

## Article (refereed)

---

**May, Linda; Carvalho, Laurence.** 2010. Maximum growing depth of macrophytes in Loch Leven, Scotland, United Kingdom, in relation to historical changes in estimated phosphorus loading. *Hydrobiologia*, 646 (1). 123-131. [10.1007/s10750-010-0176-0](https://doi.org/10.1007/s10750-010-0176-0)

© Springer Science+Business Media B.V. 2010

This version available <http://nora.nerc.ac.uk/8655/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the authors and/or other rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

**This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.**

[www.springerlink.com](http://www.springerlink.com)

Contact CEH NORA team at  
[noraceh@ceh.ac.uk](mailto:noraceh@ceh.ac.uk)

**Title**

Maximum growing depth of macrophytes in Loch Leven, Scotland, in relation to historical changes in estimated phosphorus loading

**Authors**

Linda May and Laurence Carvalho

Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB,  
Scotland, UK

Telephone: +44 (0) 131 445 8537, Fax: +44 (0)131 445 3943

Corresponding author: [lmay@ceh.ac.uk](mailto:lmay@ceh.ac.uk)

**Keywords:**

Phosphorus, lake, macrophytes, external loading, maximum growing depth, eutrophication, restoration, water quality indicator

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**

Eutrophication is a common problem of shallow lakes situated in lowland areas. In their natural state, most shallow lakes would have clear water and a thriving aquatic plant community. However, eutrophication often causes turbid water, high algal productivity, and low species diversity and abundance of submerged macrophytes. In severe cases, these impacts can have serious economic consequences on local communities. A key indicator of the ecological health of lake ecosystems is the maximum growing depth (MGD) of aquatic plants. However, few existing studies have yet quantified the relationship between changes in external phosphorus (P) input to a lake and associated variation in MGD. This study examines the relationship between these parameters in Loch Leven, a shallow, eutrophic loch in Scotland, UK. A baseline MGD value from 1905 and a series of more recent MGD values collected between 1972 and 2006 are compared to estimated phosphorus loads to the lake over a period of eutrophication and recovery. The main factors that affect MGD within the loch are explored and the effectiveness of this parameter as an indicator of eutrophication and recovery in shallow lakes is considered. The results suggest a close relationship between changes in MGD of macrophytes and changes in the external P load to the loch over the study period. Variation in MGD macrophytes also seemed to reflect the “light history” that submerged macrophytes had been exposed to over the 5 year period prior to sampling, rather than responding to short term, within year, variations in water clarity. This suggests that changes in macrophyte MGD may be a good indicator of overall, long term, changes in water quality that occur during the eutrophication and restoration of shallow lakes.

## **Introduction**

Eutrophication is a common problem in shallow lakes situated in lowland areas. This is because lowland catchments are often the focus of intensive agricultural activities, industrial development and population growth. These activities tend to generate nutrient laden runoff and discharges of effluent that enter the drainage system and, ultimately, the lake.

In their natural state, most shallow lakes would have clear water and a thriving aquatic plant community (Scheffer, 1998). However, as a result of eutrophication, many such lakes now suffer from turbid water, high algal productivity, and low species diversity and abundance of submerged macrophytes (Scheffer, 1998). In severe cases, the amenity value of these lakes is significantly reduced due to the appearance of nuisance, and sometimes toxic, algal blooms during the summer months. These can have serious economic impacts on local communities and cause an increase in water treatment costs for supply companies and downstream users (LLCMP, 1999; Drikas et al., 2001).

The need to improve water quality in these lakes is now widely recognised and, in many cases, a range of remediation measures are now being considered. Most of these are based on the assumption that reducing the external nutrient input to the lake will restore its water quality to pre-enrichment conditions (Sand-Jensen et al., 2008). However, water quality improvements in response to such management actions can be difficult to predict in shallow, lowland lakes (Moss et al., 2005), especially when the

reduction in external load is followed by an increase in nutrient release from the sediments that may last for many years (Sas, 1989).

A key indicator of the ecological health of lake ecosystems is the maximum growing depth (MGD) of aquatic plants. This is considered to be a good indicator not only of water quality (particularly water clarity), but also of the physical habitat complexity of a site and its potential for supporting a rich associated biodiversity (Jeppesen et al, 1998). However, with the exception of Sand-Jensen et al. (2008), no existing studies have yet quantified the relationship between changes in external phosphorus (P) input to a lake and any associated variation in the MGD of macrophytes. This main aim of this paper is to determine the relationship between MGD of macrophytes and estimated annual P load to Loch Leven, a shallow, eutrophic loch in Scotland, UK, over a period of eutrophication and recovery. In addition, the main factors that affect macrophyte MGD within the loch are explored and the effectiveness of this parameter as an indicator of eutrophication and recovery in shallow lakes is considered.

### **Site description**

Loch Leven is a shallow, eutrophic loch in lowland Scotland, UK (Figure 1), which has a surface area of 13.3 km<sup>2</sup>, and mean and maximum depths of 3.9 m and 25.5 m, respectively. The loch has been a key focus of long term water quality monitoring activities for almost 40 years, with more than 150 biological, chemical and physical variables being recorded here at approximately fortnightly intervals over this period (May & Spears, submitted). These data have been supplemented by water quality data

for the period 1905 to 1968 that were obtained from the literature (Table 1; May et al., submitted).

Records of the aquatic plants within the loch date back more than 100 years. Changes in the species composition over this period are described by Dudley et al. (submitted). These authors describe the current community as comprising *Chara* spp., *Potamogeton berchtoldii* / *pusillus*, *Nitella* / *Tolypella*, *Callitriche hermaphroditica*, *Potamogeton perfoliatus*, *Potamogeton filiformis* / *pectinatus*, *Elodea canadensis*, *Zannichellia palustris*, *Eleocharis acicularis*, *Myriophyllum* spp., *Potamogeton praelongus*, *Ranunculus* spp. and *Littorella uniflora*.

