# LOCH LEVEN RESEARCH

# Long-term variation and regulation of internal phosphorus loading in Loch Leven

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Published online: 3 November 2011 © Springer Science+Business Media B.V. 2011

Abstract Long-term monitoring data (1968–2008) were used to investigate internal phosphorus (P) loading following external P loading reduction in shallow Loch Leven, Scotland. A whole-lake sediment P inventory (upper 3 cm of sediment; 2005) suggested a release-potential of 29.7 tonnes (t) from the release sensitive sediment P pools. 18.5 t was contained within shallow water sediments (<4.5 m water depth) with 7.6 t in deeper water sediments below the photic zone (>5 m water depth). The "observed" release (<5.1 t), estimated using a water column P mass balance approach (1989–2008), was <5.1 t, indicating

Guest editors: L. May & B. M. Spears / Loch Leven: 40 years of scientific research

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the presence of regulating mechanisms. Observed P release declined between 1989 and 2008, with the exception of 2003–2006. Observed P release estimates were positively correlated with annual average water column P concentration after 1989, highlighting the role of internal loading in maintaining poor water quality conditions after management intervention. Multiple regression analysis suggested that internal loading was driven by the wave mixed depth in spring (positive driver), summer water temperature (positive driver) and spring water clarity transparency (negative driver). The potential importance of biological and physico-chemical feedback mechanisms in the regulation of benthic–pelagic coupling and water quality in Loch Leven are discussed.

# Introduction

Elevated phosphorus (P) inputs to Loch Leven from its catchment over many decades (May et al., 2011) resulted in a deterioration of water quality, including high water column total P (TP) concentrations, increased phytoplankton biomass and, consequently, decreased water clarity (Bailey-Watts & Kirika, 1999; Carvalho et al., 2011), and a reduction in macrophyte biomass (expressed as maximum growing depth; May

& Carvalho, 2010). In an attempt to improve water quality, external P inputs to the loch were reduced by more than 60% between the 1970s and 1990s (Bailey-Watts & Kirika, 1999; May et al., 2011). The lake responded slowly and significant improvements in water quality as a result of this management activity have been observed only recently (D'Arcy et al., 2006). This suggests a recovery period of at least 20 years at this site (1989–2008; Fig. 1).

It is generally accepted that this prolonged recovery is driven by re-equilibration processes ("internal loading"), whereby sediment P that has been accumulated over periods of high external loading is released to the overlying water column during the period of recovery in shallow lakes (Sas, 1989). The magnitude of internal loading may diminish slowly as a result of P relinquishment from the system or may be disrupted (capped) relatively quickly through the establishment of natural buffering systems at the sediment–water interface (e.g. macrophytes and benthic algae; Scheffer, 2001; Mehner et al., 2008).

It is hypothesised that a switch in water column nutrient source dependency from the catchment to the sediment has occurred in Loch Leven. This phenomenon is commonly observed in shallow lakes following the reduction of external P loading (Sas, 1989; Jeppesen et al., 2005; Søndergaard et al., 2005). However, although attempts have been made to investigate the importance of internal loading in Loch Leven, through sediment P inventories and water column mass balance estimates, little is known about changes in the relative importance of internal versus external loading across the well documented history of eutrophication and subsequent management and recovery at this site.

Holden & Caines (1974) acknowledged the potential importance of sediment P sources in driving water quality at Loch Leven between 1964 and 1971. They estimated that the mass of dormant release sensitive P (i.e. that associated with Fe and, therefore, releasable under reducing conditions) in the upper 4 cm of sediment was about 20 t P. Using a water column mass balance approach they also estimated that P cycling between the sediments and the water column amounted to a maximum sediment release of 136 kg TP day<sup>-1</sup>, a maximum sediment release of 88 kg TP day<sup>-1</sup>. Advances in chemical speciation techniques facilitated a more comprehensive assessment of sediment P fractions in 1990, immediately



**Fig. 1** Monthly average TP concentrations in the water column of Loch Leven, 1968–2008

after significant P loading reductions (Farmer et al., 1994). The authors found that a large proportion ( $\sim 30\%$ ) of the 68.8 t of TP contained in the upper 4 cm of sediments within the loch was release sensitive. A more recent study (2004–2005; i.e. during the recovery period) found significant spatial (with overlying water depth) and seasonal variations in P composition and concentrations within the active layer of surface sediment (upper 3 cm; Spears et al., 2006, 2007). This work clearly highlighted the need to include annual and spatial averages in constructing representative sediment P inventories.

