ISSN 1393 – 6670

NATIONAL PARKS AND WILDLIFE SERVICE

BENTHIC VEGETATION IN IRISH MARL LAKES: MONITORING HABITAT 3140 CONDITION 2011 TO 2018

Cilian Roden, Paul Murphy & James Ryan

An Roinn Tithíochta,
Rialtais Áitiúil agus Oidhreachta
Department of Housing,
Local Government and Heritage

IRISH WILDLIFE MANUALS 124

Front cover, small photographs from top row:

Limestone pavement, Bricklieve Mountains, Co. Sligo, Andy Bleasdale; **Meadow Saffron** *Colchicum autumnale*, Lorcan Scott; **Garden Tiger** *Arctia caja*, Brian Nelson; **Fulmar** *Fulmarus glacialis*, David Tierney; **Common Newt** *Lissotriton vulgaris*, Brian Nelson; **Scots Pine** *Pinus sylvestris*, Jenni Roche; **Raised bog pool**, Derrinea Bog, Co. Roscommon, Fernando Fernandez Valverde; **Coastal heath**, Howth Head, Co. Dublin, Maurice Eakin; **A deep water fly trap anemone** *Phelliactis* sp., Yvonne Leahy; **Violet Crystalwort** *Riccia huebeneriana*, Robert Thompson

Main photograph:

Cooloorta/Travaun Lough in 2018, Cilian Roden

Benthic vegetation in Irish marl lakes: monitoring habitat 3140 condition 2011 to 2018

Cilian Roden, Paul Murphy[1] & James Ryan

[1]Eireco

Keywords: Irish marl lakes, charophyte algae, cyanobacterial crust, submerged vegetation zones, Annex I habitat 3140, conservation condition, euphotic depth, total phosphorus, water colour

Citation: Roden, C., Murphy, P. & Ryan, J. (2020) Benthic vegetation in Irish marl lakes: monitoring habitat 3140 condition 2011 to 2018. *Irish Wildlife Manuals*, No. 124. National Parks and Wildlife Service, Department of Housing, Local Government and Heritage, Ireland.

The NPWS Project Officer for this report was: Áine O Connor; aine.oconnor@chg.gov.ie

This IWM was edited by Áine O Connor

ISSN 1393 – 6670

An RoinnTithíochta, Rialtais Áitiúil agus Oidhreachta, 90 Sráid an Rí Thuaidh, Baile Átha Cliath 7, D07 N7CV
Department of Housing, Local Government and Heritage, 90 North King Street, Dublin 7, D07 N7CV

Contents

Executive Summary

Marl lakes have a rich and distinctive flora dominated by charophyte (stoneworts) and other algae and Irish marl lakes are home to charophyte species that are rare or absent from neighbouring countries. This vegetation constitutes the Habitats Directive Annex I habitat 'Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.' (habitat code 3140). Shallow, well-mixed marl lakes are more common and larger in Ireland than most other parts of Europe, thus Ireland has significant responsibility for the protection of this habitat. However, there has been a steady erosion of habitat quality in Ireland.

The benthic vegetation of 29 Irish marl lakes was analysed using data collected between 2007 and 2018. Vegetation was described using snorkelling, which provided precise data on depth distribution and species composition. The results showed that lakes in good conservation condition are characterised by a flora with few vascular plants but abundant charophytes, and a characteristic cyanobacterial (cyanophyte) crust community. Up to five vegetation zones can occur in marl lakes, each dominated by a characteristic charophyte species. The extent of the cyanobacterial crust, the number of charophyte species, the number of charophyte vegetation zones and charophyte cover as a proportion of total vegetation cover were positively correlated with euphotic depth (maximum depth of vegetation colonisation). Conversely, low euphotic depth correlated with increased proportion of vascular plants. In turn, euphotic depth is inversely related to average lake total phosphorus and water colour. It was concluded that near pristine Irish marl lakes are characterised by euphotic depth of greater than 7 m, high charophyte vegetation abundance and species diversity, a large expanse of cyanobacterial crust and a small proportion of vascular plants.

An Appendix with site reports for all marl lakes surveyed in 2012 and 2018 is provided as a separate pdf-file.

Acknowledgements

We thank all those who have helped us during our work on marl lakes. Dr Áine O Connor has been a mainstay of the project in everything from commissioning work to editing final reports and helping us to think through our ideas. Dr Deirdre Tierney and the other staff of the Environmental Protection Agency (EPA) have generously provided data about many of our study sites. Dr Philip Doddy discussed the role of cyanobacterial crusts. Dr Klaus van de Wyer, John Bruinsma and Richard Lansdown participated in surveys of east Co. Clare lakes and Lough Bane.

Introduction

Hard-water or marl lakes are more common and larger in Ireland than in some neighbouring E.U. states. This abundance is reflected in the presence of species ranging from charophytes (*e.g. Chara tomentosa*), to crustaceans (*e.g.* White-clawed Crayfish *Austropotamobius pallipes*) and insects (*e.g. Ochthebius nilssoni*) (Nelson *et al*., 2019; O'Callaghan *et al*., 2009) that are rare or absent from neighbouring countries. They are also the location of some of the country's finest Brown Trout *Salmo trutta* fisheries (*e.g.* Lough Mask and Lough Corrib) (Reynolds, 1998). Thus, Ireland has a European responsibility to protect this habitat. However, there has been a steady erosion of habitat quality, including increasing chlorophyll levels, loss of unique populations of species such as Arctic Char *Salvelinus alpinus* and some charophyte species, and a possible decrease in water clarity, with the consequence that the depth of the euphotic zone or the area covered by benthic vegetation is decreasing (Doddy *et al*., 2019a; NPWS, 2008; Roden & Murphy, 2013; Stewart & Church, 1992). In addition, introduced species, especially *Lagarosiphon major*, are severely damaging certain lakes such as Lough Corrib.

While Irish marl lakes have been the subject of much research, descriptions of submerged, littoral vegetation based on snorkelling/scuba observation are not common (King & Caffrey, 1998). Heuff and Ryan did study a wide variety of lakes by snorkel survey including several marl lakes (Heuff, 1984), while John *et al*. (1982) examined a number of Co. Westmeath hard-water lakes. King and others (King & Champ, 2000; Krause & King, 1994) studied submerged vegetation of Lough Corrib and Lough Carra using grapnel samples. Roden (1999, 2000, 2001) and Bruinsma *et al*. (2009) used snorkel/scuba to map vegetation in hard-water lakes both on carboniferous limestone and calcareous machair. While all these surveys provide an outline of the vegetation of hard-water lakes and confirm the dominance of certain charophyte species, they were completed before the widespread use of GPS and are thus only approximate in positioning.

More recent work by the Irish Environmental Protection Agency (EPA) lake survey teams has provided geo-referenced, grapnel data on vegetation. However, only the snorkel/scuba surveys provide visual descriptions of *in situ* vegetation structure and components. Roden (2008, 2009, 2010) produced a detailed map of Lough Bane in Co. Westmeath, using snorkelling and GPS positioning of relevés and transects. This work yielded precise spatial data on vegetation zones and depths. It is noteworthy that this survey of the hard-water Lough Bane established both the presence of a previously un-described deep water bryophyte unit and a new station for the rare *Chara denudata*, thus illustrating the value of direct visual inspection. In 2011, the authors mapped the vertical and horizontal distribution of vegetation of three large Irish marl lakes (Loughs Bunny, Carra and Owel) (Roden & Murphy, 2013), and followed this in 2012 with less-detailed survey of 25 additional Irish marl lakes, again using the geo-referencing and snorkel technique. In 2018, a repeat survey of 10 lakes included many of those examined in 2011 and 2012. The results of all of the snorkel surveys between 2007 and 2018 are considered in this report.

This work has allowed a general description of Irish marl lake vegetation to be proposed; major features include a vegetation dominated by cyanobacterial (cyanophyte) crusts in shallow water giving way to extensive charophyte communities at depth. A typical depth zonation of plant communities occurring in many marl lakes is as follows

- Cyanobacterial crust (termed 'krustenstein' in Roden & Murphy (2013))
- *Chara curta*
- *Chara rudis* and aquatic angiosperms
- *Chara virgata*
- *Chara denudata* or *Nitella flexilis* agg.

A constant but rarely emphasised feature is the relative scarcity of vascular plants in these lakes. They are also distinguished by considerable euphotic depths (see definition over-leaf) exceeding 7 m and reaching 12 m in some cases. Many examples, unfortunately, show signs of nutrient enrichment such as the destruction of the cyanobacterial crust, expansion of vascular plants and decrease in euphotic depth.

Roden & Murphy (2013) proposed a set of measurements based on benthic vegetation, which would allow an assessment of the conservation or ecological condition of a marl lake. Important factors proposed included maximum depth of colonisation, number of charophyte species and extent of cyanobacterial crust. The survey work in 2012 and 2018 provided an extensive data base which allowed the validity and suitability of these and other indicators to be assessed.

The present report summarises the results of marl lake surveys undertaken by the authors since 2007, relates benthic vegetation to environmental factors including water colour, transparency, and nutrient concentration, and attempts to define the characteristics of 'near pristine' marl lakes on Carboniferous limestone. This main report includes the results of these analyses. An Appendix with site reports for all marl lakes surveyed in 2012 and 2018 is provided as a separate pdf-file A companion *Irish Wildlife Manuals* volume (Roden *et al*., 2020) contains prescriptions for how to survey marl lake vegetation and methods to assess its conservation condition, while papers by Doddy *et al*. (2019a, b) describe how the cyanobacterial crust of Irish marl lakes responds to eutrophication.

Euphotic depth is used throughout this report to mean the maximum depth, below water surface, at which attached macrophytes (including bryophytes and charophytes) grow (*i.e.* the base/bottom of the littoral zone or maximum depth of vegetation colonisation). In marl lakes, algae are most commonly encountered at this maximum euphotic depth. Occasionally, a thin (5 mm) cyanobacterial mat occurs below the euphotic depth, or unattached plants of *Lemna trisulca* may drift down.

2 Methods

This chapter provides details of the different surveys that informed this *Irish Wildlife Manuals*. It includes information on site selection, field survey of benthic vegetation using snorkelling techniques, sources of physico-chemical data for the lakes and the analytical methods used.

2.1 Surveys and site selection

Submerged vegetation data from five separate snorkel-based surveys were used in this study in order to cover marl lakes in a range of conservation conditions from near-pristine to fundamentally altered states (see Table 1) (Bruinsma *et al*., 2009; Roden, 2008, 2009, 2010; Roden & Murphy, 2013). Cyanophyte crust data are from Doddy (2019), Doddy *et al*. (2019a, b). Surveys 3, 4 and 5 were commissioned by NPWS specifically to assess the conservation condition of the habitat 'Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.' (habitat code 3140) in the selected lakes. Data from surveys 4 and 5, the 2012 and 2018 surveys, are here reported for the first time (see site reports in Appendix III).

Table 1 Surveys from which data were used in this report.

	Survey	Survey Year(s)	Purpose	Commissioned/ funded by
1	Lough Bane water level study (Roden 2008, 2009, 2010)	2007-2010	Impact of lake level change	Meath County Council
2	Survey of east Co. Clare lake vegetation (Bruinsma *et al*., 2009)	2009	Floristic and vegetation survey	The Heritage Council
3	Survey of Loughs Bunny, Carra and Owel (Roden & Murphy, 2013)	2011	Conservation condition assessment	NPWS
4	Survey of 25 marl lakes (this report)	2012	Conservation condition assessment	NPWS
5	Survey of 10 marl lakes (this report)	2018	Conservation condition assessment	NPWS
6	Cyanobacterial Communities in Limestone Lakes & Pools in Ireland (Doddy *et al*., 2019a)	2016, 2017	PhD study	GMIT, NPWS

In 2011 (survey number 3), the pilot project to assess the conservation condition of habitat 3140 in marl lakes selected three lakes of recognised high-conservation-value across a wide geographic spread (Counties Clare, Mayo and Westmeath). Each of the three lakes is protected within a Special Area of Conservation (SAC). The methods followed those pioneered in the Lough Bane study (survey number 1) (Roden, 2008, 2009, 2010). See Roden & Murphy (2013) for full details.

The 2012 survey (number 4) applied the condition assessment methods developed in 2011 to a broader range of 25 marl lakes. Sites were selected, based on existing data and expert knowledge, to cover the range of conservation conditions (*Good*, *Poor* and *Bad*) and were located both inside and outside of SACs.

