.

The results presented here clearly show that Loch Leven macrophyte community is becoming more diverse (both in terms of species richness and evenness) and also becoming more similar to the species recorded in 1907. Palaeobotanical studies of aquatic plant macrofossils at Loch Leven (Salgado et al., 2010), however, show that 1907 was not an undisturbed baseline. In the 17^{th} and 18^{th} century even less competitive isoetids, such as *Isoetes lacustris* and *Lobelia dortmanna*, were abundant and by 1907 the loch was probably already altered not only by nutrients, but also by liming in the catchment (Salgado et al., 2010). Additional to the changes in land use and farming practices, there were substantial changes to the outflow and water level of the loch, which were made in the mid 1830s. These modifications lowered the water level by 1.4 m and converted 4.5 km^2 of aquatic habitat to farmland (May & Spears, submitted). This raises the question of what recovery target is appropriate.

Two of the main reasons that Loch Leven is so valued ecologically, are the internationally renowned over-wintering and breeding bird community (Quinn et al., submitted) and the brown trout fishery (May & Spears, submitted). There are indications that both of these communities, and the benthic invertebrates that form a key part of their diet, have responded to attempts to restore water quality in the loch (Gunn et al., submitted; Quinn et al., submitted; Winfield et al., submitted). These broader recovery trends may be, in part, associated with the recovery observed in the macrophyte community. Increased abundance and diversity of plants could provide greater physical habitat structure for invertebrates (vandenBerg et al., 1997; Warfe & Barmuta, 2006), more productive and variable food sources for dabbling ducks and herbivorous birds, such as coot and swan (Moreno-Ostos et al., 2008; Perrow et al., 1997) and more physical habitat for fish feeding and breeding (Warfe & Barmuta, 2006).

The comparison of multiple aquatic plant surveys has provided more evidence (additional to other papers in this special issue) that Loch Leven is currently undergoing recovery from eutrophication, at least since 1993. This is most evident when looking at species richness, at both the whole lake and smaller scales, and species evenness. The plant community has regained many, but not all, of the taxa that were present in 1907, so cannot yet be said to have returned to a state similar to that observed by West (1910). It is unlikely that the plant community will ever return to its pre-industrial state, due to changes in land use, and the regulation of the loch’s outlet, which are likely never to be reversed.

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Tables

Table 1. Sources of data, showing year of survey, total number of samples collected, and the literature source.

Year	**Samples**	**Source**
1907	unknown	West (1910)
1966	853	Jupp *et al.* (1974)
1972	744	Jupp *et al.* (1974)
1975	556	Britton (1975)
1986	190	Robson (1986)
1993	233	Murphy and Milligan (1993)
1999	233	Griffin and Milligan (1999)
2008	255	CEH internal study

Table 2. List of taxa, which were used for analyses, found in Loch Leven in surveys included in this paper, including an indication of relative abundance where the information was available (an ‘x’ indicates that no abundance information was available). Abundance data are standardised point frequency, expressed as a percentage. All numbers have been rounded up to the nearest integer for clarity.

Taxa	**1907**	**1966**	**1972**	**1975**	**1986**	**1993**	**1999**	**2008**
Chara spp.	x	97	30	37	56	56	52	22
Potamogeton berchtoldii / P. pusillus	x			1		1	8	21
Nitella / Tolypella	x	1	13	28				19
Callitriche hermaphroditica	x		3	1	3	6	10	14
Potamogeton perfoliatus	x		1	1	6	7	7	7
Potamogeton filiformis / P. pectinatus	x	1	25	28	21	5	19	7
Elodea canadensis	x	2	1	2	2	6	1	6
Zannichellia palustris		1	30	5	13	21	2	5
Eleocharis acicularis	x			2		1	2	1
Myriophyllum spp.	x	1	1					1
Potamogeton praelongus	x							1
Ranunculus spp.	x							1
Littorella uniflora	x		1	1	2	1	2	1
Potamogeton crispus		2	1	1	1	2		
Potamogeton gramineus	x							
Potamogeton lucens	x							