The hydrology of the loch is not regulated naturally. Water level is controlled by a series of sluice gates that were installed in the mid-1800s and, since then, have been manually adjusted on a daily basis to control the rate of discharge at the outflow (Sargent & Ledger, 1992). As a result, although water levels can vary widely over the winter period, the pattern of change from May to September (i.e. during the macrophyte growing period) is very similar each year (Figure 2). This results in an initial water level of about 107.2 m.a.s.l. at the end of April, which then declines in a more or less linear way over the summer period and culminates in a minimum water level of about 106.7 m.a.s.l. towards the end of September.

The catchment of the loch covers an area of 145 km<sup>2</sup> and comprises mainly agricultural land (~80%), with some areas of rough grazing and woodland in the uplands (Castle et al., 1999) that are situated at some distance from the loch. Sources of pollution from domestic waste water in the area comprise a small town and a few

scattered farms and villages (Frost, 1996). Until recently, the number of people living here had changed very little, with the resident population increasing from 7,500 in 1930 to 7,800 people in the 1990s. Although there is little industry in the area, a woollen mill situated on the side of the loch was responsible for discharging large quantities of P-laden effluent into the loch *via* one of the inflow streams from the mid 1950s to the late 1980s (Holden & Caines, 1974; Caines & Harriman, 1976; Bailey-Watts & Kirika, 1987; Bailey-Watts & Kirika, 1999; May et al., submitted).

## **Methods**

The absolute maximum growing depth (MGD) of submerged, rooted, vascular plants (macrophytes) in the loch were obtained from the literature, which records surveys carried out from 1905 to 2006 (West, 1910; Jupp et al., 1974; Bailey-Watts, 1979; Robson, 1986, 1990; Murphy & Milligan, 1993; Griffin & Milligan, 1999; Spears et al., 2009), and from personal observations made by one of the authors (Table 2). The absolute MGD was the deepest point at which macrophytes were recorded in the loch. All of the surveys were conducted along transects using a boat. In all surveys, except West (1910), samples of vegetation were obtained at intervals along transects using a 'drag rake' attached to a piece of rope. The drag rake consisted of two opposing garden rake heads fastened together back-to-back and covered by a coarse wire mesh, as described by Jupp et al. (1974). Generally, over 200 samples were taken from more than 30 transects providing an accurate estimate of the MGD (Spears et al., 2009). The MGD from 2004 and 2006 was the deepest point measured from only three transects, although these transects were explicitly chosen from previous surveys as being those where macrophytes consistently grow deepest in the loch. The

sampling method, number of transects and sample points from the West (1910) survey are unknown. The results do, however, indicate that the West survey was very comprehensive, being carried out alongside a bathymetric survey that comprised 538 depth soundings (Murray & Pullar, 1910). All of the surveys were undertaken at similar times of year (usually August/September).

Phosphorus loads to the loch were not available for the early 1900s, so the value for 1905 was derived from an in-lake P concentration of  $65 \mu\text{g l}^{-1}$  (Bennion, pers. comm.), which had been inferred from palaeolimnological data using a diatom-TP transfer coefficient (Bennion et al., 2004). The corresponding P load was back calculated from this value using the measured loch flushing rate for 1905 (Sargent & Ledger, 1992) and the lake response model of Dillon & Rigler (1974).

Phosphorus loads to the loch had been measured in 1972, 1975, 1976, 1985, 1995 and 2005 (May et al., submitted), but most of these years (apart from 1972 and 1975) did not align exactly with macrophyte survey dates between 1972 and 2006. So, P loads for several of these MGD years had to be interpolated from years in which the P load had been measured. The exact methods of calculation for each interpolated value are shown in Table 1. In outline, the P load was estimated from the nearest measured value after adjustment for any documented change in point source discharges of P that had occurred in the intervening period, e.g. upgrades to waste water treatment works or changes to industrial processes (LLCMP, 1999). Phosphorus in runoff from diffuse sources was assumed to be similar in both years because there was little inter-annual variation in rainfall between 'measured' and 'estimated' years (Table 2). Even if there had been more variation in rainfall between years, it is unlikely that this would have



caused large variations in overall P load to the loch, because external P load from this catchment has, until very recently, always been heavily dominated by point source discharges (60-80% of the P load until the mid 1990s).

Weekly/fortnightly data on water transparency, in-lake P concentrations and water level were obtained from long-term monitoring records for the loch held by the Natural Environment Research Council, UK. These records span the period 1968 to 2006 (May & Spears, submitted).

## **Results**

Variation in the maximum growing depth (MGD) of macrophytes recorded in 1905 and from 1972 to 2006 is shown in Figure 3. Although initially high (4.9 m in 1905), MGD had fallen to 1.5 m by the late 1960s. This value then increased slightly to 2.5 m - 3.0 m in the late 1970s, and fell again to about 2 m in the early 1990s. By the late 1990s, macrophytes had begun to colonise deeper areas again, with MGD progressively increasing from 3.6 m to 4.5 m between 1999 and 2006.

Corresponding variation in external P loads to the loch between 1905 and 2006 is summarised in Figure 4. The data show that P input was relatively low (i.e. about  $5 \text{ t y}^{-1}$  or  $0.38 \text{ g P m}^{-2} \text{ y}^{-1}$ ) in the early 1900s, but had risen to  $20 \text{ t y}^{-1}$  ( $1.54 \text{ g P m}^{-2} \text{ y}^{-1}$ ) by 1985. From the mid 1980s onwards, the external P load fell progressively to about 40 per cent of the level recorded in 1985 as a result of management activities within the catchment (May et al., submitted).

When these two sets of data are combined (Figure 5), there appears to be a strong inverse relationship between macrophyte MGD and external P load to the loch over the entire study period. In 1905, when the P load was only about  $5 \text{ t y}^{-1}$ , the MGD was about 4.9 m. As the P load increased and decreased between the mid 1960s and mid 1990s, MGD varied accordingly, reaching a value of less than 2 m when P loads were highest. From the mid 1990s onwards, the MGD progressively increased, reaching around 4.5 m by 2006. These changes appear to track the progress of the 60 percent reduction in external P load to the loch that was achieved between 1985 and 2005 (Figure 4).