Characteristic water column TP peaks in late summer/early autumn, which are typically driven by internal loading, have been recorded in Loch Leven since 1989 (Fig. 1, lower panel; Spears et al., 2006, 2008). Such peaks are commonly observed in "recovering" shallow lakes (Sas, 1989; Søndergaard, 2007) at this time of year when external nutrient inputs are low. At Loch Leven, there is also a trough in the hydrograph at this time of year (Smith, 1974). For these reasons, changes in water column TP concentration over this period can be attributed fairly reliably to internal loading.

Recent studies have highlighted strong spatial zonation in relation to the environmental drivers of sediment P release in Loch Leven. Dominant nutrient cycling mechanisms are synthesised from Spears et al. (2006, 2007, 2009), the spatial distribution of dominant autotrophic groups is summarised from Spears (2007) and Spears et al. (2009) and the substrate composition and light attenuation are summarised from Calvert (1974) and unpublished data (2004–2005), respectively. In shallow, photic zones, P release is expected to be driven by wind induced disturbance of sediments and diffusive release across an aerobic sediment-water interface (Fig. 2; Table 1). In these zones, sediment oxygen concentrations are likely maintained through a combination of wind induced wave mixing (Spears & Jones, 2010) and benthic primary production (Spears et al., 2008). Sediment P release in deeper, relatively undisturbed, aphotic sediments is likely dominated by diffusive release across an aerobic (especially in cooler, windy winter/spring) or anoxic (especially in warm, calm summer/autumn) sediment-water interface (Spears et al., 2007). Although the relative importance of these processes is known to vary seasonally and interannually, the combined effects of these drivers have not been quantified.

In Loch Leven, wave mixing of sediments and, therefore, the threat of disturbance driven P-release is lowest in summer and highest in winter (Spears & Jones, 2010). In contrast, temperature driven release, through enhanced diffusion rates (shallow and deep water sediments) or the onset of anoxia and resultant release of reductant-soluble P (more likely in deep water sediments), is more important in summer and autumn (Spears et al., 2007, 2008). The effects of benthic autotrophs in reducing sediment P release are likely to be strongest during summers with high temperatures (Spears et al., 2008) that follow an intense spring clear water phase.

The objectives of this article are (1) to use sediment P concentration data to create a whole loch sediment P inventory and partition this spatially according to overlying water depth, (2) to use water column TP fluctuations, associated with apparent internal loading processes, to estimate long-term variations in the magnitude of apparent internal P loading, and (3) to investigate the relative seasonal effects of temperature, wind induced wave mixing, and water transparency (Secchi depth) on long-term variations in internal loading.

# Methods

# Study site

Loch Leven (Fig. 3) is a large (13.3  $\text{km}^2$  surface area) shallow (mean depth 3.9 m) eutrophic loch in east central Scotland (latitude 56°10′N, longitude 3°30′W). The loch has a long and well documented history of eutrophication problems, with catchment management during 1970s-1990s resulting in a significant reduction in external P loading (Bailey-Watts & Kirika, 1999; D'Arcy et al., 2006; May et al., 2011). The period of high external loading (1968–1989) was characterised by high baseline TP concentrations apparently masking any seasonal TP trends (Fig. 1). The external TP load was halved between 1985 (20 t TP per year) and 1995 ( $\sim 8$  t TP per year) and appears to have changed little between 1995 and 2005 (8 t TP per year) (May et al., 2011). About 65% of this reduction was conducted between 1970 and 1987 the remaining 25% occurring between 1993 and 1997 (LLAMAG, 1993). A change in the TP signal is evident post 1989 where autumnal internal loading peaks are observed coupled





 Table 1
 Estimated zonation of functional autrotrophs in Loch Leven based on data from 2004 to 2006; depth ranges represent zones of dominance based on spatial assessments of biomass

Zone	Dominant autotrophic group	Dominant substratum	Depth (m)	Loch surface area (%)	Incident light reaching sediment surface (%)	Nutrient cycling mechanism
1	Microalgae/emergent vegetation	Sand/stones	<1.0	21	100.0–16.1	Aerated, diffuse, disturbance
2	Macrophytes	Sand/mud	1.0–3.5	37	16.0–1.4	Aerated, diffuse, disturbance
3	Microalgae	Mud	3.6–5.5	23	1.3–0.1	Aerated diffuse, undisturbed
4	Detritus	Mud	>5.5	19	0.1–0.0	Aerated/anoxic, undisturbed

with a drop in baseline TP. The magnitude of this peak is observed to fluctuate and is lowest during 2000–2003 and 2007–2008.