The 2018 survey (number 5) focussed on monitoring lakes in *Good* and borderline *Good-Poor* condition within SACs. Indications of ecological decline in these lakes would be a highly significant, negative indicator of the national conservation status of the habitat, especially given that the 2012 survey had demonstrated a majority of marl lakes had *Poor* or *Bad* conservation condition.

Paired physico-chemical data were required for the analyses of environmental supporting conditions and these were not available for some of the more remote lakes surveyed in 2012 and 2018. As a result, data from Bruinsma *et al*. (2009) for four marl lakes were incorporated and these, as well as Ballycuirke from Doddy *et al*. (2019a) provided examples of highly-degraded lakes.

Table 2 lists the marl lakes from the five surveys for which data were available and considered within this report.

Table 2 List of marl lakes considered in this report. The names of the 29 lakes used in the analyses of environmental drivers are emboldened. Grid reference is for the approximate centroid of the lake in Irish Grid. Surveys are numbered 1 to 5 as per Table 1. Year(s) gives the year(s) the lake was surveyed for submerged macrophytes. If the lake is within a Special Area of Conservation, the site code and name are given in the 'SAC' field. Site reports for the 32 lakes surveyed in 2011, 2012 and/or 2018 are provided in Appendix III.

Lake name	County	Grid reference	Survey	Year(s)	SAC
Aillebrack	Galway	L5856643406	4	2012	002074, Slyne Head Peninsula SAC
Annaghmore Lough	Roscommon	M8997283651	4	2012	001626, Annaghmore Lough (Roscommon) SAC (SAC is not selected for habitat 3140)
Lough Arrow	Sligo, Roscommon	G7899112053	4, 6	2012	001673, Lough Arrow SAC
Ballycuirke Lough	Galway	M2298731623	6	2017	000297, Lough Corrib SAC
Ballyeighter Lough (1)	Clare	R3571294040	4	2012	001926, East Burren Complex SAC
Ballyeighter (Lough) 2	Clare	R3352892434	4	2012	001926, East Burren Complex SAC
Lough Bane	Meath, Westmeath	N5476671293	1, 5	2007, 2008, 2009, 2010, 2018	002120, Lough Bane and Lough Glass SAC
Bleach Lough	Limerick	R4445954653	4	2012	
Brick Lough	Galway	M6354013918	4	2012	
Lough Bridget	Clare	R5599280222	2	2009	
Lough Bunny	Clare	R3749196757	3, 5, 6	2011, 2018	001926, East Burren Complex SAC
Lough Carra	Mayo	M1766272566	3, 5, 6	2011, 2018	001774, Lough Carra Mask Complex SAC
Clonlea Lough	Clare	R5092373481	2	2009	
Cooloorta Lough	Clare	R3533496517	4, 5, 6	2012, 2018	001926, East Burren Complex SAC
Lough Corrib	Galway, Mayo	M2669836252	4, 6	2012	000297, Lough Corrib SAC
Lough Cullaun	Clare	R3156290586	4	2012	001926, East Burren Complex SAC
Cullaunyheeda	Clare	R4843574671	4, 6	2012	
Lough Derravaragh	Westmeath	N4237366758	4, 6	2012	
Lough Ennell	Westmeath	N3987946565	4, 6	2012	000685, Lough Ennell SAC
Errit Lough	Roscommon	M5391485143	4	2012	000607, Errit Lough SAC
Fahy Lough	Galway	L5681455539	4	2012	001309, Omey Island Machair SAC
Finn Lough	Clare	R4324569592	4, 6	2012	
Lough George	Clare	R3426891522	5	2018	001926, East Burren Complex SAC
Lough Hackett	Galway	M3068649236	4	2012	
Inchicronan	Clare	R3937485947	2	2009	

Lake name	County	Grid reference	Survey	Year(s)	SAC
Lough Lene	Westmeath	N5107368421	1, 4, 6	2007, 2012	002121, Lough Lene SAC
Lough Mask	Mayo, Galway	M1070363710	4, 6	2012	001774, Lough Carra Mask Complex SAC
Melmore Lough	Donegal	C1285743568	5	2018	000194, Tranarossan and Melmore Lough SAC
Muckanagh Lough	Clare	R3712392809	4, 5, 6	2012, 2018	001926, East Burren Complex SAC
Lough Owel	Westmeath	N4032258331	3, 5, 6	2011, 2018	000688, Lough Owel SAC
Lough Rea	Galway	M6153815480	4, 5, 6	2012, 2018	000304, Lough Rea SAC
Rosroe Lough	Clare	R4439669018	2	2009	
Spring Lough	Monaghan	H8610603952	4	2012	
Summerhill Lough	Monaghan, Fermanagh	H4906627952	4	2012	001786, Kilroosky Lough Cluster SAC
Urlaur Lough	Mayo	M5114188814	4	2012	001571, Urlaur Lakes SAC
Walshpool Lough	Mayo	M2163284137	4, 6	2012	
White Lough	Meath, Westmeath	N5115473108	1, 5	2007, 2018	001810, White Lough, Ben Loughs and Lough Doo SAC

2.2 Macrophyte vegetation survey methods

The marl lake vegetation survey methods described in detail in Roden *et al.* (2020) were broadly used in all five surveys. Transects running from the shore to beyond the euphotic depth were surveyed by snorkelling. Relevés (2 m x 2 m) were taken along the transect, each sampling a homogenous area of vegetation with a depth difference less than 20 cm. At least one relevé was sampled in each distinct vegetation zone, and with every increase in depth of 1 m and/or horizontal distance of 20 m. Field measurements included species composition and cover, euphotic depth, transect and relevé positions.

- The 2007 survey of Lough Bane was designed to produce an accurate map of marginal and submerged vegetation, and a total of seven transects and two additional marginal vegetation samples, were examined (Roden, 2008). At White Lough and Lough Lene, the control sites, three and one transects, respectively, were surveyed (Roden, 2008).
- Mapping the submerged vegetation was also an aim of the 2011 survey, so a larger number of samples (more than 400 relevés) were taken from a large number of transects (Roden & Murphy, 2013).
- In 2012 and 2018, at least two transects were sampled per lake.
- Methods for the 2009 east Clare survey differed slightly in that line transects were examined rather than relevés, and only a single transect was sampled in each lake (Bruinsma *et al*., 2009).

Macrophyte specimens were taken, where necessary, for determination. All taxa were determined to species level with the exception of the cyanobacterial crust (see Doddy *et al*. 2019a).

2.3 Physico-chemical data

Data for total phosphorus, water colour and alkalinity were available for most lakes from the EPA monitoring programme. To provide a general estimate of nutrient concentrations and alkalinity values over the sampling period, the data for 2010–2016 were averaged to give mean figures for each lake. For Cooloorta and Finn Loughs, two samples were collected at geographically separated areas in each lake in 2016, and analysed in a commercial laboratory (Glan-Uisce Teo, Galway), as EPA data were not available.

2.4 Data analyses

Vegetation analyses used data for all 25 lakes surveyed in 2012 (survey 4) and the 10 lakes surveyed in 2018 (survey 5). Vegetation units were determined using cluster analysis, with groups distinguished at the 50% similarity level. Indicator species analysis was then used to define the members of each species group with the method of Dufrêne and Legendre. Relevé data from 2012 and 2018 surveys were analysed separately.

Analyses of vegetation and environmental drivers, including species depth distribution, used data for the 29 lakes emboldened in Table 2 from all surveys (1-6). Vegetation data collected in 2012 and 2018 (surveys 4 and 5) were not included in these analyses where

1. There were no corresponding water chemistry data for the lake or
2. The lake was a coastal 'machair' lake, where the influence of the sea likely leads to a naturally different water chemistry; machair lakes are also naturally shallow; and
3. Data from Lough Carra were not used in some analyses, as the lake is very complex with several basins differing greatly in ecological quality, so average lake values were thought to be of limited use.

The key vegetation metrics derived were euphotic depth, the number of vegetation zones, number of charophyte species, and relative cover of charophytes, crust and vascular plants and these were calculated as the averages across all transects in a lake. An additional metric, the charophyte and cyanophyte crust ('krustenstein') score (C&K score) was also calculated for each lake. The C&K score is a measure of the combined cover of charophytes and cyanophyte crust as a proportion of the total vegetation cover (cyanophyte crust, charophytes bryophytes and vascular plants). While cyanophyte/cyanobacterial crust is a very important component of the highest quality marl lakes (Doddy *et al*., 2019a), it is restricted to shallow waters and has low cover relative to charophytes. In practice, therefore, the addition of crust cover to the charophyte cover does not greatly increase the C&K score. Similarly, bryophytes have limited extent in most marl lakes, so the remaining fraction (*i.e.* the inverse of the C&K score) is effectively the proportionate cover of vascular plants. Roden *et al*. (2020) provide further information on all vegetation metrics.

As noted in Section 2.3, the available EPA physico-chemical data for 2010–2016 were averaged for each lake. An environmental index was created by combining values for total phosphorus and water colour, by multiplying average concentrations for each (see also Roden *et al*., 2020).

Graphs were prepared using the Mac OSx programme Datagraph. Multivariate analyses were performed using PC-ORD version 6. A principal components analysis was run using vegetation and environmental data.

3 Results

Appendix I provides the main summary vegetation and water chemistry data for the 29 lakes used in the analyses of environmental supporting conditions. The values give are averages across all transects and physico-chemical samples for each lake. As the EPA water chemistry dataset covered the period 2010-2016, the vegetation data presented in Appendix I are for 2011 and 2012, rather than 2018. Appendix I also provides the abbreviations used for lakes in the figures provided.

3.1 Separating marl lakes from other Irish lakes

A comparison of the lakes described in this survey with lakes characterised by *Najas*-type lake vegetation such as *Isoetes lacustris* or *Nitella translucens* (data from Roden *et al*, in prep.) shows a complete separation on the basis of alkalinity (Figure 1). Only two marl lakes, Ballycuirke and Corrib, Co. Galway, have alkalinity < 100 mg/l $CaCO_3$, while none of the soft-water group has alkalinity > 75 mg/l $CaCO_3$. The most alkaline of the soft-water group, Kindrum Lough, Co. Donegal, is of interest because it contains two charophyte species (*Chara rudis* and *Chara curta*) in vegetation otherwise typical of soft-water lakes. Conversely, *Isoetes lacustris* occurs in nearly all the soft-water group and does not occur in any of the marl lakes surveyed.

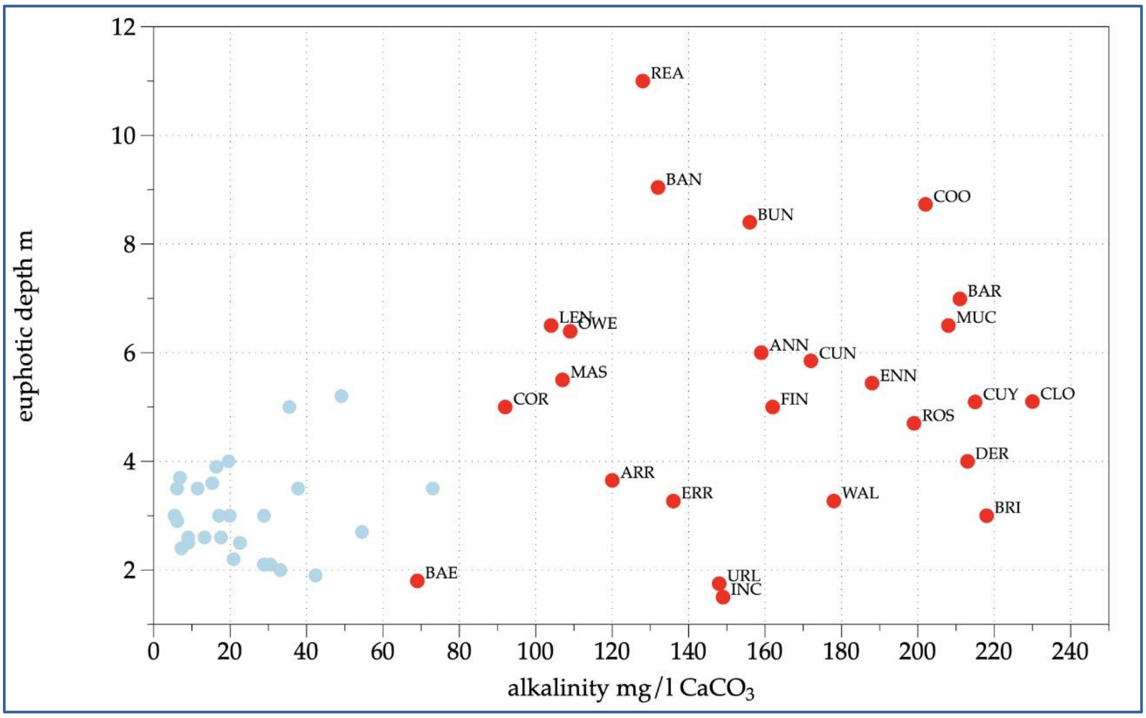

Figure 1 Alkalinity and lake euphotic depth for marl lakes and soft-water (*Najas*) lakes. Labelled red discs show marl lakes, unlabelled blue discs show soft-water or *Najas* lakes (data from Roden *et al.*, in prep.). See Appendix I for key to the lake names used.