A close relationship was found between MGD and the average of the annual mean Secchi disk transparency readings collected over the previous 5 year period (Figure 6), although there was little evidence that MGD responded to shorter term variation in this parameter. This suggests that MGD provides an integrated response to long term changes in water clarity rather than a more immediate response to short term variation in this parameter.

## **Discussion**

There are comparatively few studies of the response of lakes to reduced nutrient loads and most of those that do exist have largely focused on changes in phytoplankton species and abundance (Anderson et al, 2005; Jeppesen et al., 2005). In some cases, these changes have been found to have knock-on effects on macrophyte communities, altering their species composition and abundance (Nichols & Lathrop, 1994; Egertson et al., 2004; Valley & Drake, 2007) and having an impact on their maximum growing

depth (Søndergaard et al., 2005). It is widely believed that this is because submerged macrophytes fail to thrive when phytoplankton densities are high (Jones et al., 2002; Scheffer 1998). It is well established that phytoplankton densities tend to be high when in-lake phosphorus (P) concentrations are high, and that these P concentrations are often linked to the magnitude of the external P load (OECD, 1982; Jeppesen et al., 2005).

This study has clearly shown that the maximum growing depth (MGD) of macrophytes in Loch Leven varied markedly between 1972 and 2006, apparently reflecting changes in the estimated P loading to the loch from external sources over that period. The most recent MGD values (4.2 m in 2004 and 4.5 m in 2006) are very similar to the baseline value of 4.9 m that was recorded in 1905, i.e. before serious eutrophication problems began. As increasing MGD is one of the key targets for lake restoration at this site (LLCMP, 1999), it is important to identify the main factors that have contributed to this response.

One possible explanation is that the observed changes in MGD were actually only apparent effects caused by variation in water level or of variation in the management of the outflow, rather than changes in P load. This is an important consideration for two reasons. Firstly, MGD is measured relative to a baseline that is defined by the water level in the loch at the time of each survey and secondly because significant inter- and intra-annual variations in water level over the growing season could also affect the depth of macrophyte colonisation. However, examination of the loch level records for the years in which macrophyte surveys were undertaken showed that, although loch level varied by more than 1 m over the year as a whole, temporal

changes in water level over the macrophyte growing season (April to September) were remarkably similar each year and variability during the macrophyte survey period (usually August to September) was very small ( $\pm 0.2$  m) compared with the large change in MGD over the study period (3.5 m). The reason for this consistent water level is because summer water levels are controlled by the manual operation of sluice gates on the outflow. It can, therefore, be concluded that the variations in macrophyte MGD recorded were real and unlikely to be caused by variation in water level.

Another possibility is that, in some way, changes in the external P load to the loch had indirectly affected the depth distribution of the macrophytes over time, possibly through their impact on in-lake P concentrations and water clarity values, following the classic series of events described by many authors including Scheffer (1998) and Jeppesen et al. (2005). However, the data do not completely support this hypothesis in Loch Leven. Recent trends in annual mean P concentrations within the loch over the period 1969 – 2008 (Carvalho et al., submitted) seem to suggest that there is little direct relationship between this parameter and the variation in macrophyte MGD that has been reported here. In fact, according to these authors, the biggest fall in P concentrations in Loch Leven occurred in the early 1970s, before any improvements were seen in the aquatic macrophytes, and P concentrations were increasing in the mid-1990s, when MGD recovery was most pronounced. This suggests that the link between P load and macrophyte MGD is not mediated simply through changes in in-lake P concentration. As has been shown in other studies of recovery from nutrient enrichment, other factors, such as biological resilience, may influence the response of MGD to nutrients (Scheffer, 1998; Jeppesen et al., 2005).

Spence (1982) suggests other factors that may also be important in determining the MGD of macrophytes in lakes, including sediment conditions, topography, gradient, wind/wave action, water temperature and under water light climate. Other authors suggest that differences in sampling methods can also affect the determination of this parameter (Canfield et al., 1985; Spears et al., 2009). However, it is generally believed that wind/wave action and light availability are probably the most important of these (Spence, 1982; Vant et al., 1986; Riis & Hawes, 2003). The possible impact of these factors on the MGD of macrophytes at Loch Leven is explored below.

Since macrophyte MGD in Loch Leven changed markedly over the last 100 years, it seems unlikely that any of these changes were caused by environmental factors that have remained stable over that period. So, it was concluded that unsuitable sediments, topography, gradient and variation in sampling methods were unlikely to be important drivers of the observed changes. Also, it seems unlikely that long term variation in wind/wave action is the main cause of this variation, because this study has shown a very strong link between MGD and external P load that would be difficult to explain in terms of this parameter. Although temperature gradients have been identified as limiting the depth distribution of macrophytes in deep, clear water lakes (Dale, 1986), this effect is unlikely to occur in a shallow, well mixed lake, such as Loch Leven, which shows very little temperature variation over depth within the top 5 m of the water column (May, 1980). Indeed, Pearsall (1920) and Spence (1964, 1982) found no evidence of temperature limitation of macrophyte MGD occurring in any lakes within the British Isles.