The substrate of Loch Leven is mainly sand and is dominated mainly by cobbles at depths of less than 2 m, and by silt and organic mud at depths of greater than 2 m (Calvert, 1974; Spears et al., 2006).

# Estimating the sediment P inventory

Sediment P concentrations across a gradient of 1.5–22.5 m overlying water depth (Reed Bower site

also sampled; 3.5 m water depth) were reported by Spears et al. (2007). Surface sediments were sampled using a Jenkin surface sediment sampler. Sediment P pools were quantified using the modified Psenner extraction scheme (Farmer et al., 1994). Annual average concentrations of sediment P pools (labile, reductant-soluble and total sediment P) were calculated for the upper 3 cm of surface sediments, using monthly concentrations between April 2004 and April 2005, and extrapolated over a range of water depths (Table 2). Labile and reductant-soluble P were combined as release sensitive sediment P. These annual **Fig. 3** Bathymetric map of Loch Leven showing the location of the Reed Bower sampling site



 Table 2
 Estimates of sediment surface area, TP content of upper 3 cm of sediment, and release sensitive (labile and reductant-soluble sediment P pools) P for given depth ranges in Loch Leven 2005

Depth range (m)	Sediment	area	TP content		Release sensitive P		
	(km <sup>2</sup> )	(% lake area)	(tonnes)	(% Total)	(tonnes)	(% Total)	
2.0-4.4	5.44	39.6	62.5	67.9	18.6	20.1	
4.5-6.9	1.87	13.6	18.8	20.4	7.0	7.6	
7.0–9.4	0.37	2.7	3.3	3.4	1.4	1.5	
9.5–11.9	0.23	1.7	2.1	2.3	0.8	0.9	
12.0-14.4	0.16	1.1	1.4	1.5	0.5	0.5	
14.5–16.9	0.17	1.2	1.5	1.6	0.5	0.6	
17.0–19.4	0.11	0.8	0.9	1.0	0.4	0.4	
19.5–21.9	0.09	0.7	0.8	0.9	0.3	0.3	
22.0-25.0	0.07	0.5	0.5	0.6	0.2	0.2	
Total	8.49	61.9	92.0		29.7	32.3	

average concentrations were converted to mass of P (tonnes) by correcting for the annual average dry weight of sediment and the surface area of the loch bed for each depth class (Kirby, 1971).

# Estimating long-term variations in internal loading

Water samples for TP analysis were collected at a twoweek interval from the Reed Bower sample site (Fig. 3) using an integrated water column sampler deployed to about 25 cm above the sediment surface. Only values for 1989–2008 were used in the analyses that follow. When open water sampling was deemed to be impractical (e.g. due to ice cover), surface water samples were collected from the outflow. The method used for TP analysis was as described by Wetzel & Likens (2000), with an added acidification step (0.1 ml of 30% H<sub>2</sub>SO<sub>4</sub> was added to the samples before addition of persulfate).

Internal loading was estimated using a water column mass balance approach. The magnitude of the May–September internal loading peak (I-Load<sub>M-S</sub>; Fig. 1, lower panel; Spears et al., 2006, 2008) was

corrected for loch volume to estimate the mass of P release (tonnes) required to effect the observed change in water column TP concentration. This was conducted for each year during the recovery period (1989–2008). The troughs (generally May–June) and peaks (generally August–September) were manually selected from the raw TP concentration data to represent the lowest and highest values, respectively, corresponding to the peak in each year. These peaks occur in the summer, during periods of low external loading and, as such, this method represents an estimate of I-Load<sub>M-S</sub> (Carvalho et al., 1995).

I-Load<sub>M-S</sub> was plotted against annual average water column TP concentration for each year, the covariance between the two being quantified using correlation analysis (n = 19;  $\alpha = 0.05$ ) following normality criteria testing using the Anderson–Darling test (P > 0.05; Townend, 2004). All statistical analyses were conducted using Minitab version 15.