Potamogeton obtusifolius	x	1
Potamogeton x *zizii*	x	

Figures

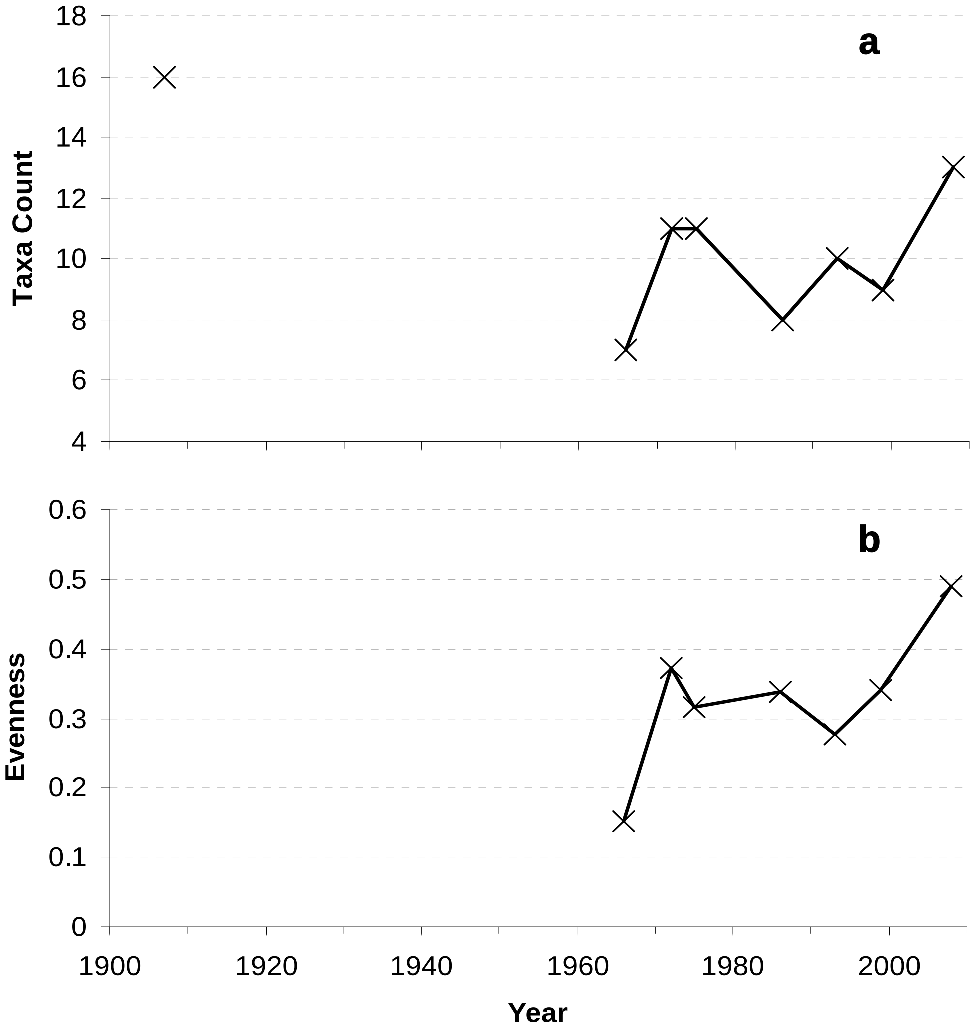

Figure 1. Counts of taxa (a) and evenness of taxa distribution (b) from all Loch Leven macrophyte surveys presented in this paper. The taxa are as described in the methods section.