It is generally believed that one of the most important factors restricting macrophytes to the shallow areas of Loch Leven is decreased water clarity caused by increased phytoplankton densities during cultural eutrophication (Jupp & Spence, 1977). However, to date, there has been little hard evidence of this. Initially, when this was investigated on a year-on-year basis, the long term monitoring data seemed to suggest that there was no direct relationship between MGD and water clarity at this site. This unexpected result appeared to contrast markedly with the findings from other studies such as Chambers & Kalff (1984), Skubinna et al. (1995), Middleboe & Markager (1997), Jeppesen et al (2005) and Sand-Jensen et al. (2008). However, further investigation revealed a very close relationship between macrophyte MGD and the overall average of the annual mean water transparency values recorded at this site over the 5 year period preceding the date of sampling. This supports the assertion put forward by Canfield et al. (1985), Rørslett & Johansen (1995) and Schwarz & Hawes (1997) that submerged aquatic plants tend to integrate water clarity conditions over time in relation to their depth penetration, and that “light history” is more likely to determine MGD than water clarity at or around the time of sampling

The impact of water clarity on the depth distribution of macrophytes may also be exacerbated by the extent of epiphyte growth on the surface of the plants, as this also limits the amount of light available to the macrophytes for growth. Sand-Jensen (1990) outlines the importance of this shading effect by providing evidence that, in some cases, epiphytes are more important than phytoplankton for attenuating light before it reaches submerged macrophytes. As there are no records of epiphyte growth associated with the long term data on macrophyte distribution at Loch Leven, the importance of this effect at this site could not be tested. However, because epiphyte

growth is often positively related to nutrient availability, this could certainly be a contributory factor in the development of the strong relationship between MGD and external P load that has been observed at this site.

## **Conclusions**

There is documentary evidence that increasing annual loads of P from the catchment, especially between the 1960s and the mid 1980s, were responsible for increasing eutrophication problems at Loch Leven in the 1970s and 1980s (LLCMP, 1999). Restoration measures were put in place that resulted in a 60 per cent reduction in P load to the loch by the mid 1990s (Bailey-Watts & Kirika, 1999). Changes in MGD at this site seem to reflect these changes in external P load. Variation in MGD also appears to reflect the “light history” that submerged macrophytes have been exposed to over the 5 year period prior to sampling, although not to short term, within year, variations in water clarity. This suggests that changes in macrophyte MGD may be a good indicator of the overall, long term changes in water quality that occur during the eutrophication and restoration of shallow lakes.

## **Acknowledgements**

We are grateful to the Loch Leven Trustees for daily outflow records and to Helen Bennion, University College London, for an estimate of the P concentration in Loch Leven in 1905 based on palaeolimnological records. We are particularly indebted to the Montgomery family, the owners of the loch, for their continuing support for, and interest in, our research. This research was funded by Scottish Natural Heritage, the

Scottish Environment Protection Agency and the Natural Environment Research Council, UK.

## **References**

Anderson, N.J., Jeppesen, E. & Søndergaard, M., 2005. Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. *Freshwater Biology* 50: 1589 – 1593.

Bailey-Watts, A.E., 1979. The monitoring of Loch Leven macrophytes. Final report to the Nature Conservancy Council. Contract no. F3/03/73, 15 pp., 4 Tables, 8 Figures.

Bailey-Watts, A.E. & Kirika, A., 1987. A re-assessment of the phosphorus inputs to Loch Leven (Kinross, Scotland): rationale and an overview of results on instantaneous loadings with special reference to runoff. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 78: 351 - 367.

Bailey-Watts, A.E. & Kirika, A., 1999. Poor water quality in Loch Leven (Scotland) in 1995, in spite of reduced phosphorus loadings since 1985: the influences of catchment management and inter-annual weather variation. *Hydrobiologia* 403: 135-151.

Bennion, H., Fluin, J. & Simpson, G.L., 2004. Assessing eutrophication and reference conditions for Scottish freshwater lochs using subfossil diatoms. *Journal of Applied Ecology* 41: 124-138.



Britton, R.H., 1975. Survey of aquatic macrophytes in Loch Leven, August 1975. In: Loch Leven Research Group Annual Report, 1975: 18-26.

Caines, L.A. & Harriman, R., 1976. Chemical investigations. In: Loch Leven Research Group Annual Report, 1976: 1-2.

Canfield, D.E. Jr., Langeland, K.A., Linda, S.B. & Haller, W.T., 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *Journal of Aquatic Plant Management* 23: 25-28.

Castle, K., Frost, C.A. & Flint, D., 1999. The Loch Leven Project – Buffer strips in practice on a catchment scale. *Aspects of Applied Biology* 54: 71 – 78.

Chambers, P.A. & Kalff, J., 1984. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. *Canadian Journal of Fisheries and Aquatic Science* 42: 701-709.

Dale, H.M., 1986. Temperature and light: the determining factors in maximum depth distribution of aquatic macrophytes in Ontario, Canada. *Hydrobiologia* 133: 73-77.

Drikas, M., Chow, C.W.K., House, J. & Burch, M.D. 2001. Using coagulation, flocculation, and settling to remove toxic cyanobacteria. *Journal of the American Water Works Association* 93: 100-111.

Dudley, B., Gunn, I.D.M., Carvalho, L., Proctor, I., O'Hare, M.T., Murphy, K.J. & Milligan, A., 2010. Changes in aquatic macrophyte communities in Loch Leven – evidence of recovery from eutrophication? *Hydrobiologia*, submitted.

Egertson, C.J., Kopaska, J.A. & Downing, J.A., 2004. A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia* 524: 145-156

Frost, A., 1996. Loch Leven and diffuse pollution. In: Petchey, A., D'Arcy, B. & Frost, A. (eds.) *Diffuse Pollution and Agriculture*. Proceedings of a conference held in Edinburgh, 12 – 14 April 1995: 174-182.

Griffin, L.R. & Milligan, A.L., 1999. Submerged macrophytes of Loch Leven, Kinross. Report to Scottish Natural Heritage. Contract no. BAT/LH07/99/00/75, 40 pp, 2 appendices.

Holden, A. V. & Caines, L. A., 1974. Nutrient Chemistry of Loch-Leven, Kinross. *Proceedings of the Royal Society of Edinburgh Section (B)* 74: 101-121.

Holden, A. V., Caines, L. A. & Harriman, R., 1975. Chemical investigations. In: *Loch Leven Annual Report, 1975*, 34 pp.