Mean euphotic depth is also greater in marl lakes than in the soft-water group (Figure 2). Although the existence of soft-water lakes with greater euphotic depths is very possible, there are few records from Irish lakes. Heuff (1984) notes that the corrie lake Coumshinguan Lough, Co. Waterford, had a Secchi depth of 12.5 m but the actual depth of vegetation was only 5 m.

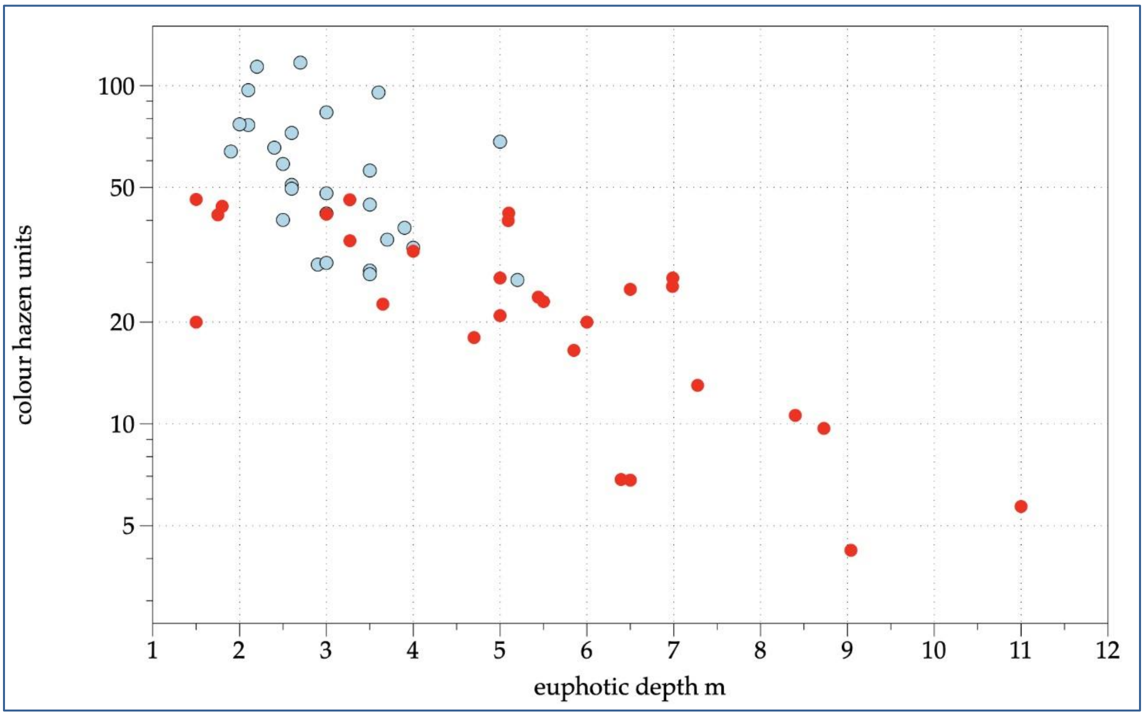

Figure 2 Colour and euphotic depth for marl and soft water lakes. Red discs show marl lakes, blue discs show soft-water or *Najas* lakes.

3.2 The species of marl lakes

Table 3 lists the commonest species in the 2012 and 2018 surveys. In 2012, 22 species accounted for 80% of all records and nine of these were charophytes. In 2018, 16 species accounted for 80% of all records and eight of these were charophytes. Cyanobacterial crust was also abundant in both surveys. The remainder were vascular plants. A very similar group of species was abundant both in 2012 and 2018. The species listed in Table 3 constitute the core flora of the marl lakes surveyed.

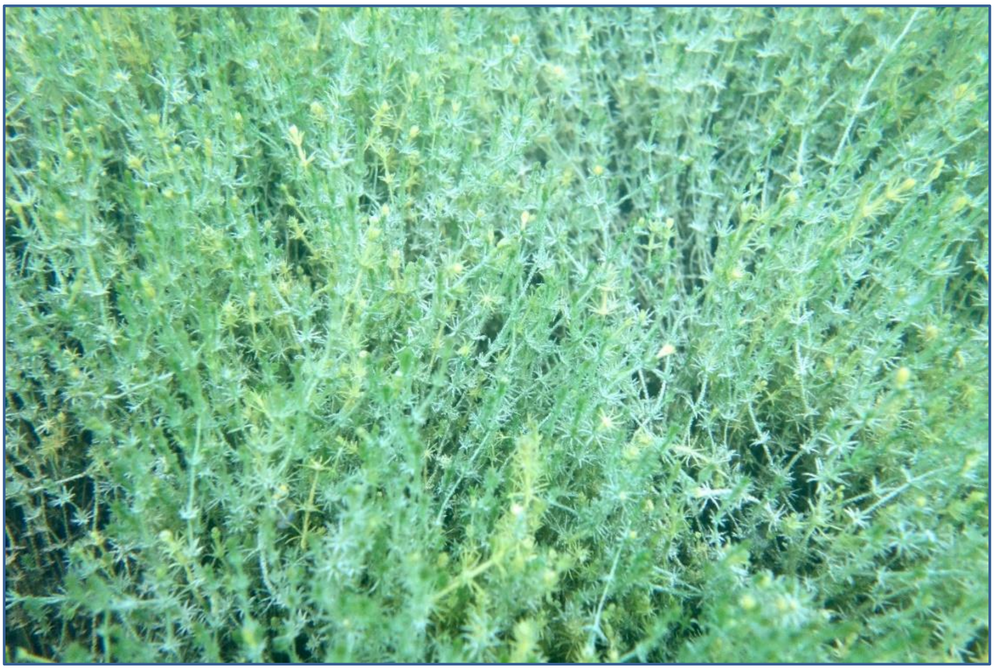

Figure 3 *Chara curta* in a marl lake. See Appendix III site reports for more photographs of marl lake vegetation.

Table 3 The commoner species ranked in order of frequency based on the 2012 survey. Records accounting for 80% of the total of 2,453 records made, are shown. 2018 frequency ranking are shown for comparison. Cum. % is the % total of all records made in the 2012 survey. A record is defined as a species present in a relevé or sample.

Species	number of records	Cum. Total	Cum. %	2012 rank	2018 rank
Chara rudis	278	278	11.3	1	2
Chara curta	236	514	20.5	2	1
Chara virgata	256	770	30.7	3	3
Cyanobacterial crust	149	919	36.6	4	4
Chara contraria	144	1063	42.3	5	7
Chara aculeolata	95	1158	46.1	6	5
Chara tomentosa	83	1241	49.4	7	9
Phragmites australis	72	1313	52.3	8	19
Elodea canadensis	68	1381	55.0	9	11
Schoenoplectus lacustris	68	1449	57.7	10	12
Chara virgata var. *annulata*	67	1516	60.4	11	13
Potamogeton perfoliatus	61	1577	62.8	12	8
Nuphar lutea	60	1637	65.2	13	10
Utricularia vulgaris/australis	59	1696	67.5	14	6
Chara aspera	56	1752	69.8	15	42
Ophrydium versatile	45	1797	71.6	16	30
Myriophyllum verticillatum	39	1836	73.1	17	14
Potamogeton gramineus	34	1870	74.5	18	15
Chara denudata	34	1904	75.8	19	17
Lemna trisulca	39	1943	77.4	20	45
Littorella uniflora	32	1975	78.7	21	27
Myriophyllum alterniflorum	32	2007	79.9	22	16

3.3 Vegetation units in marl lakes

The vegetation data were analysed using cluster analysis and the constituent species of each group distinguished using indicator species analysis. The results of the indicator species analyses for the 2012 and 2018 surveys are provided in Appendix II. Table 4 compares the groups found in both surveys. Figures 4 and 5 show the average depth and euphotic depth of the dominant species in each group in the 2012 and 2018 surveys. A large number of angiosperm species occur as populations confined to one or two lakes. For example *Ceratophyllum demersum* occurs in Finn Lough and Lough Hackett, while *Myriophyllum verticillatum* only occurs in Lough Carra. It is not possible to include such species, when grouping the vegetation of the lakes data set as a whole. Either one treats such populations as unique ecological groupings or regards them as chance additions to the dataset. In marked contrast, most charophyte species and the cyanobacterial crust are found in most lakes of the data set.

Table 4 A comparison of the vegetation units distinguished in the 2012 and 2018 surveys. 'ISA' is Indicator Species Analysis.

proposed vegetation units	2012 survey		2018 survey	
	Group	Species with highest ISA values in each group	Group	Species with highest ISA values in each group
Cyanobacterial crust group	4	Cyanobacterial crust, *Chara virgata* var. *annulata*, *Littorella uniflora*	1	Cyanobacterial crust
Chara curta group	9	*Chara curta*, *Chara aculeolata*, *Chara contraria*	2	*Chara curta*, *Chara aculeolata*
Chara rudis group	2	*Chara rudis*, *Nuphar lutea*	3	*Chara rudis*, *Nuphar lutea*
Potamogeton perfoliatus group	1	*Potamogeton perfoliatus*, *Myriophyllum spicatum*	10, 13	*Potamogeton perfoliatus*, *Nuphar lutea*
Chara virgata group	6	*Chara virgata*	4	*Chara virgata*
Elodea group	10	*Elodea canadensis*, *Lemna trisulca*	5	*Elodea canadensis*, *Lemna trisulca*, Bryophytes, *Hippuris vulgaris*
Chara denudata group	12	*Chara denudata*, *Tolypella glomerata*	6	*Chara denudata*, *Nitella flexilis* agg.

The following groups were distinguished in the cluster analyses and were found in both the 2018 and 2012 data sets.

3.3.1 Cyanobacterial crust

This group is well developed in marl lakes where it covers most hard surfaces. Occasional charophyte species occur, especially *Chara virgata* var. *annulata* and more rarely, plants of *Littorella uniflora*. It is confined to the shallowest water with an average depth of about 1 m.

3.3.2 *Chara curta* group

This group occurs in slightly deeper water than cyanobacterial crust, where it can form a near monoculture over large areas (see Figure 3), however other species such as *Chara tomentosa* and *Chara contraria* may occur. Vascular plants are rare.

3.3.3 *Chara rudis* group

This group, like the *Chara curta* group, can form near monocultures, but it often contains some vascular plant species especially *Nuphar lutea* and *Schoenoplectus lacustris*. In marl lakes with a central doline, *Chara rudis* and associated vascular plants can occur along the break in slope at a depth of 2-3 m. In Lough Rea and Lough Owel, the *Chara rudis* group is often replaced by stands of *Chara contraria*. Conversely, in lakes with a reduced euphotic depth, the *Chara rudis* group can be the only charophyte vegetation present.

3.3.4 *Chara virgata* group

This group occurs at depths at 5 m and deeper. It contains few associate species, other than occasional mixed stands with *Chara contraria* or *Chara denudata*.

3.3.5 *Potamogeton perfoliatus* group

This is not a widespread grouping and is commonest in machair loughs rather than marl lakes, however occasional plants occur in the *Chara rudis* group, especially in lakes with shallower euphotic depths.

3.3.6 *Elodea* group

This group is more typical of lakes with shallower euphotic depths, *Elodea canadensis* is the most widespread member but *Lemna trisulca* occurs in lakes with euphotic depth < 7 m.

3.3.7 *Chara denudata* group

Chara denudata is found at the bottom of the euphotic zone in a minority of marl lakes (Lough Owel, Lough Carra, and Lough Corrib). Perhaps significantly, the other species in this group, *Nitella flexilis* and *Tolypella glomerata*, are also charophytes that lack a cortex along the main axes. This may be an adaption to low light.

Comparable units or groups were recognised by Roden & Murphy (2013) in Lough Carra, Lough Owel and Lough Bunny in 2011, and by Roden (2008) in Lough Bane.