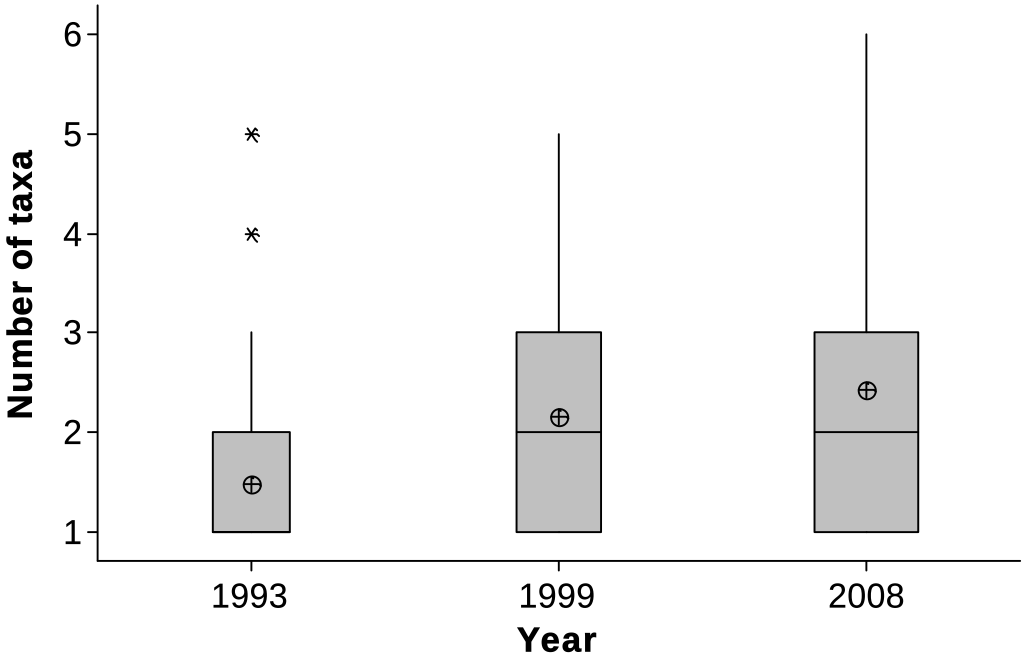

Figure 2. Number of taxa found in each sample 1993, 1999 and 2008 expressed as boxplots including 25th percentile, median, 75th percentile and 90th percentile. Note that for 1993, the median was 1. Outliers (stars) and the mean are also shown (crossed circle).

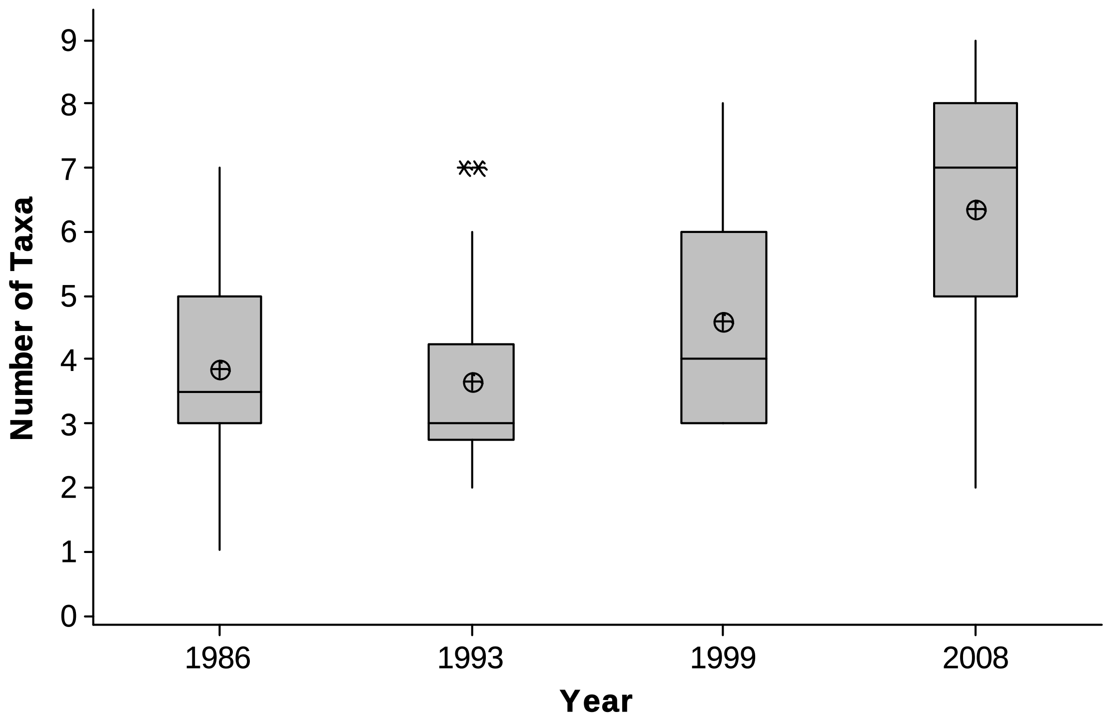

Figure 3. Number of taxa found in each survey sector of macrophyte surveys of Loch Leven in 1986, 1993, 1999 and 2008 expressed as box plots, including 10th and 25th percentiles, median, and 75th and 90th percentiles. Outliers (stars) and the mean are also shown (crossed circle).