Jeppesen, E., Søndergaard, M., Søndergaard, M. & Christoffersen, K. (Eds) 1998. *The structuring role of submerged macrophytes in lakes*. Springer Verlag, New York.

Jeppesen, E., Sondergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, R., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Kohler, J., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Noges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Schelske, C.L., Straile, D., Tatrai, I., Willen, E. & Winder, M., 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology* 50: 1747-1771.

Jones, J.I., Young, J.O., Eaton, J.W. & Moss, B., 2002. The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interactions between submerged plants and periphyton. *Journal of Ecology* 90: 12-24.

Jupp, B.P., Spence, D.H.N. & Britton, R.H., 1974. The distribution and production of submerged macrophytes in Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh (B)* 74: 195 – 208.

Jupp, B.P. & Spence, D.H.N., 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. *Journal of Ecology* 65: 175 – 186.

LLCMP, 1999. Loch Leven Catchment Management Plan: The Report of the Loch Leven Area Management Advisory Group, 93 pp.

May, L., 1980. Ecology of planktonic rotifers at Loch Leven, Kinross-shire. Ph.D Thesis, Paisley College of Technology, 180 pp.

May, L., Defew, L. & Bennion, H., submitted. Historical changes in external phosphorus loads to Loch Leven, 1905 to 2005. *Hydrobiologia*.

May, L. & Spears, B.W., submitted. A history of scientific research at Loch Leven. *Hydrobiologia*.

Middleboe, A.L. & Markager, S., 1997. Depth limits and minimum light requirements for freshwater macrophytes. *Freshwater Biology* 37: 553-568.

Moss, B., Barker, T., Stephen, D., Williams, A.E., Balayla, D.J., Beklioglu, M. & Carvalho, L., 2005. Consequences of reduced nutrient loading on a lake system in a lowland catchment: deviations from the norm? *Freshwater Biology* 50: 1687 – 1705.

Murphy, K.J. & Milligan, A., 1993. Submerged macrophytes of Loch Leven, Kinross, August 1993. Report to Scottish Natural Heritage. Contract no. 937/F2A/5.3/224, 27 pp, 4 Figures, 8 Maps, 2 Appendices.

Nichols, S.A. & Lathrop, R.C., 1994. Cultural impacts on macrophytes in the Yahara lakes since the late 1800s. *Aquatic Botany* 47: 225-247.

OECD, 1982. Eutrophication of waters: monitoring, assessment and control. OECD, Paris, 154 pp.

Pearsall, W.H., 1920. The aquatic vegetation of English lakes. *Journal of Ecology* 8: 163-201.

Riis, T. & Hawes, I., 2003. Effect of wave exposure on vegetation abundance, richness and depth distribution of shallow water plants in a New Zealand lake. *Freshwater Biology* 48: 75-87.

Robson, T.O., 1986. Loch Leven Kinross Macrophyte Survey, August 1986. Final Report to the Nature Conservancy Council. Contract no. HF3-03-208(46), 43 pp.

Robson, T.O., 1990. Macrophyte survey August 1990. Report to Nature Conservancy Council. Contract no. 21.F2B.219.DA01, 40 pp.

Rørslett, B. & Johansen, S.W., 1995. Dynamic response of submerged macrophyte, *Isoetes lacustris*, to alternating light levels under field conditions. *Aquatic Botany* 56: 223 -224.

Sand-Jensen, K., 1990. Epiphyte shading – its role in resulting depth distribution of submerged aquatic macrophytes. *Folia Geobotanica and Phytotaxonomica* 25: 315-320.

Sand-Jensen, K., Pedersen, N. L., Thorsgaard, I., Moeslund, B., Borum, J. & Brodersen, K.P., 2008. 100 years of vegetation decline and recovery in Lake Fure, Denmark. *Journal of Ecology* 96: 260-271.

Sargent, R. J. & Ledger, D. C., 1992. Derivation of a 130 year run-off record from sluice records for the Loch Leven catchment, south-east Scotland. *Proceedings of the Institution of Civil Engineers Water, Maritime and Energy* 96: 71-80.

Sas, H. (ed.), 1989. *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*. Acad. Verlag. Richarz GmbH Berlin, Germany, 497 pp.

Scheffer, M., 1998. *Ecology of Shallow Lakes*. Kluwer Academic Publishers, Dordrecht.

Schwarz, A. & Hawes, I., 1997. Effects of changing water clarity on characean biomass and species composition in a large oligotrophic lake. *Aquatic Botany* 56: 169-181.

Skubbina, J.P., Coon, T.G. & Batterson, T.R., 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw bay, Lake Huron. *Journal of Great Lakes Research* 21: 476 – 488.

Søndergaard, M., Jeppesen E., Jensen, J.P. & Lildalamsinck, S., 2005. Water Framework Directive: ecological classification of Danish lakes. *Journal of Applied Ecology* 42: 616.

Spears, B.M., Gunn, I.D.M, Carvalho, L., Winfield, I.J., Dudley, B., Murphy, K. & May, L., 2009. An evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven, Scotland. *Aquatic Botany* 91: 75-81.

Spence, D.H.N., 1964. The macrophyte vegetation of freshwater lochs, swamps and associated fens. In Burnett, J.H. (ed.) *The Vegetation of Scotland*. Oliver & Boyd, Edinburgh: 306–425.

Spence D.H.N., 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* 12: 37-124.

Valley, R.D. & Drake, M.T., 2007. What does resilience of a clear-water state in lakes mean for the spatial heterogeneity of submersed macrophyte biovolume? *Aquatic Botany* 87: 307–319.

Vant, W. N., Davies-Colley, R. J., Clayton, J.S. & Coffrey, B.T., 1986. Macrophyte depth limits in north island New Zealand lakes of differing clarity. *Hydrobiologia* 137: 55-56.

West, G., 1910. An epitome of a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habitat in several lake areas in Scotland. In Murray, J. & Pullar, L. (eds.) *Bathymetrical Survey of the Freshwater Lochs, Volume I*. Challenger Office, Edinburgh: 156–260.