# Identifying the long-term drivers of internal loading

The effects of water clarity (Secchi depth), wind induced wave mixed depth, and temperature on the magnitude of I-Load $_{M-S}$  were assessed between 1989 and 2007, excluding 2000-2002 due to lack of wind data (n = 16). Secchi depth was recorded at the Reed Bower sampling site (Fig. 3) at roughly two-weekly intervals. Monthly mean temperatures were calculated from daily measurements recorded at a weather station on the shore by Kinross Estates. Average daily temperatures were calculated as the arithmetic mean of the maximum and minimum daily temperatures recorded. Gaps in the on-shore weather data were filled using a regression equation that related 30 years of air temperature records from Loch Leven  $(T_{Leven})$  to those recorded at Leuchars  $(T_{\text{Leuchars}})$ , a weather station situated about 44 km north-east of the loch (http://www.metoffice.gov.uk/climate/uk/stationdata/). This was as follows:

 $T_{\text{Leven}} = 1.023 \times T_{\text{Leuchars}} - 0.9938(r^2 = 0.9885)$ 

Daily average wind speed and direction for Loch Leven was provided by Kinross Estates. Daily wave mixed depths, averaged over six sampling locations across the loch (see Spears & Jones, 2010) were estimated as a function of effective fetch, and wind speed and direction, using simple wave theory (Smith, 1974; Douglas & Rippey, 2000).

All data were averaged, first by month and then by season (winter: December to February; spring: March to May; summer: June to August; autumn: September to November).

The normality of each data population was assessed using an Anderson–Darling test and assumed normal given P > 0.05 (Townend, 2004). The combined effects of temperature, Secchi depth, and depth of the wave mixed layer on I-Load<sub>M-S</sub> were investigated using stepwise multiple regression analysis that included seasonal and annual averages of each of the three drivers. Planned multiple regression was conducted using the output of the stepwise multiple regression and the resultant model was validated against estimates of I-Load<sub>M-S</sub>.

# Results

## Sediment P inventory

The depth range of sediment studied (2.0-25.0 m) represents about 62% of the surface area of the loch (Table 2). Depth range 2.0-4.4 m (40% loch surface area) had the highest surface sediment TP (62.5 t; 68% of whole loch sediment TP estimate) and release sensitive P mass (18.6 t; 20% of whole loch sediment TP estimate). This was followed by the 4.5-6.9 m depth range which contained 19 t of sediment TP (20% whole loch sediment TP) and 7 t of release sensitive P (8% whole loch sediment TP). Only 11 t sediment TP (11% whole loch sediment TP) and 4 t release sensitive P (4% whole loch sediment TP) was contained within the depth range 7.0-25.0 m (9% loch surface area).

Long-term variation in internal loading

During the recovery period, internal loading (I-Load<sub>M-S</sub>) was highest (5.0 t TP) in 1991 and lowest in 2002 (1.1 t TP) (Fig. 4). However, overall, there was a steadily declining trend in I-Load<sub>M-S</sub> from 1989 to 2002. This was followed by a temporary increase in values between 2003 and 2006, followed by a large decrease observed in 2007 to a value that was sustained in 2008. Annual average water column TP concentrations were significantly and positively correlated with I-Load<sub>M-S</sub> (correlation coefficient = 0.794; P = < 0.001).

**Fig. 4** Internal load estimates and annual mean TP concentration for Loch Leven, 1989–2008



Identifying the drivers of internal P loading

The effects of temperature, Secchi depth, and wave mixing on internal loading were first assessed using stepwise multiple regression analysis. A significant result was returned in which the spring wave mixed depth had the largest effect, followed by summer air temperature and then by spring Secchi depth (Table 3). Standard multiple regression analysis was then used to construct the following I-Load<sub>M-S</sub> model:

$$I-Load_{M-S}(t TP) = -5.86 + 2.03Zc + 0.53T - 0.75 SD$$

where I-Load<sub>M-S</sub> is the Internal P load (t TP), Zc is the wave mixed depth (m), *T* is the summer air temperature (°C), SD is the Secchi depth (m).

The fit of the modelled data to the measured data is shown (Fig. 5). There was a significant correlation (correlation coefficient = 0.84; P < 0.001) between modelled and "observed" I-Load<sub>M-S</sub>.