The relationships between the various dominant species is shown in Figures 4 and 5 which illustrates the average position of each species in relation to depth and euphotic depth in 2012 and 2018. In general, each charophyte group occurs at a characteristic depth, with cyanobacterial crust in the shallowest water followed by the *Chara curta* group, then the *Chara rudis* and *Chara virgata* zones and finally the less common *Chara denudata* zone. An exception is the *Chara contraria* zone. This species, along with *Chara aspera* and *Chara virgata* var. *annulata*, occurs sporadically in shallow water, but *Chara contraria* also occurs at great depth in Lough Rea and Lough Owel. The angiosperm groups are characterised by lower average euphotic depths, compared to charophytes.

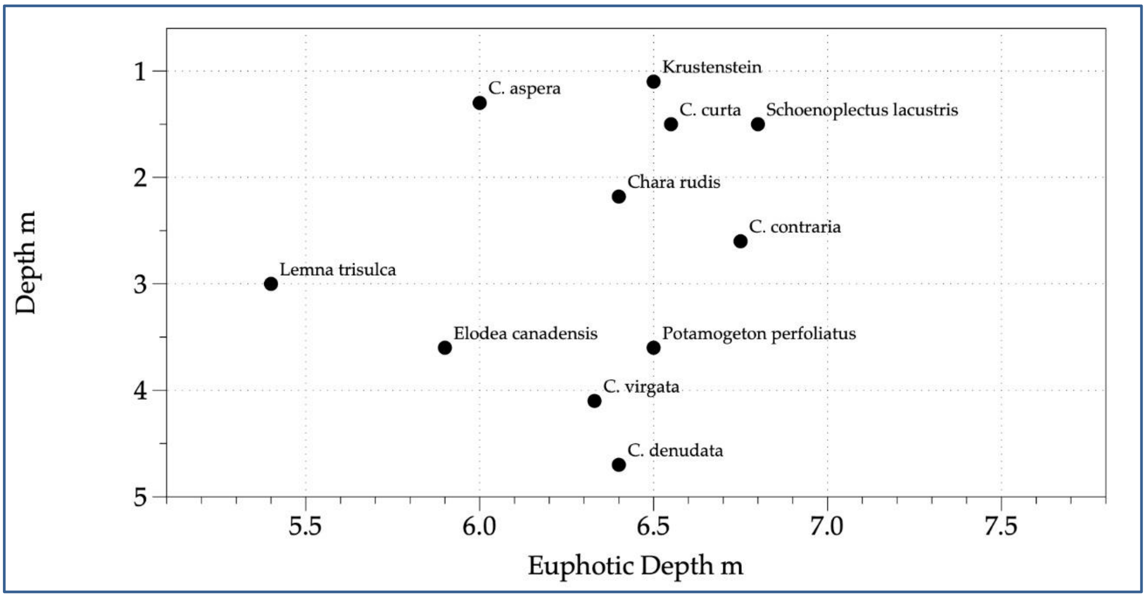

Figure 4 Average depth and euphotic depth for commoner species recorded in the 2012 marl lake survey

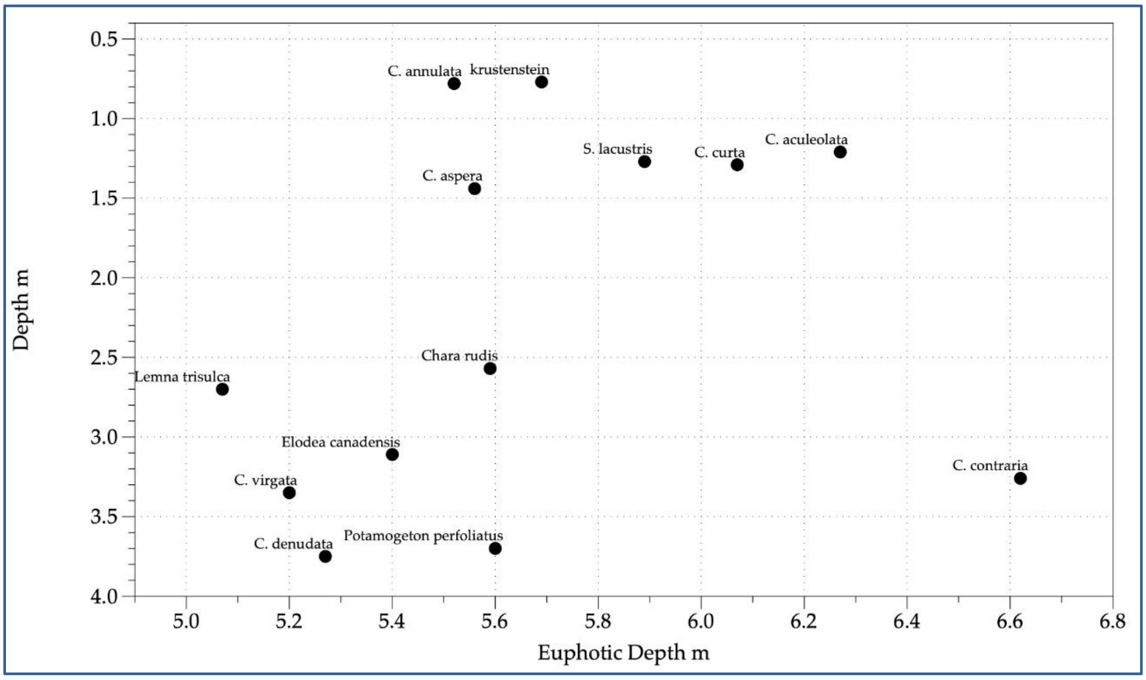

Figure 5 Average depth and euphotic depth for commoner species recorded in the 2018 marl lake survey.

These data can also be visualised by plotting all species records against relevé depth and transect euphotic depth. The distribution of charophyte species, except *Chara hispida* and *Chara vulgaris*, and the more abundant angiosperms are shown (Figures 6 to 9). The diagrams confirm the vertical zonation of charophytes in these lakes and a tendency of angiosperms to be more abundant as lake euphotic depth declines.

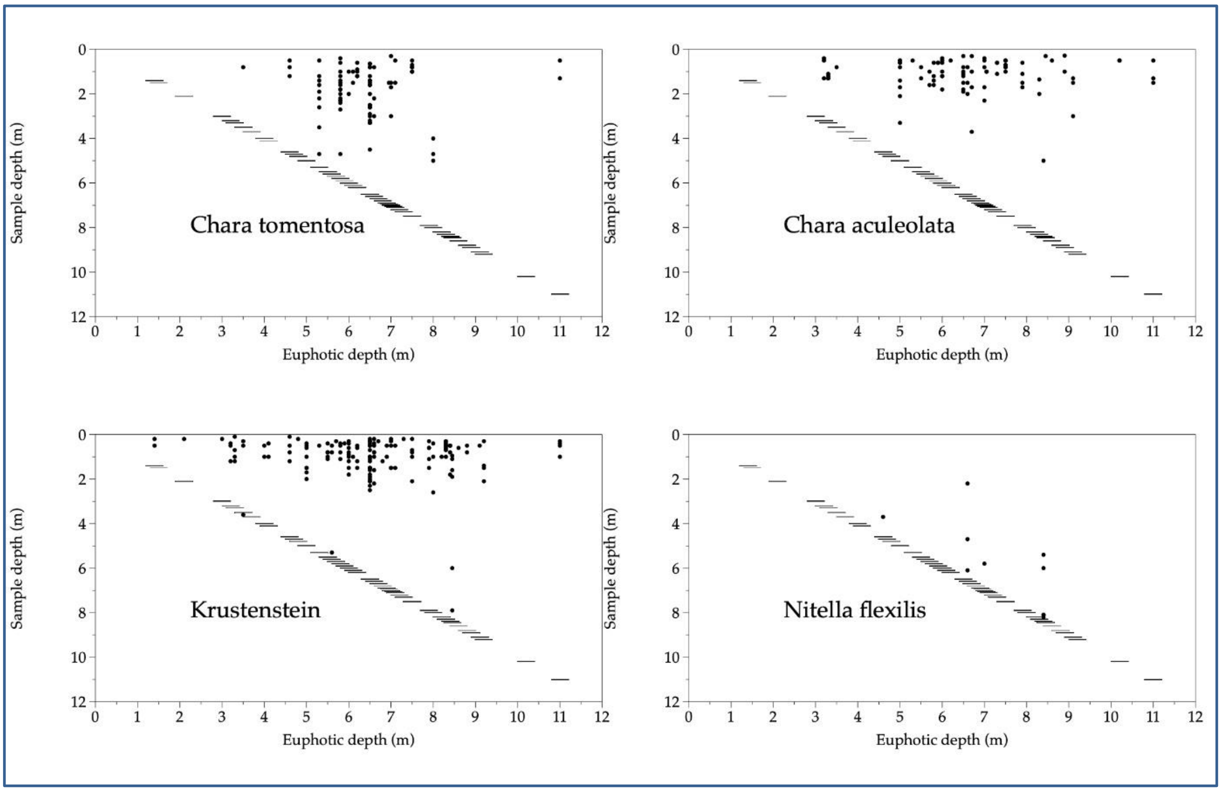

Figure 6 Depth/euphotic depth records for *Chara tomentosa*, *Chara aculeolata*, cyanobacterial crust ('Krustenstein') and *Nitella flexilis* in the 2012 marl lake surveys. Dots represent individual presence records, horizontal lines forming diagonal bar crossing each diagram are euphotic depths of each transect.

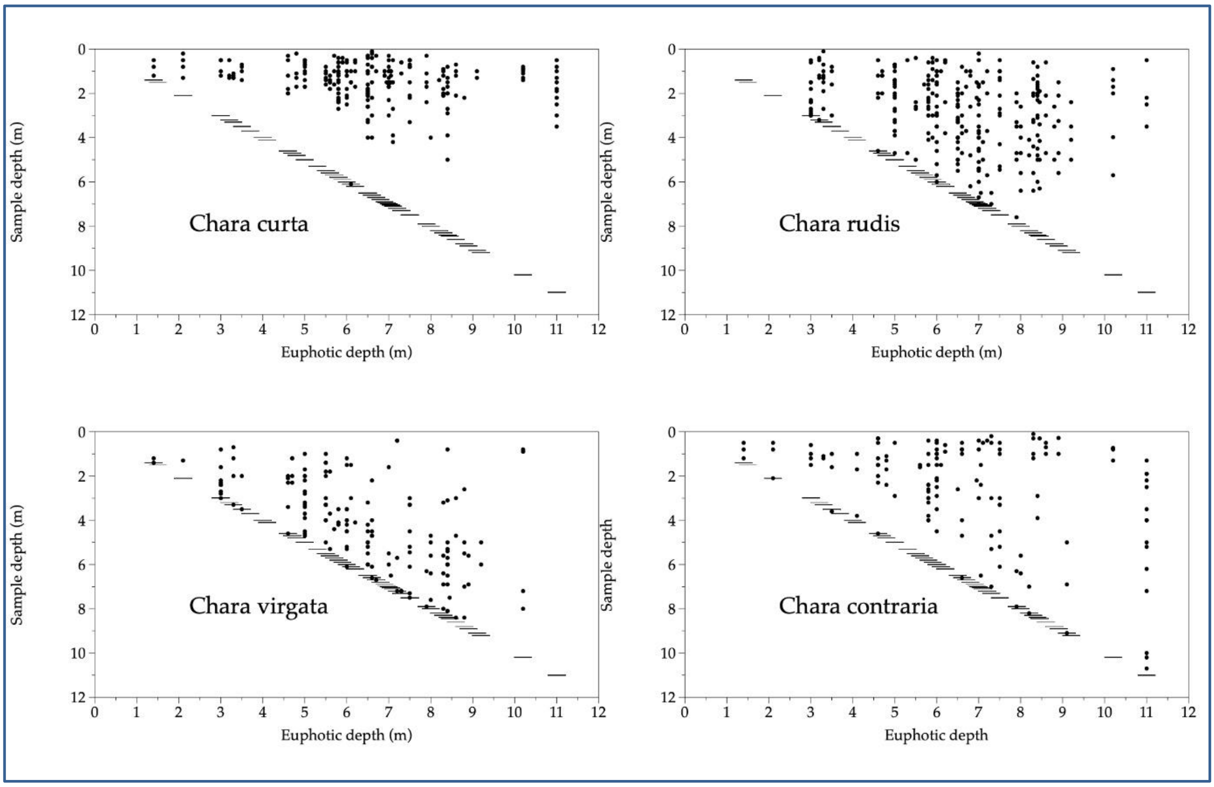

Figure 7 Depth/euphotic depth records for *Chara curta*, *Chara rudis*, *Chara virgata* and *Chara contraria* in the 2012 marl lake surveys. Dots represent individual presence records, horizontal lines forming diagonal bar crossing each diagram are euphotic depths of each transect.