## Tables

Table 1. Methods used to estimate external total phosphorus (P) loads to Loch Leven between 1905 and 2006 for years that correspond to macrophyte growing depth measurements.

<b>Year</b>	<b>Method of estimation</b>	<b>References</b>
<b>1905</b>	Estimated from in-lake P concentration of $65 \mu\text{g l}^{-1}$ (Bennion, <i>pers. comm.</i> ) and measured loch flushing rate using the equation of Dillon & Rigler (1974)	Sargent & Ledger (1992); Bennion et al. (2004)
<b>1972</b>	Measured data	Holden & Caines (1974)
<b>1975</b>	Measured data	Caines & Harriman (1976)
<b>1978</b>	Estimated as the measured P load for 1976	Caines & Harriman (1976)
<b>1986</b>	Estimated as the measured P load for 1985	Bailey-Watts et al. (1987)
<b>1990</b>	Calculated as the measured P load for 1985 minus the known reduction in annual P load from an industrial source (i.e. 6.29 t)	Bailey-Watts et al. (1987); LLCMP (1999)
<b>1993</b>	Calculated as the 1990 value minus the 1.7 t reduction in P load achieved by upgrading a waste water treatment works	LLCMP (1999)
<b>1999</b>	As for 1993, as all point source upgrades had been completed by this date	LLCMP (1999)
<b>2004</b>	Midway between 1999 and 2005 value	
<b>2006</b>	Estimated as the measured 2005 value as no known changes in external P sources had occurred since then	May et al. (submitted)



Table 2. Variation in annual rainfall between the years for which phosphorus (P) load to Loch Leven was estimated and the years on which these estimated values were based.

<b>'Estimated' year</b>	<b>Rainfall (mm)</b>	<b>'Measured' year</b>	<b>Rainfall (mm)</b>	<b>Variation</b>
1978	996	1976	970	+ 2.7%
1986	1136	1985	1154	+ 1.5%
1990	1254	1985	1154	+ 8.7%
1993	1219	1985	1154	- 5.6%
1999	1122	1985	1154	- 2.8%
2004	986	1995 & 2005	941 (average)	+ 4.8%
2006	1066	2005	1004	+ 6.2%

Table 3. Maximum growing depth (MGD) of submerged macrophytes in Loch Leven in 1905, and 1972 – 2006, showing survey method used.

<b>Year</b>	<b>Macrophyte MGD (m)</b>	<b>Survey method</b>	<b>Reference</b>
<b>1905</b>	4.9	Unknown	West, 1910
<b>1972</b>	1.5	Drag rake	Jupp et al., 1974
<b>1975</b>	3.0	Drag rake	Britton, 1975
<b>1978</b>	2.6	Drag rake	Bailey-Watts, 1979
<b>1986</b>	1.8	Drag rake	Robson, 1986
<b>1990</b>	1.8	Drag rake	Robson, 1990
<b>1993</b>	2.0	Drag rake & grapnel	Murphy & Milligan, 1993
<b>1999</b>	4.0	Drag rake & grapnel	Griffin & Milligan, 1999
<b>2004</b>	2.9	Drag rake	Carvalho, <i>pers comm.</i>
<b>2006</b>	4.5	Drag rake	Spears et al, 2009

## **Figure legends**

Figure 1. Map of Great Britain showing the location of Loch Leven (inset) within Scotland.

Figure 2. Variation in water level at Loch Leven for the years in which maximum growing depth (MGD) of macrophytes was determined, where available.

Figure 3. Changes in maximum growing depth (MGD) of submerged macrophytes in Loch Leven between 1972 and 2006 in comparison with historical data collected in 1905.

Figure 4. Measured (grey triangles) and estimated (black diamonds) annual external total phosphorus (TP) loads to Loch Leven.

Figure 5. Relationship between maximum growing depth (MGD) of macrophytes and annual external total phosphorus (TP) load to Loch Leven for various years between 1905 and 2006.

Figure 6. Relationship between maximum growing depth (MGD) of macrophytes in Loch Leven and water clarity expressed as the average of the 5-year antecedent values of annual mean Secchi disk reading (SDR).