# Discussion

Distribution of sediment P in relation to the regulation of release

The difference between the mass of release sensitive P in the sediments (total 29.7 t P) and the mass of P required to raise the water column P concentration during the internal loading peak in Loch Leven in 2005 ( $\sim$ 4 t TP) is large. This suggests that only a small

Table 3	Results	of the	multiple	linear	regression	analysis	s of	drivers	of	internal	load	at	Loch	Leven	ı

Predictor	Coefficient		SE coefficient	Т		Р	
Constant	-5.8	36	3.3	-1.	8	0.11	
Spring wave mixed depth 2.03		)3	0.7		9	0.02	
Summer air temperature	0.52		0.2 2.8		8	0.02	
Spring Secchi depth	-0.75		0.5	-1.	6	0.15	
Analysis of variance	DF	SS	MS	F	Р		
Regression	3	6.3	2.1	8.39	0.006		
Residual error	9	2.2	0.2				
Total	12	8.5					
	S = 0.49		$R^2 = 0.74$		$R^2$ (adj.) =	0.65	

SE standard error, DF degrees of freedom, SS sum of squares, MS mean square



Fig. 5 Relationship between modelled internal load and measured internal load for Loch Leven, 1989–2008 ( $r^2 = 0.84$ ; P < 0.001)

amount of the sediment P pool is responsible for the observed changes in water column TP during internal loading events at this site. This situation is often observed in shallow lakes and can be explained by considering spatial variation in lake bed characteristics in relation to the available P stock (Boström et al., 1988).

The spatial distribution of sediment P pools in Loch Leven was assessed in 2004/2005 (Spears et al., 2007, 2008). These studies highlighted co-variation between reductant-soluble sediment P concentrations, bottom water dissolved oxygen concentrations and benthic algal biomass, patterns that are consistent with observations from other lakes (van Luijn et al., 1995; Jin et al., 2006). Macrophytes have also been reported to reduce sediment P release through similar mechanisms in lakes (Granéli & Solander, 1998), although this has not been directly quantified in Loch Leven. In 2005, sediment P release may have been buffered by benthic autotrophs in sediments at a depth of between 1.0 and 5.5 m in Loch Leven; the lower boundary being regulated by light attenuation. It follows that sediment P release will have been unimpeded by benthic autotrophs in regions of the loch bed that lie more than 5.5 m below the water surface. Further, deeper water sediments in Loch Leven were susceptible to net-heterotrophy resulting in reduced dissolved oxygen concentrations in bottom waters and the reduction of redox-sensitive P complexes associated with an increase in sediment P release (Spears et al., 2007). This was significantly enhanced in the warmer summer months (Spears et al., 2007).

In 2005, 7 t of release sensitive P was estimated to be contained within surface sediments in the aphotic zone (i.e. >5.5 m overlying water depth). This compares with some 23 t of release sensitive P in the photic zone (i.e. <5.5 m overlying water depth). Due to strong concentration gradients in dissolved P across the sediment water interface (Spears et al., 2007), it is unlikely that diffusive P release from aerobic sediments in the photic zone is negligible (Jiang et al., 2006; Spears et al., 2008). However, release mechanisms such as wind induced wave disturbance (Søndergaard et al., 1992) and bioturbation (Andersson et al., 1988) are also likely to be important in these well aerated zones. In contrast, the dominant release mechanisms in the aphotic zone are more likely to be driven by temperature related microbial deoxygenation of surface sediments and the associated release of redox-sensitive P complexes (Boström et al., 1988; Spears et al., 2007).

Understanding the long-term regulation of internal loading

Under the present external P loading regime and photic depth, the magnitude of internal P loading in Loch Leven is driven mainly by variations in weather. Specifically, internal loading appears to increase as a result of high wind and turbidity in spring and high temperature in summer. The direct relationship between internal loading and summer temperature is well documented and results from direct increase in solute mobility across concentration gradients coupled with the metabolic scrubbing of dissolved oxygen by benthic heterotrophs and associated reduction of redox-sensitive sediment P complexes (Søndergaard, 1989; Jenson & Andersen, 1992; Spears et al., 2008). The spring Secchi depth reflects the light conditions at the sediment surface during the period of benthic autotroph establishment and is probably a good proxy for summer benthic autotrophic biomass (Canfield et al., 1985). Phillips et al. (2005) linked improvements in spring water clarity with increased summer benthic algal biomass and reduced summer internal loading. The mechanisms behind spring wave mixing with respect to the regulation of the magnitude of internal load are less easily explained. Wave mixing in spring may result in sediment disturbance which can enhance sediment nutrient release (Søndergaard et al., 1992) and inhibit the establishment of benthic autotrophs (macrophytes: Jupp & Spence, 1977, Doyle, 2001; microalgae: Cyr, 1998a). The negative effects of wave action on the biomass of the macrophytes Potamogeton filiformus and P. Pectinatus in Loch Leven have been well documented, with up to 80% of the biomass reduction in these species being attributed to wave action and the associated deterioration of substrate towards a coarser nutrient poor material (Jupp & Spence, 1977). This suggests that the buffering capacity of benthic autotrophs may be reduced under high wind conditions in Loch Leven. Additionally, high wave induced mixing has been linked to the focusing of sediments from shallow waters to deeper waters (Hilton, 1985; Cyr, 1998b) and may represent the relocation of P from the photic to the aphotic zone, thus increasing overall sediment P release.