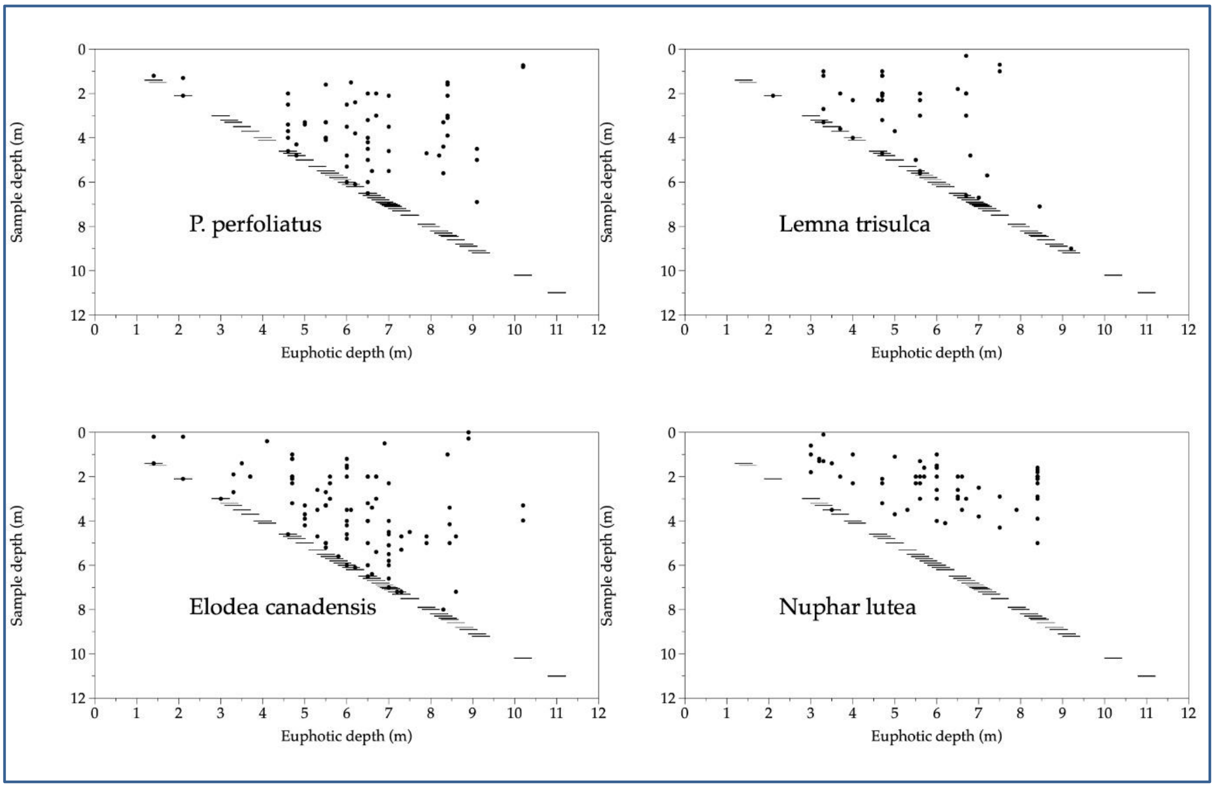

Figure 8 Depth/euphotic depth records for *Potamogeton perfoliatus*, *Lemna trisulca*, *Elodea canadensis* and *Nuphar lutea* in the 2012 marl lake surveys. Dots represent individual presence records, horizontal lines forming diagonal bar crossing each diagram are euphotic depths of each transect.

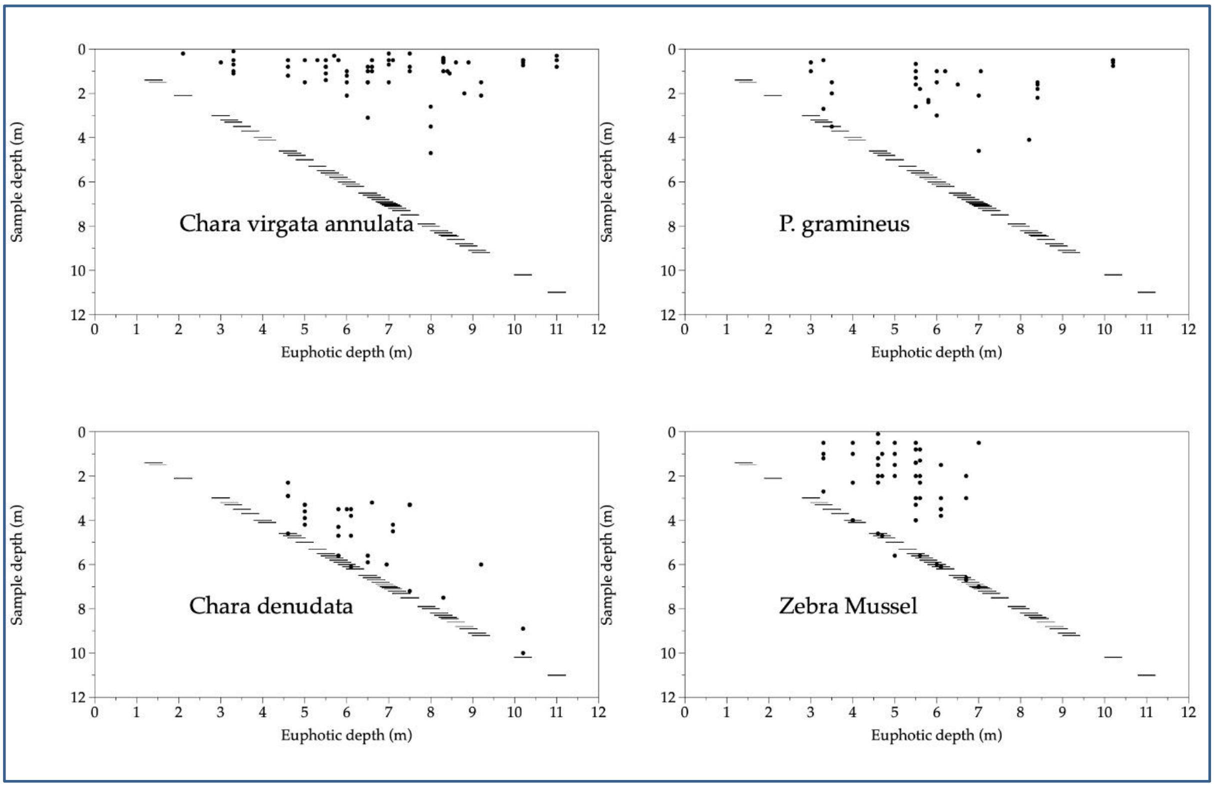

Figure 9 Depth/euphotic depth records for *Chara virgata* var *annulata*, *Potamogeton gramineus*, *Chara denudata* and Zebra Mussel in the 2012 marl lake surveys. Dots represent individual presence records, horizontal lines forming diagonal bar crossing each diagram are euphotic depths of each transect.

Some species occupy a specific depth range along all transects regardless of euphotic depths: some occur in shallow water (0-2m) (cyanobacterial crust, *Chara virgata* var. *annulata*, *Chara aculeolata*); a second group occurs in slightly deeper water (1 - 4 m) (*Chara curta, Potamogeton gramineus*); *Chara rudis* occupies the entire range of depths, except for very shallow and deep water; while *Chara contraria* is even more widespread. For other species, the depth at which they occur increases with euphotic depth: *Nuphar lutea*, *Chara virgata*, *Chara denudata* and *Nitella flexilis*. Certain species appear confined to lakes with euphotic depth of less than seven metres: Zebra Mussel *Dreissena polymorpha*, *Lemna trisulca*.

The diagrams (Figures 6 to 9) also show additional patterns as follows

- Below about 7 m depth, angiosperms are scarce or absent
- Above 7 m, angiosperms can occur to the base of the euphotic depth
- *Chara rudis* shares this distribution
- On transects with a euphotic depth of greater than 7 m, both angiosperms and *Chara rudis* are concentrated in mid water depths between 1 m and 5 m, being replaced by *Chara virgata*, *Chara contraria* or *Chara denudata* in deeper water
- This distribution might be related to a frequent feature of Irish marl lakes: a break in slope between a shallow (1-3 m) shelf and a central deeper doline (> 12 m). We have noted that in certain lakes (*e.g.* Lough Bunny) angiosperms (*Potamogeton perfoliatus*, *Hippuris vulgaris* and *Nuphar lutea*) are confined to this break in slope.

3.4 The relationship between vegetation and lake environment

Several parameters measured in field survey can be expressed quantitatively including number of charophyte species per lake, euphotic depth and proportion of charophytes in total vegetation cover. In turn these values can be compared with quantitative measures of the lake environment including alkalinity, total phosphorus and water colour. In Appendix I these summary data are shown for the lakes in this report. A number of factors were found to be significantly correlated, as detailed in the following sub-sections.

3.4.1 Lake vegetation and euphotic depth

Lakes with a greater euphotic depth have higher charophyte cover in their benthic vegetation (Figure 10). With euphotic depths of 6 m and greater, lakes have charophyte cover above 0.6 (60%). At lower euphotic depths (less than 6 m), charophyte cover falls and charophyte vegetation is absent in lakes with euphotic depth less than 3 m (with the exception of Urlaur Lough). Charophyte cover and euphotic depth are positively correlated ($p < 0.001$). Conversely, vascular plant cover is negatively correlated with euphotic depth ($p < 0.05$) Although a linear regression line is fitted to the data (Figure 10), the relationship between euphotic depth and charophyte cover may also be seen as three patterns or sections: 1) with consistently high charophyte cover at euphotic depths > 6 m; 2) with great variation between 3 m and 6 m; and 3) no charophyte cover below 3 m euphotic depth. The outliers of Urlaur, Errit, Walshpool are discussed below.

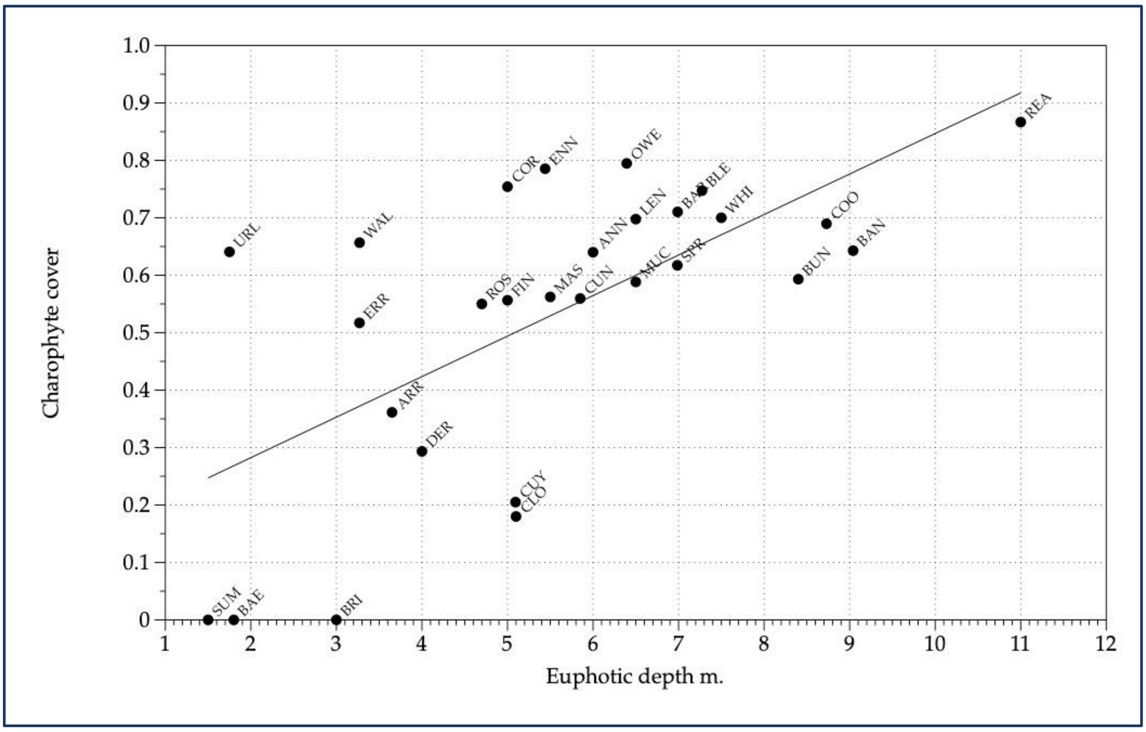

Figure 10 Lake average charophyte cover plotted against lake average euphotic depth. See Appendix I for key to the lake names used.