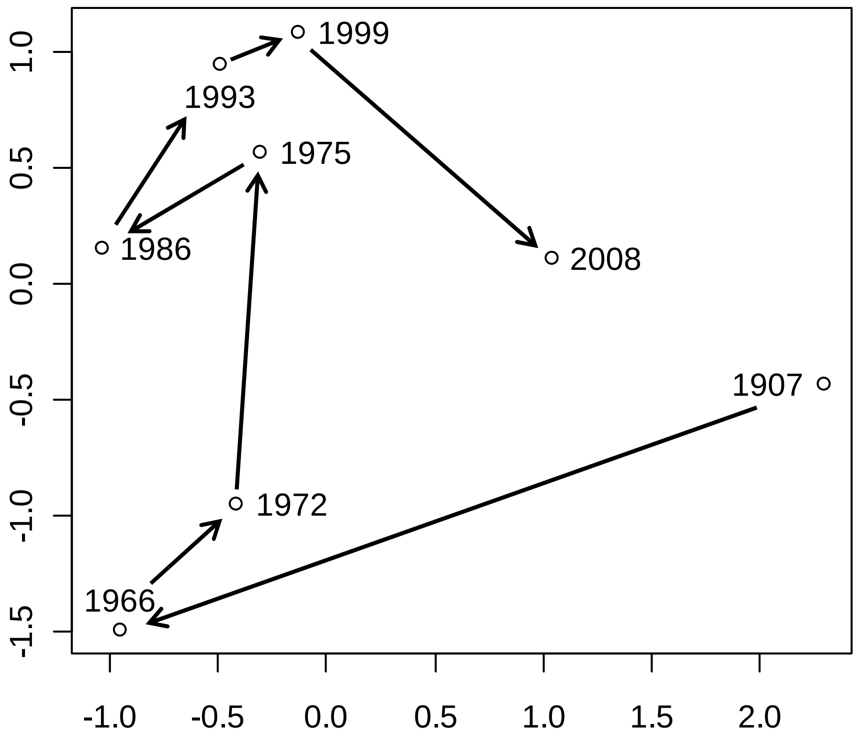

Figure 4. MDS plot of species occurrence presence/absence data from all surveys. Methods are as explained in the text. Arrows have been added to illustrate apparent progression in aquatic plant community composition between surveys.

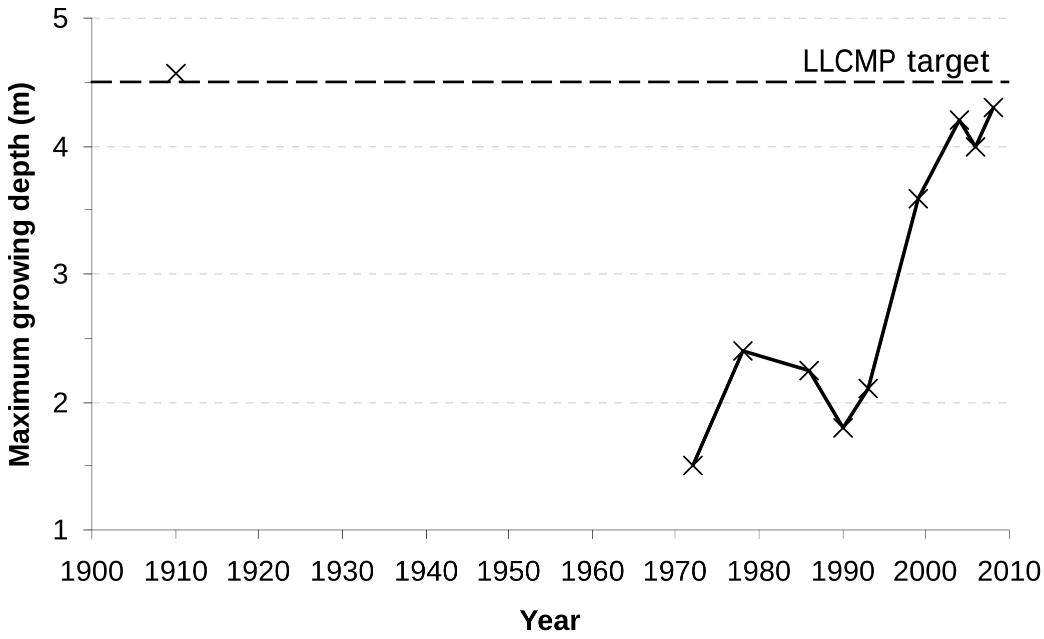

Figure 5. Maximum depth colonised by aquatic plants for all years in which the data are available. The dashed line represents the target set by the Loch Leven Catchment Management Plan (LLCMP, 1999).