Other studies have highlighted the important role of benthic autotrophs, macrophytes in particular, as drivers of both positive and negative feedbacks through which "recovering" shallow lakes can alternate between clear water macrophyte and turbid phytoplankton-dominated states (Rip et al., 2005; van Nes et al., 2007). The switch between positive and negative feedback mechanisms has also been linked to climate change (i.e. the North Atlantic Oscillation). These effects are many and are linked mainly through direct relationships between indices of the NAO (calculated by comparing sea level atmospheric pressures in the northern (Southwest Iceland) and southern (Gibraltar) reach of the northern hemisphere (Jones et al., 1997)) and precipitation, wind and temperature (Straile et al., 2003). Effects can include variations in nutrient loading from the catchment as a result of high precipitation (Monteith et al., 2000; Rip, 2007), variations in the wave mixed zone and potential sediment disturbance (Loch Leven: Spears & Jones, 2010), and variations in zooplankton grazing rates associated with the intensity of the spring clear water phase (Scheffer et al., 2001).

The low internal loading events of 2007 and 2008 in Loch Leven were characterised by low spring wind speeds, low summer temperatures and high Secchi depths (i.e. high NAO winter index years; http://www.cru.uea.ac.uk/~timo/projpages/

nao\_update.htm). In addition, a thorough assessment of macrophyte colonisation conducted in 2008 returned a maximum macrophyte colonisation depth similar to that observed before eutrophication (4.6 m: May & Carvalho, 2010), presumably resulting in higher P uptake by both macrophytes and epiphytes (Carpenter & Lodge, 1986). However, these years were also years of high rainfall and presumably, higher flushing rates (Carvalho et al., 2011). Although the results of this study highlight the importance of climate change as a driver of internal loading, it should be noted that interactions between climate and land use drivers may override the observed relationships. Further work is required to quantify the interactions between climate change, catchment pressures and biological control of internal nutrient processes in Loch Leven.

# Conclusions

Improvements in water column TP concentration during the recovery period appear to have resulted from two different processes. First, a gradual decline in TP was observed over the 20 year period (Carvalho et al., 2011). Second, a more instantaneous decline in TP was observed in 2007. Correlation analysis suggests that one important driver of this variation in Loch Leven between 1989 and 2008 was the magnitude of internal loading. Variability in the magnitude of internal loading during the recovery period appeared to be regulated mainly by climate change variables (i.e. wind and temperature) and, to a lesser extent, indicators of water clarity (i.e. Secchi depth), rather than TP concentrations in the sediment.

Acknowledgments We would like to acknowledge Mr. Jamie Montgomery and, his father, Sir David Montgomery for their continued support, enthusiasm and assistance throughout the project. We would also like to thank Willie Wilson, of Loch Leven Fisheries, for his invaluable advice and support during the project and for the provision of weather data. Finally, we wish to thank Dr. Martin Søndergaard (NERI, Denmark) and Dr. Andrea Kelly (the Broads Authority, UK) for useful comments that led to the improvement of the manuscript. This project was funded by the Natural Environment Research Council, UK.

# References

- Andersson, G., W. Granéli & J. Stenson, 1988. The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170: 267–284.
- Bailey-Watts, A. E. & A. Kirika, 1999. Poor water quality in Loch Leven (Scotland) in 1995, in spite of reduced

phosphorus loading since 1985: the influences of catchment management and inter-annual weather variation. Hydrobiologia 403: 135–151.