A similar grouping pattern can be seen in charophyte species number (Figure 11), with the number of *Chara* species positively correlated with euphotic depth ($p < 0.001$). As charophytes often form mono-specific stands and occur as vertically zoned bands, not unlike the zonation of seaweed on a rocky shore, this correlation reflects the increasing number of charophyte zones with increasing euphotic depth. Figures 6 to 9 show that when euphotic depth is greater than 7 m, only *Chara virgata*, *Chara contraria*, *Chara denudata* or *Nitella flexilis* occur at the base of the euphotic zone. When euphotic depth is less than 7 m, *Chara rudis* and several vascular plants can occur at the base of the euphotic zone and the lower

Chara virgata zone is often absent or very reduced. Consequently, the full sequence of cyanobacterial crust and charophyte zones tends to only occur in lakes with euphotic depth > 6 m.

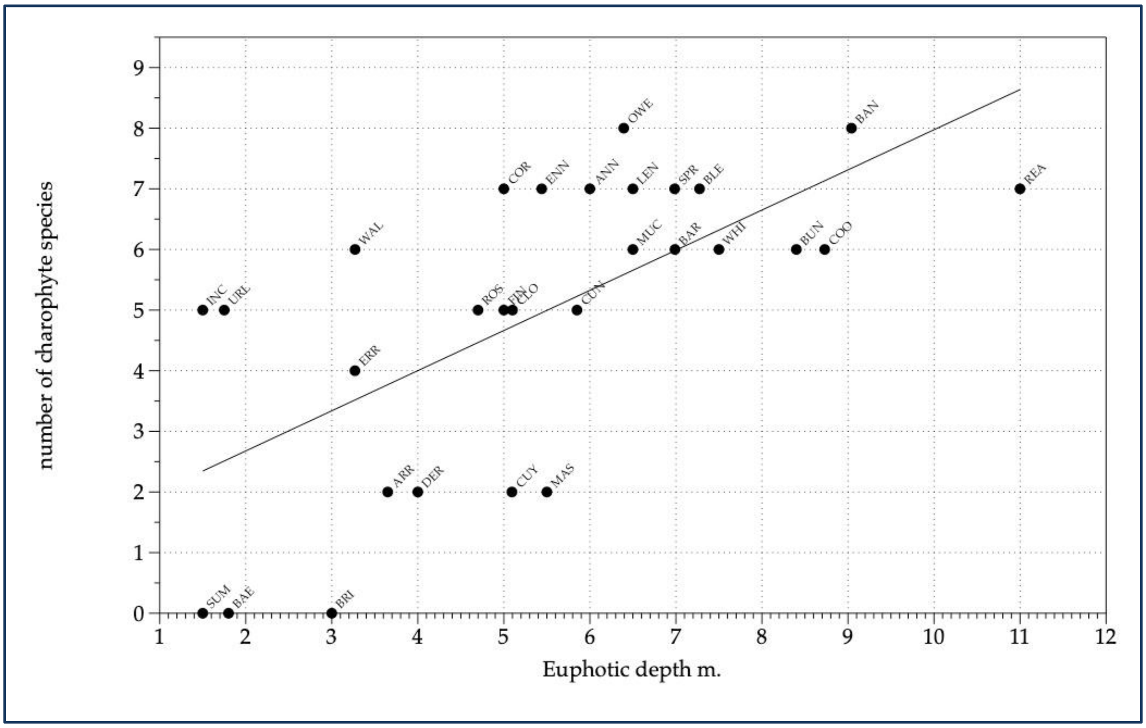

Figure 11 Lake charophyte species number plotted against lake average euphotic depth. See Appendix I for key to the lake names used.

Combining these results, it can be seen that lakes with clear water (large euphotic depth), high charophyte cover, few angiosperms and many charophyte species can be contrasted to lakes with many vascular plants, low charophyte cover and species number and shallow euphotic depth. A comparison between Lough Rea and Cooloorta, on the one hand, and Cullaunyheeda and Arrow, on the other, illustrates the differences between sites (see Figures 10, 11 and 12, and Appendix III site reports). At one extreme, euphotic depth exceeds 10 m, at least five charophyte species are recorded, and few angiosperms occur. In contrast, in the second group, euphotic depth is less than 5 m, only two species of charophyte are recorded and angiosperms are common.

Figure 12 shows a PCA diagram of the data presented in Appendix I. The analysis demonstrates an inverse relationship between euphotic depth, number of vegetation zones, charophyte species number and charophyte cover on the one hand and angiosperm cover, total phosphorus and water colour on the other hand. These relationships confirm the patterns discussed above. The diagram also shows the relationships between the lakes included in the analysis. These fall roughly along a gradient parallel to the angiosperm cover and euphotic depth vectors.

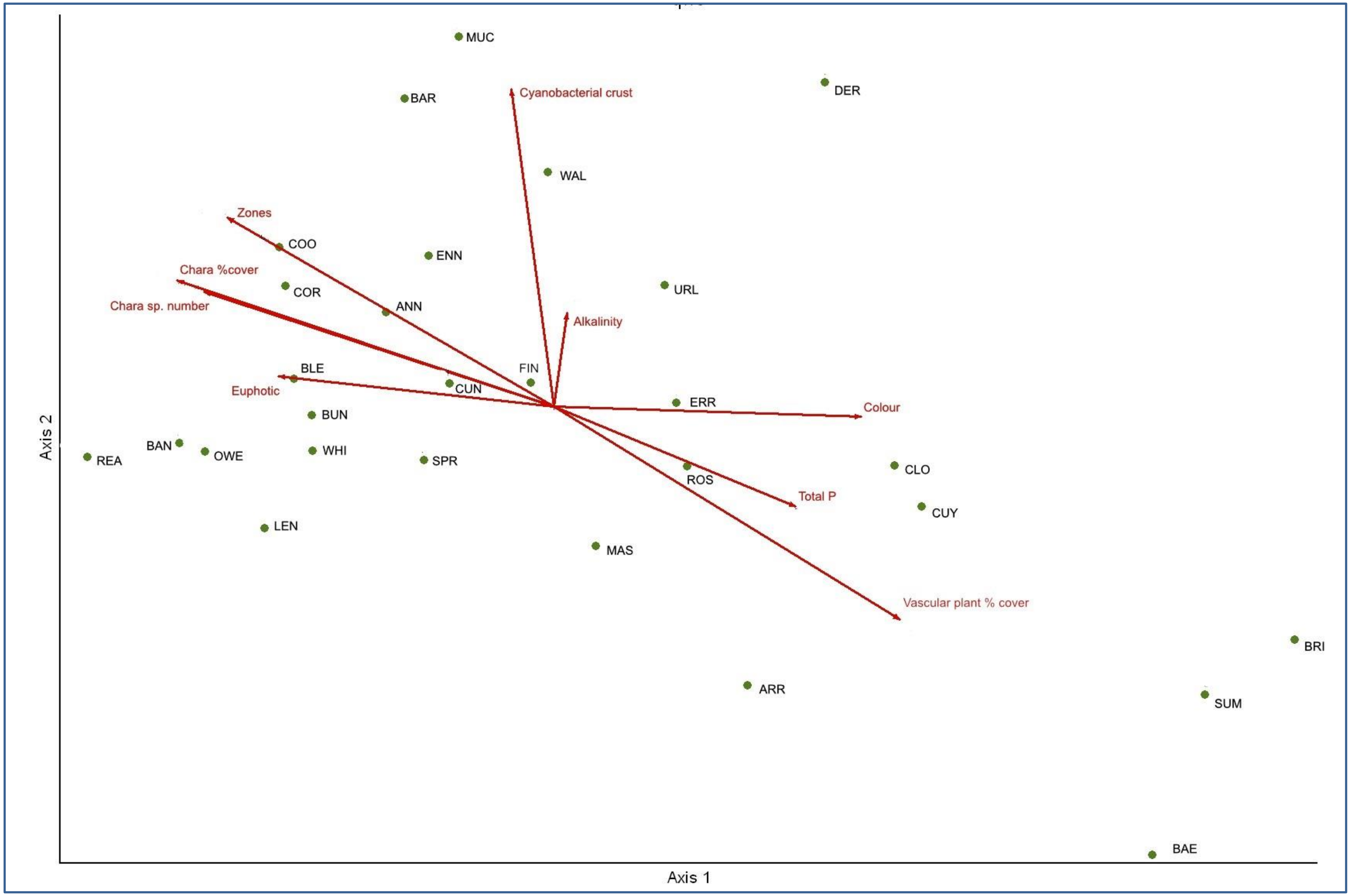

Figure 12 Principal Components Analysis (PCA) of surveyed lakes based on vegetation and environmental data (see Appendix I). Axis 1 accounts for 61.4 % of total variation while axis 2 accounts for 14%. Eigenvaules for axes 1, 2 and 3 are 5.529, 1.26 and 0.976, respectively.

3.4.2 Lake vegetation and water colour

Water colour (*i.e.* the dissolved light-absorbing compounds, as opposed to particulate matter) is negatively correlated ($p < 0.001$) with euphotic depth (Figure 13), charophyte cover (Figure 14) and charophyte species number (Figure 15). Vascular plant cover is positively correlated with water colour ($p < 0.01$). Figure 13 shows that lakes with euphotic depth greater than 6 m have colour less than 20 Hazen units. The clearest water is found in Lough Bane with colour less than 5 Hazen units, while Summerhill Lough has colour of 46 Hazen units.

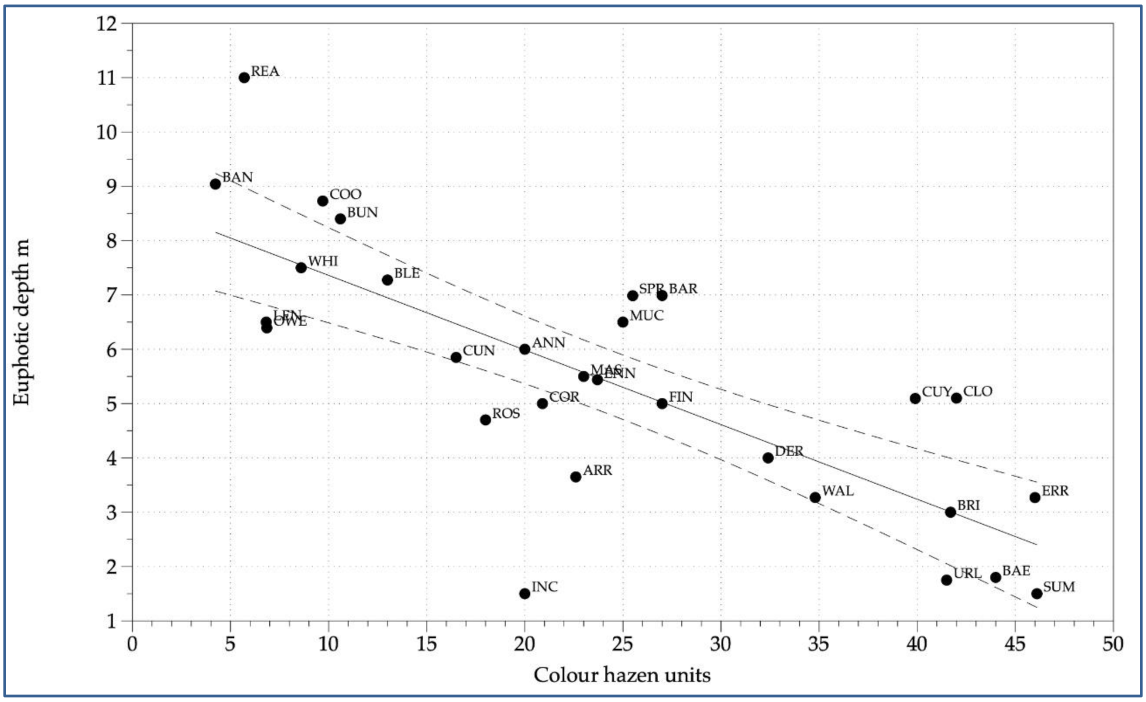

Figure 13 Average euphotic depth plotted against average lake water colour. 95%confidence limits shown. See Appendix I for key to the lake names used.