Figure 1

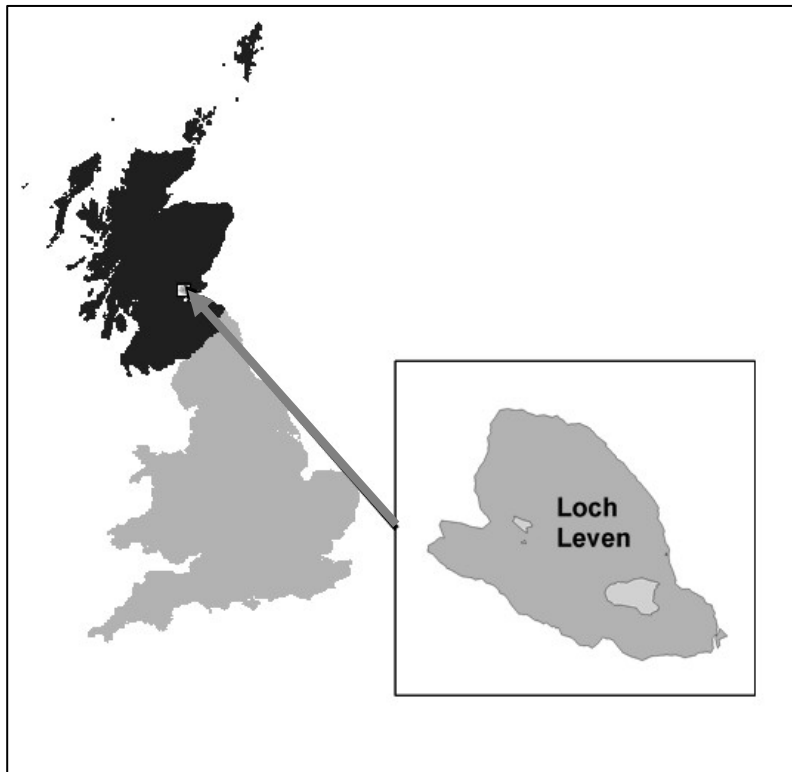


Figure 2

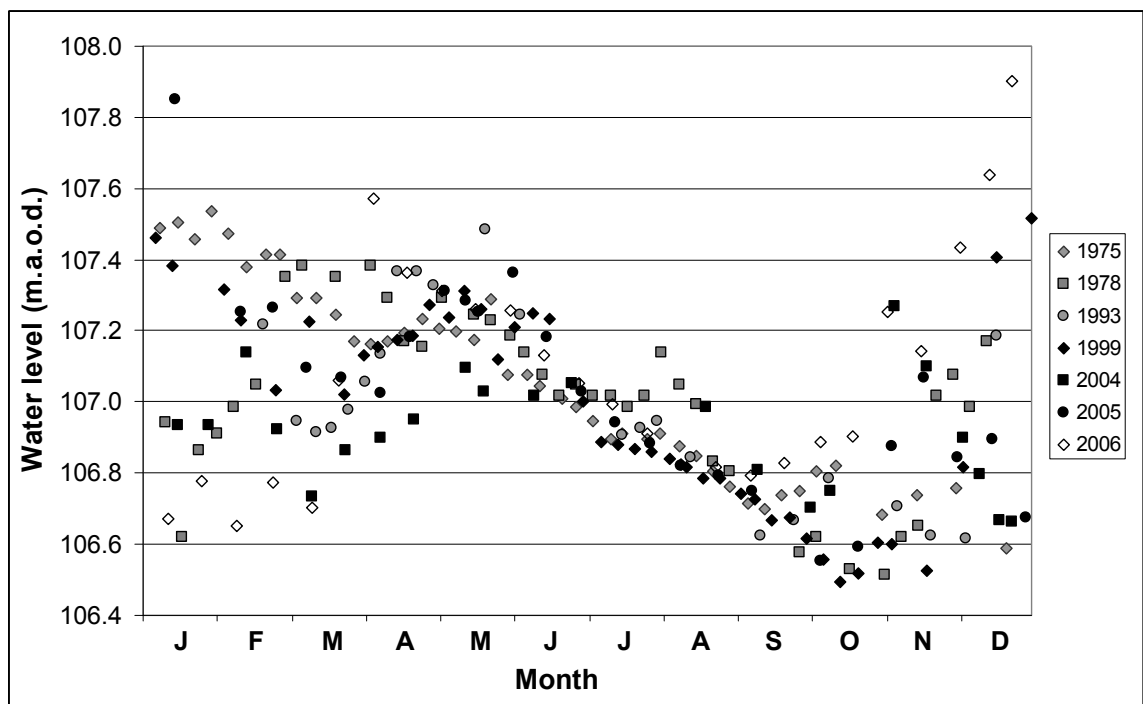


Figure 3

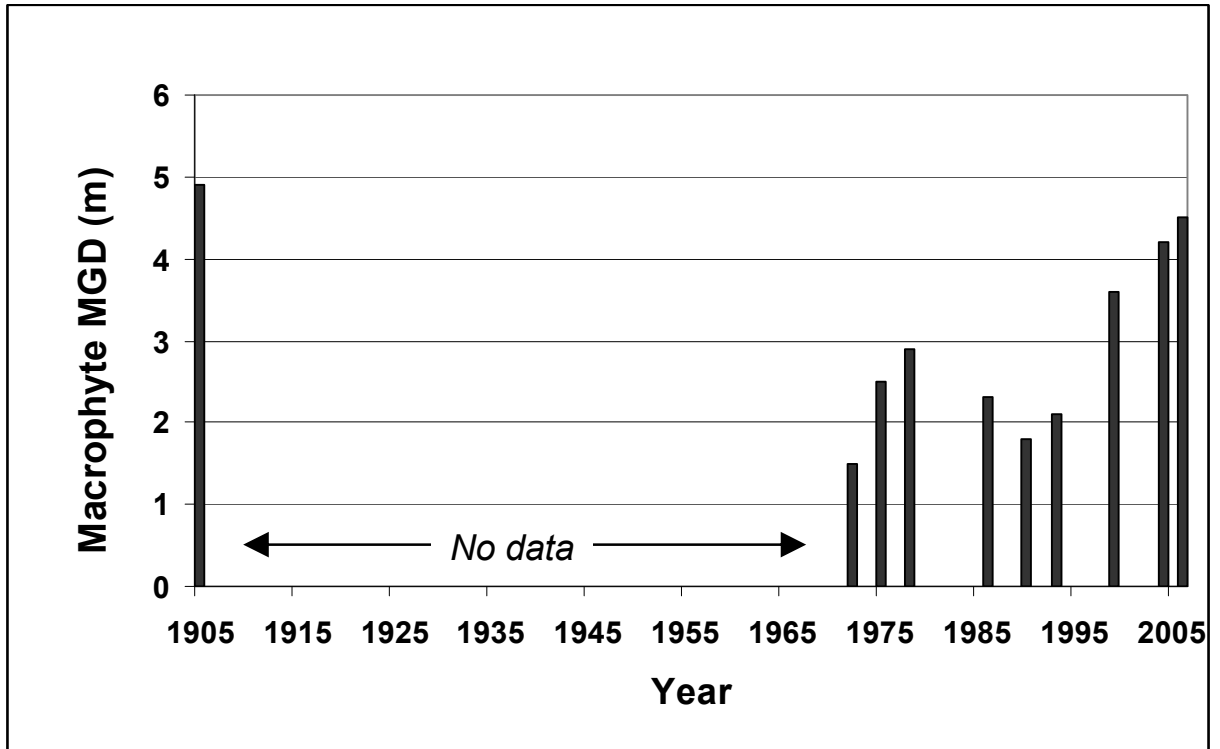