- Boström, B., J. M. Anderson, S. Fleischer & M. Jansson, 1988. Exchange of phosphorus across the sediment–water interface. Hydrobiologia 170: 229–244.
- Calvert, S. E., 1974. The distribution of bottom sediments in Loch Leven, Kinross. Proceedings of the Royal Society of Edinburgh B 74: 69–80.
- Canfield, D. E. Jr., K. A. Langeland, S. B. Linda & W. T. Haller, 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. Journal of Aquatic Plant Management 23: 25–28.
- Carpenter, S. R. & D. M. Lodge, 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26: 341–370.
- Carvalho, L., M. Beklioglu & B. Moss, 1995. Changes in a deep lake following sewage diversion – a challenge to the orthodoxy of external phosphorus control as a restoration strategy? Freshwater Biology 34: 399–410.
- Carvalho, L., C. Ferguson, I. Gunn, H. Bennion, B. Spears, A. Kirika & L. May, 2011. Water quality of Loch Leven: responses to enrichment, restoration and climate change. Hydrobiologia. doi:10.1007/s10750-011-0923-x.
- Cyr, H., 1998a. How does vertical distribution of chlorophyll vary in littoral sediments of small lakes? Freshwater Biology 40: 25–40.
- Cyr, H., 1998b. Effects of wave disturbance and substrate slope on sediment characteristics in the littoral zone of small lakes. Canadian Journal of Fisheries and Aquatic Sciences 55: 967–976.
- D'Arcy, B. J., L. May, J. Long, I. R. Fozzard, S. Greig & A. Brachet, 2006. The restoration of Loch Leven, Scotland. Water Science and Technology 53: 181–191.
- Douglas, R. W. & B. Rippey, 2000. The random redistribution of sediment by wind in a lake. Limnology and Oceanography 45: 686–694.
- Doyle, R. D., 2001. Effects of waves on the early growth of Vallisneria americanna. Freshwater Biology 46: 389–397.
- Farmer, J. G., A. E. Bailey-Watts, A. Kirika & C. Scott, 1994. Phosphorus fractionation and mobility in Loch Leven sediments. Aquatic Conservation: Marine and Freshwater Ecosystems 4: 45–56.
- Granéli, W. & D. Solander, 1998. Influence of aquatic macrophytes in lakes. Hydrobiologia 170: 245–266.
- Hilton, J., 1985. A conceptual framework for predicting the occurrence of sediment focussing and sediment redistribution in small lakes. Limnology and Oceanography 30: 1131–1143.
- Holden, A. V. & L. A. Caines, 1974. Nutrient chemistry of Loch Leven, Kinross. Proceedings of the Royal Society of Edinburgh B 74: 101–121.
- Jenson, H. S. & F. Ø. Andersen, 1992. Importance of temperature, nitrate, and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. Limnology and Oceanography 37: 577–589.
- Jeppesen, E., M. Søndergaard, J. P. Jensen, K. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangur, J. Kohler, E. H. H. R. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Noges, G. Persson,

G. Phillips, R. Portielje, S. Romo, C. L. Schelske, D. Straile, I. Tatrai, E. Willen & M. Winder, 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50: 1747–1771.

- Jiang, X., X. Jin, Y. Yao, L. Li & F. Wu, 2006. Effects of oxygen on the release and distribution of phosphorus in the sediments under the light condition. Environmental Pollution 141: 482–487.
- Jin, X., X. Jiang, Y. Yao, L. Li & F. Wu, 2006. Effects of light and oxygen on the uptake and distribution of phosphorus at the sediment–water interface. Science of the total Environment 357: 231–236.
- Jones, P. D., T. Jonsson & D. Wheeler, 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. International Journal of Climatology 17: 1433–1450.
- Jupp, B. P. & D. H. N. Spence, 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. II Wave action, sediments, and water fowl grazing. The Journal of Ecology 65: 175–186.
- Kirby, R. P., 1971. The bathymetrical resurvey of Loch Leven, Kinross. Geographical Journal 137: 372–378.
- LLAMAG, 1993. Loch Leven: the report of the Loch Leven area management advisory group. Forth River Purification Board, Edinburgh.
- May, L. & L. Carvalho, 2010. Maximum growing depth of macrophytes in Loch Leven, Scotland, United Kingdom in relation to historical changes in estimated phosphorus loading. Hydrobiologia 646: 123–131.
- May, L., L. H. Defew, H. Bennion & A. Kirika, 2011. Historical changes(1905–2005) in external phosphorus loads to Loch Leven, Scotland, UK. Hydrobiologia. doi:10.1007/s10750-011-0922-y.
- Mehner, T. M., T. Diekmann, P. Gonsiorczyk, R. Kasprzak, L. Koschel, M. Krienitz, M. Rumpf, G. Schulz & Wauer, 2008. Rapid recovery from eutrophication of a stratified lake by disruption of internal nutrient load. Ecosystems 11: 1142–1156.
- Monteith, D. T., C. D. Evans & B. Reynolds, 2000. Are temporal variations in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation? Hydrological Processes 14: 1745–1749.
- Phillips, G., A. Kelly, J. Pitt, R. Sanderson & E. Taylor, 2005. The recovery of a very shallow lake, 20 years after the control of effluent driver phosphorus. Freshwater Biology 50: 1628–1638.
- Rip, W., 2007. Cyclic state shifts in a restored shallow lake. Thesis, Wageningen University. ISBN 978-90-8504-706-3.
- Rip, W., M. R. L. Ouboter, E. H. van Ness & B. Beltman, 2005. Long term oscillation of a shallow lake ecosystem upon reduction in external phosphorus load. Archiv für Hydrobiologie 164: 387–409.
- Scheffer, M., 2001. Ecology of shallow lakes. Kluwer Academic Press, London.
- Scheffer, M., D. Straile, E. H. van Nes & H. Hosper, 2001. Climatic warming causes regime shifts in lake food webs. Limnology and Oceanography 46: 1780–1783.
- Sas, H., 1989. Lake restoration by reduction of nutrient loading. Academic Verlag Richarz, St. Augustin.