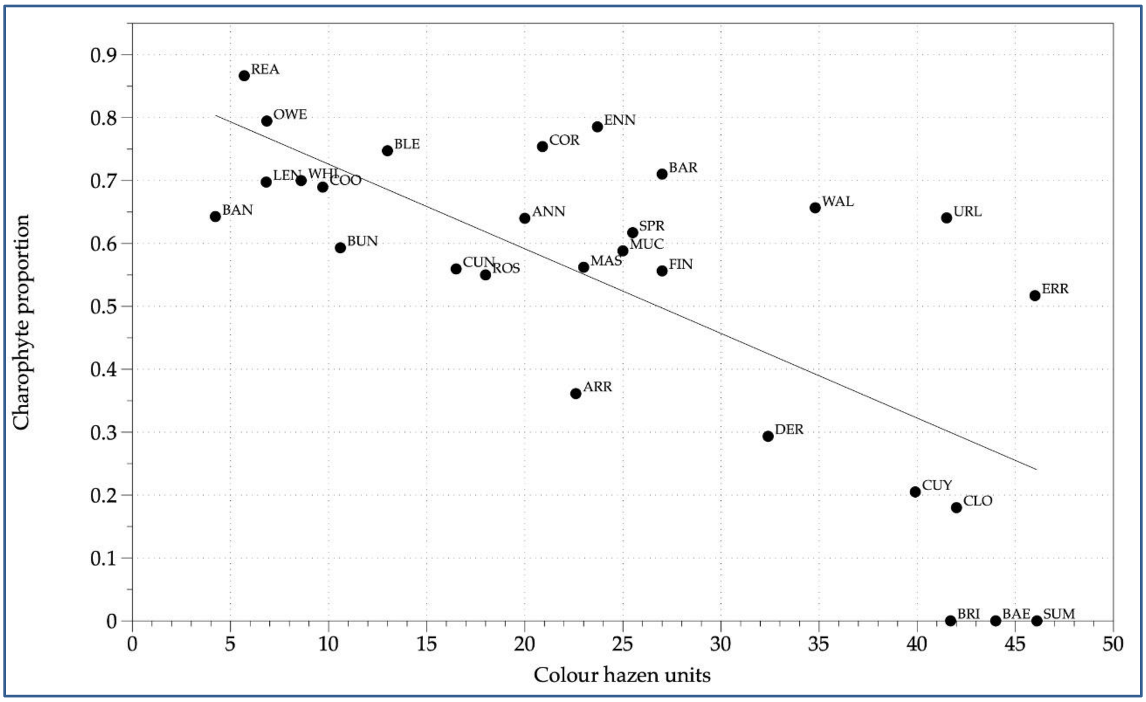

Figure 14 Charophyte cover, as a proportion, plotted against average lake water colour.

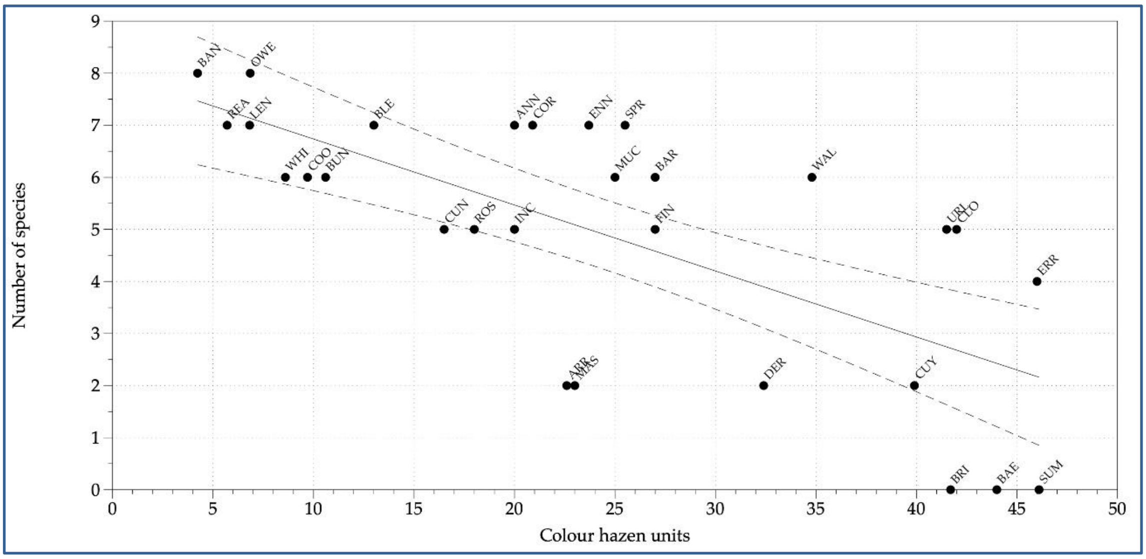

Figure 15 Number of charophyte species plotted against average lake water colour. See Appendix I for key to the lake names used.

3.4.3 Lake vegetation and total phosphorus

As in the case of water colour, euphotic depth, charophyte cover and charophyte species number are inversely related to lake total phosphorus (TP) ($p < 0.001$) (Figures 16, 17 and 18). The better fit of the power regression than the linear regression shown in Figure 16 implies that euphotic depth is more sensitive to changes in total phosphorus below 0.01 mg/l than at higher concentrations. Vascular plant cover is positively correlated ($p < 0.01$) to total phosphorus. It is notable that all lakes with total phosphorus < 0.01 mg/l have euphotic depth greater than 5.0 m, with the exception of Walshpool and Errit Loughs (Figure 16). These high-colour lakes have markedly low euphotic depths but also low values of total phosphorus.

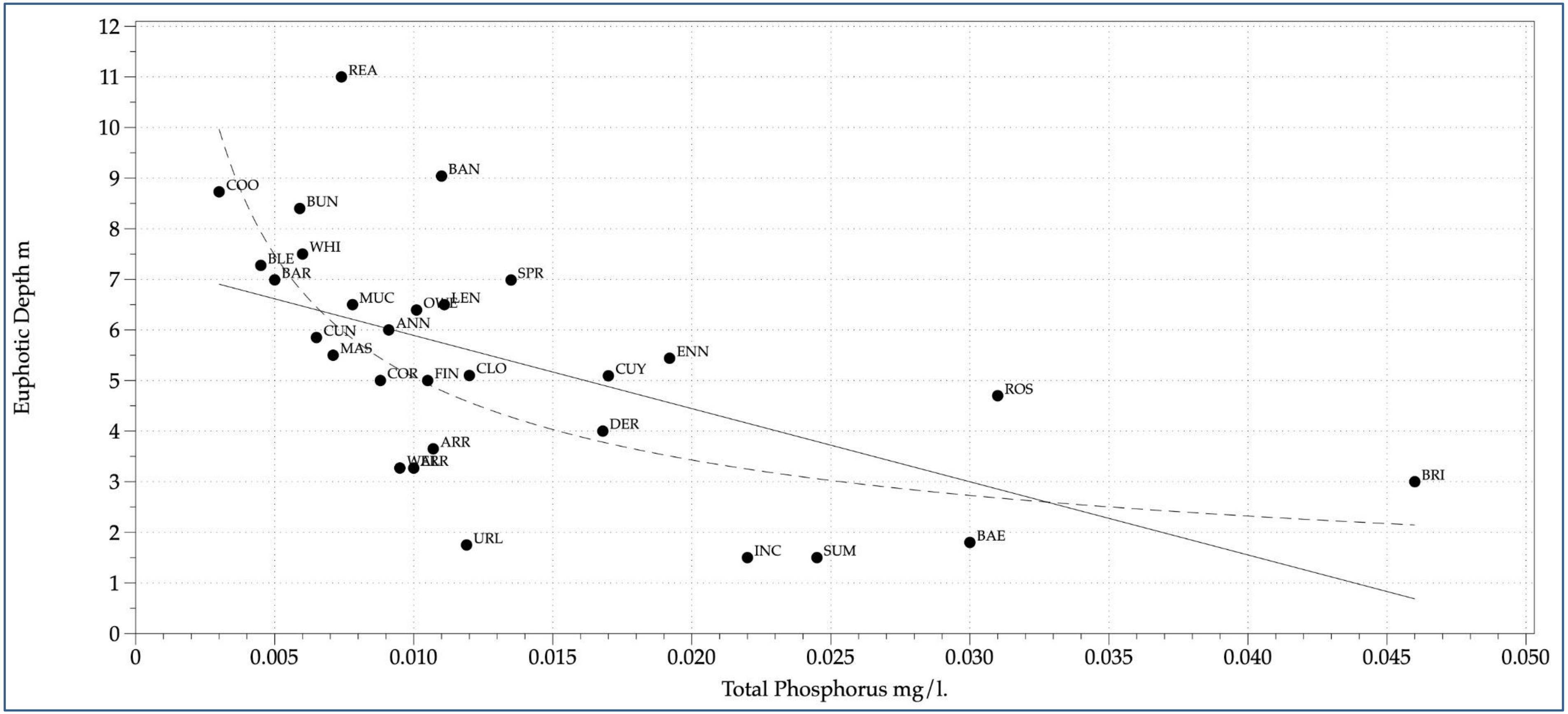

Figure 16 Average euphotic depth plotted against average lake total phosphorus. The straight line represents a linear regression of the data (r = 0.59), while the dashed line represents a power function regression (r = 0.66). See Appendix I for key to the lake names used.

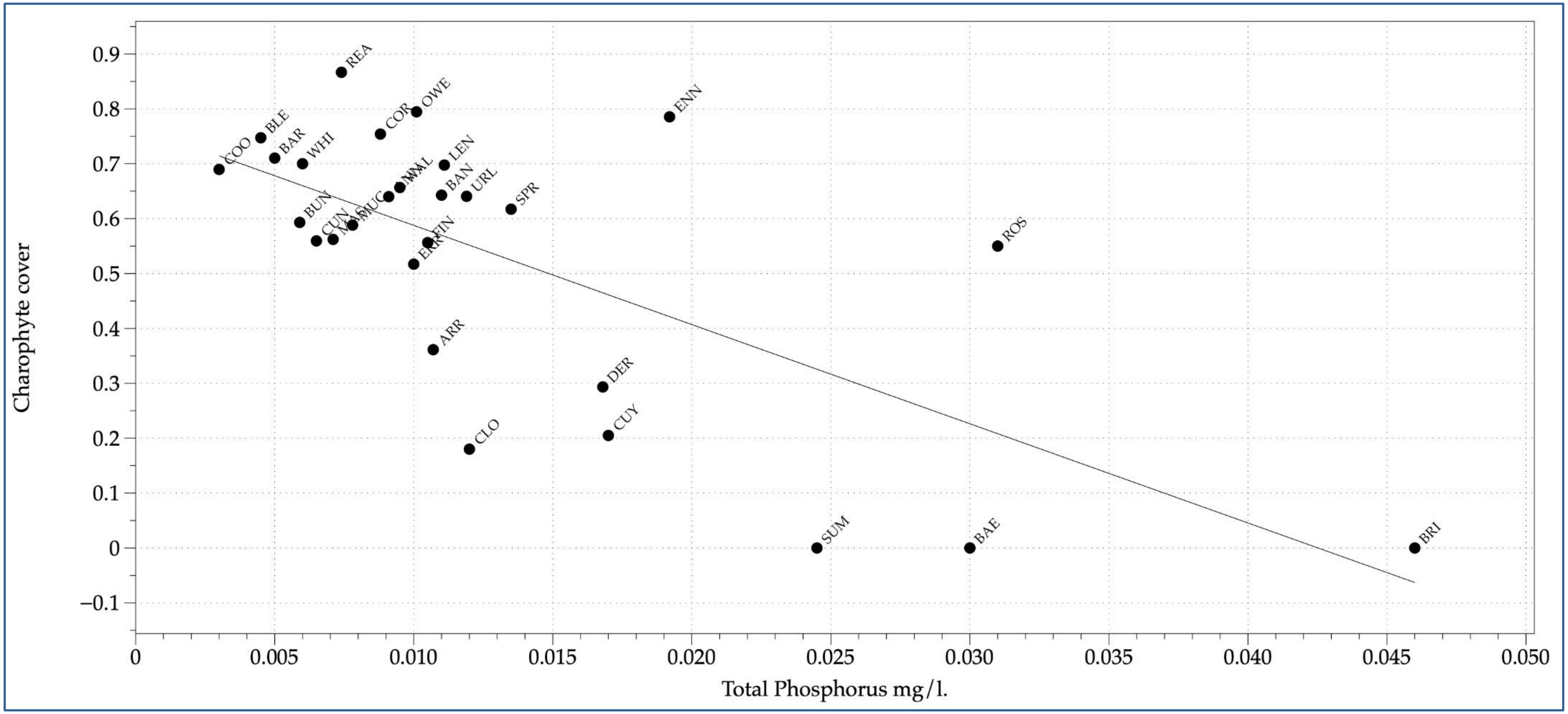

Figure 17 Charophyte cover, as a proportion, plotted against average lake total phosphorus. See Appendix I for key to the lake names used.