Figure 4

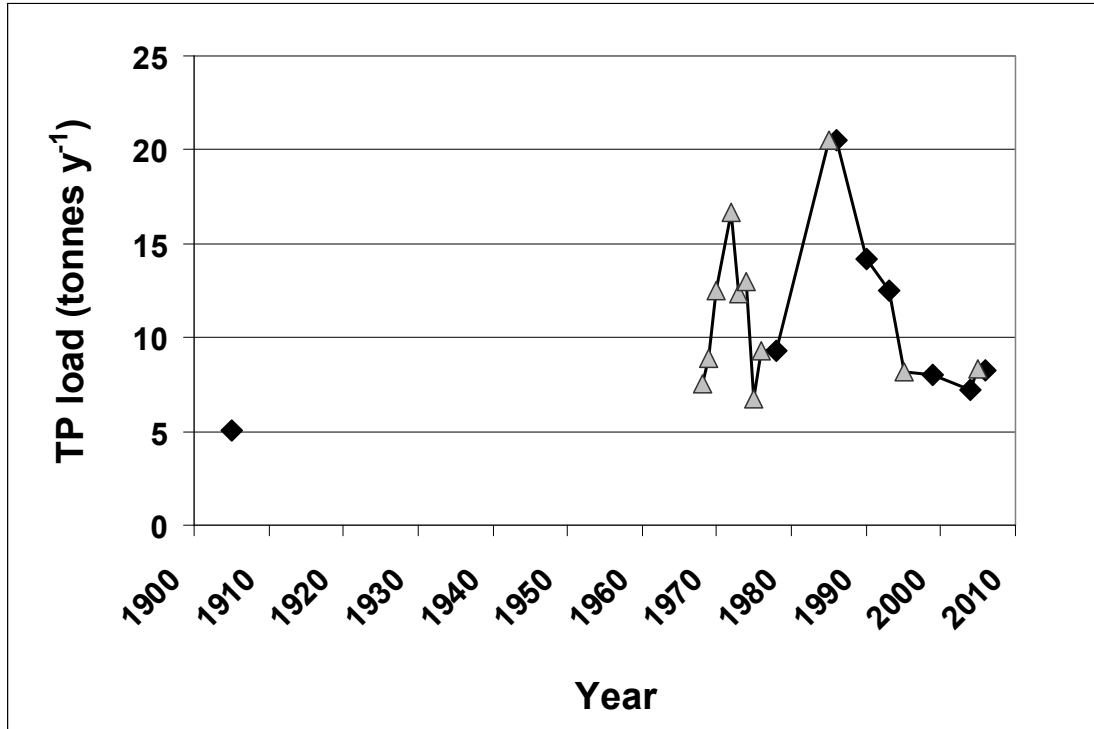


Figure 5

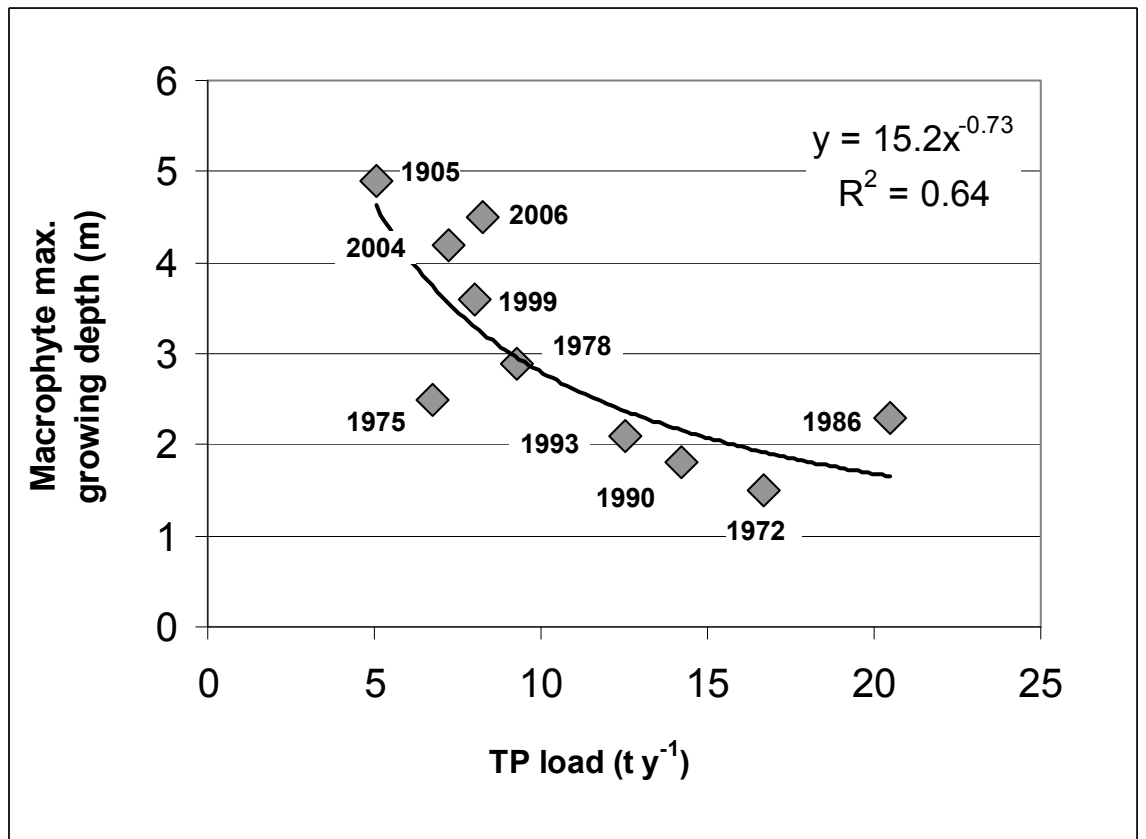


Figure 6