- Smith, I. R., 1974. The structure and physical environment of Loch Leven, Scotland. Proceedings of the Royal Society of Edinburgh B 74: 81–100.
- Søndergaard, M., 1989. Phosphorus release from a hypertrophic lake sediment: experiments with intact sediment cores in a continuous flow system. Archive für Hydrobiologie 116: 45–59.
- Søndergaard, M., 2007. Nutrient dynamics in lakes with emphasis on phosphorus, sediment and lake restorations. DSc. Thesis. National Environmental Research Institute, University of Aarhus, Denmark: 276 pp.
- Søndergaard, M., P. Kristensen & E. Jeppesen, 1992. Phosphorus release from resuspended sediment in the shallow and wind-exposed Lake Arrresø, Denmark. Hydrobiologia 228: 91–99.
- Søndergaard, M., J. P. Jensen & E. Jeppesen, 2005. Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. Freshwater Biology 50: 1605–1615.
- Spears, B. M., 2007. Benthic-pelagic nutrient cycling in shallow lakes: investigating the functional role of benthic microalgae. PhD Thesis, University of St Andrews.
- Spears, B. M. & I. Jones, 2010. The long-term (1978–2005) effects of the North Atlantic oscillation on wind-induced wave mixing in Loch Leven (Scotland). Hydrobiologia 646: 49–59.
- Spears, B. M., L. Carvalho, R. Perkins, A. Kirika & D. M. Paterson, 2006. Spatial and historical variation in sediment phosphorus fractions and mobility in a large shallow lake. Water Research 40: 383–391.

- Spears, B. M., L. Carvalho, R. Perkins, A. Kirika & D. M. Paterson, 2007. Sediment P cycling in a large shallow lake: spatio-temporal variation in P pools and release. Hydrobiologia 584: 37–48.
- Spears, B. M., L. Carvalho, R. Perkins & D. M. Paterson, 2008. The effects of light on sediment nutrient flux and water column nutrient stoichiometry in a shallow lake. Water Research 42: 977–986.
- Spears, B. M., I. D. M. Gunn, L. Carvalho, I. J. Winfield, B. Dudley, K. Murphy & L. May, 2009. An evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven, Scotland. Aquatic Botany 91: 75–81.
- Straile, D., D. M. Livingstone, G. A. Weyhenmeyer & D. G. George, 2003. The response of freshwater ecosystems to climate variability associated with the North Atlantic oscillation. Geophysical Monographs 134: 263–279.
- Townend, J., 2004. Practical statistics for environmental and biological scientists. Wiley, West Sussex.
- van Luijn, F., D. T. van der Molen, W. J. Luttmer & P. C. M. Boers, 1995. Influence of benthic diatoms on the nutrient release from sediments of shallow lakes recovering from eutrophication. Water Science and Technology 32: 89–97.
- van Nes, E., W. Rip & M. Scheffer, 2007. A theory for cyclic shifts between alternative states in shallow lakes. Ecosystems 10: 17–27.
- Wetzel, R. G. & G. E. Likens, 2000. Limnological analyses, 3rd ed. Springer-Verlag, New York.