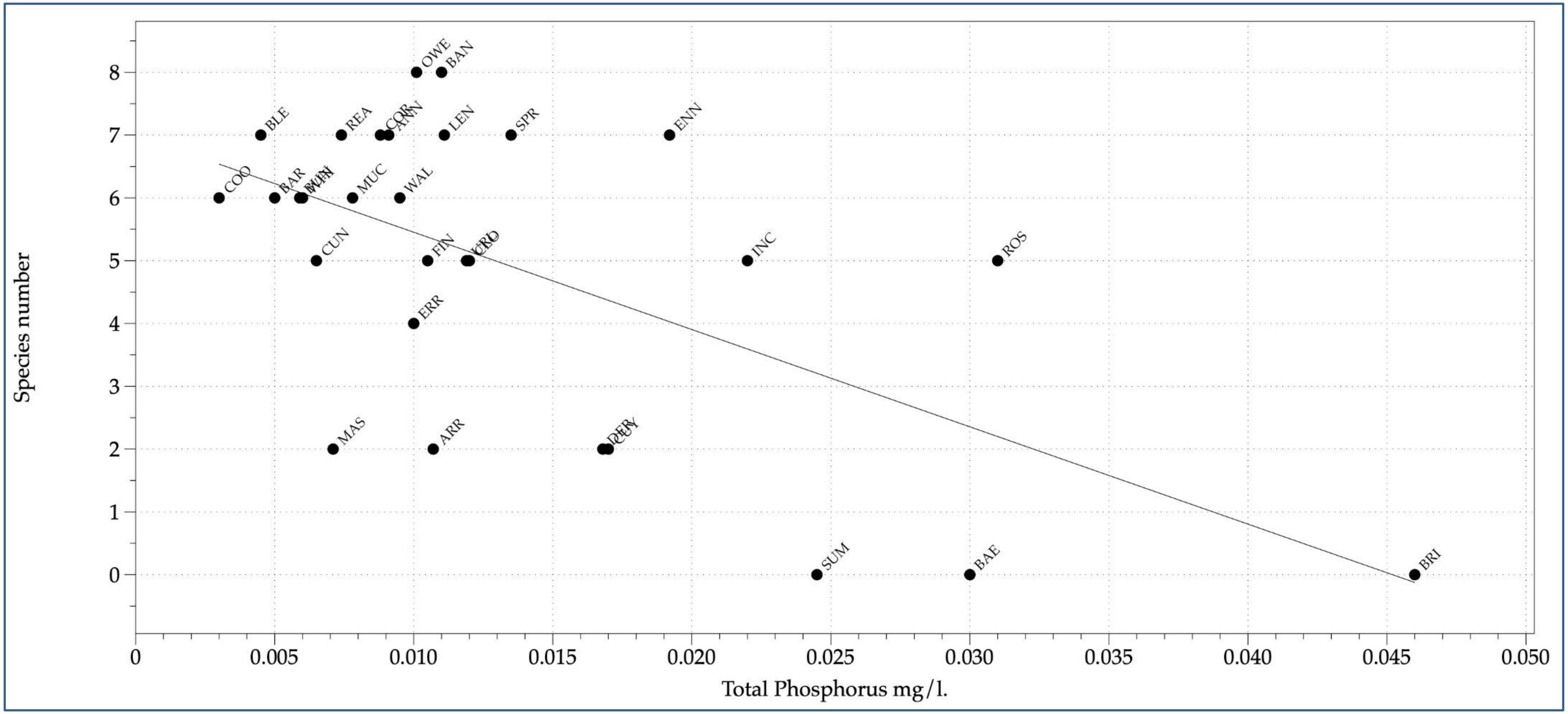

Figure 18 Number of charophyte species plotted against average lake total phosphorus. See Appendix I for key to the lake names used.

3.4.4 Relationship between total phosphorus and colour

Lakes with high charophyte diversity and cover and a deep euphotic zone have both low values for water colour and total phosphorus (Figure 19). Conversely, lakes with shallow euphotic zones and high vascular plant cover have higher values for colour and total phosphorus. But these environmental factors do not always co-vary, thus Walshpool, Urlaur and Errit have high colour (> 40 Hazen units) but low total phosphorus (< 0.12 mg/l), while Rosroe and Ennel have high total phosphorus but lower colour.

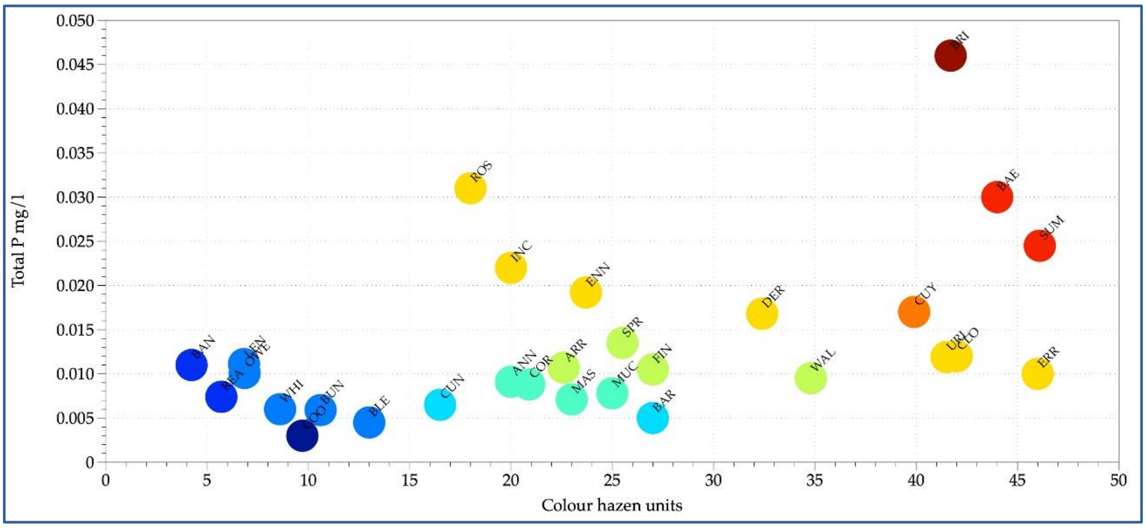

Figure 19 Water colour plotted against lake total phosphorus. See Figure 20 for further information on colours, which reflect the Index (TP × Colour) and Appendix I for key to the lake names used.

Euphotic depth, charophyte species number and charophyte cover are all measures of lake macrophyte quality. As seen above, total phosphorus and water colour show significant correlations with these measures of vegetation structure. This indicates that vegetation structure is influenced by both total phosphorus and water colour. Most lakes have either high colour and high total phosphorus, or low total phosphorus and low colour, but some outliers have high colour but low total phosphorus (Walshpool, Urlaur and Errit). Few lakes have high total phosphorus but low colour, possibly indicating the lake colour is not independent of total phosphorus.

An index of macrophyte quality can be proposed by combining total phosphorus and colour, as follows

$$\text{Index} = \text{TP (in mg/l)} \times \text{Colour (in Hazen Units)}$$

In Figure 20, the natural log of this index is plotted against lake euphotic depth, showing a highly significant correlation ($p < 0.001$) among the variables. This relationship indicates that marl lake vegetation structure as measured by euphotic depth is determined, in large part, by a combination of lake total phosphorus and water colour.

The index is also significantly correlated ($p < 0.01$) with lake charophyte species number and proportion of charophyte cover. A plot of charophyte cover against the natural log of the Index (Figure 21) however, shows a discontinuity in the relationship. Cover remains high (> 0.6) up to ln Index values of -1.0 but above a value of -0.5 collapses to near zero. This reflects a dramatic visual change in lake appearance from clear water charophyte and cyanobacterial crust dominance to darker water and vascular plant dominance. An interesting possibility is that this change is an example of alternative lake stable states as explored by Scheffer (2004) and others.

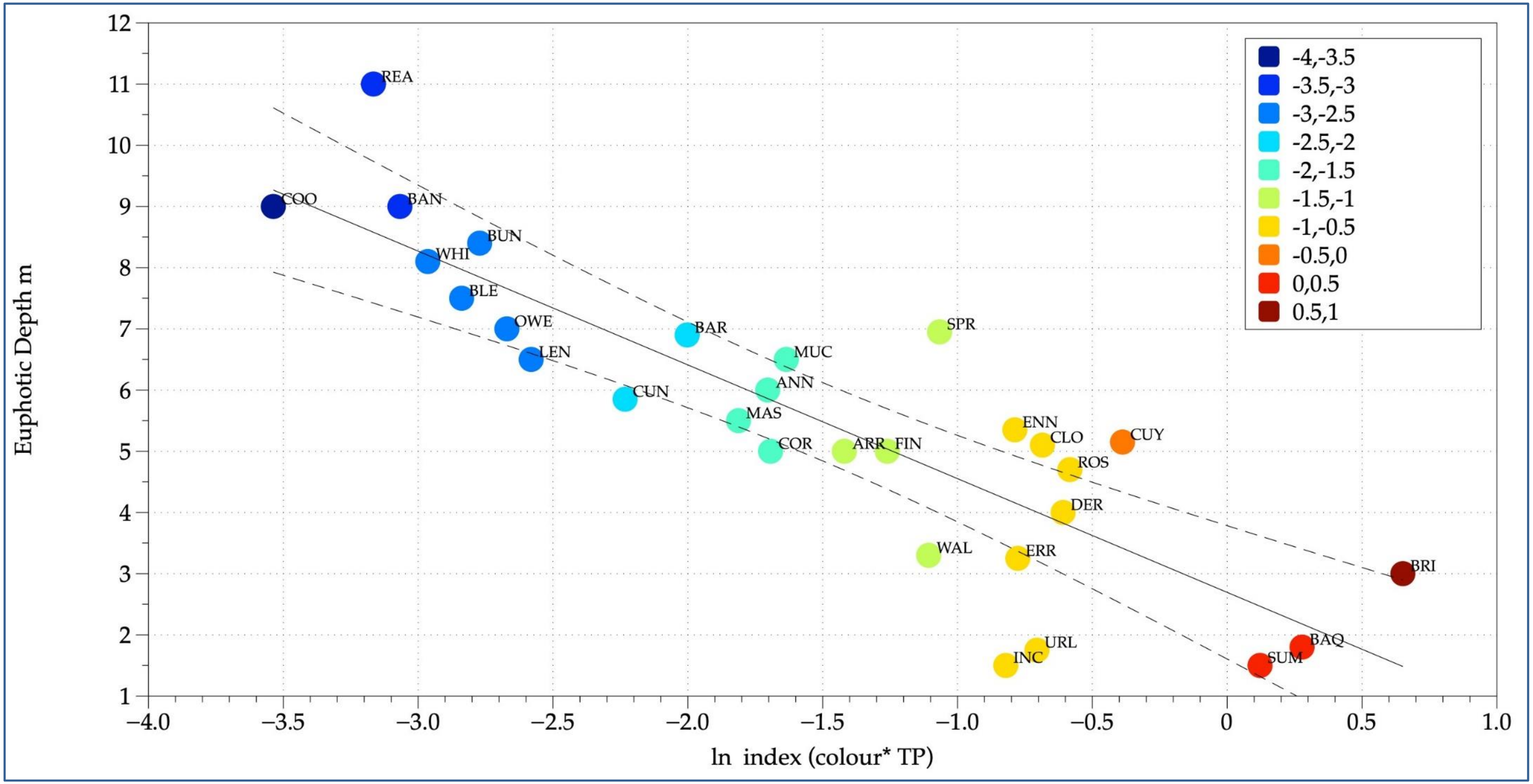

Figure 20 Average euphotic depth plotted against the log of the environmental quality index (TP × Colour). Note log scale on X-axis. Colour reflects a range of 0.5 log index units as shown on the X-axis. See Appendix I for key to the lake names used.

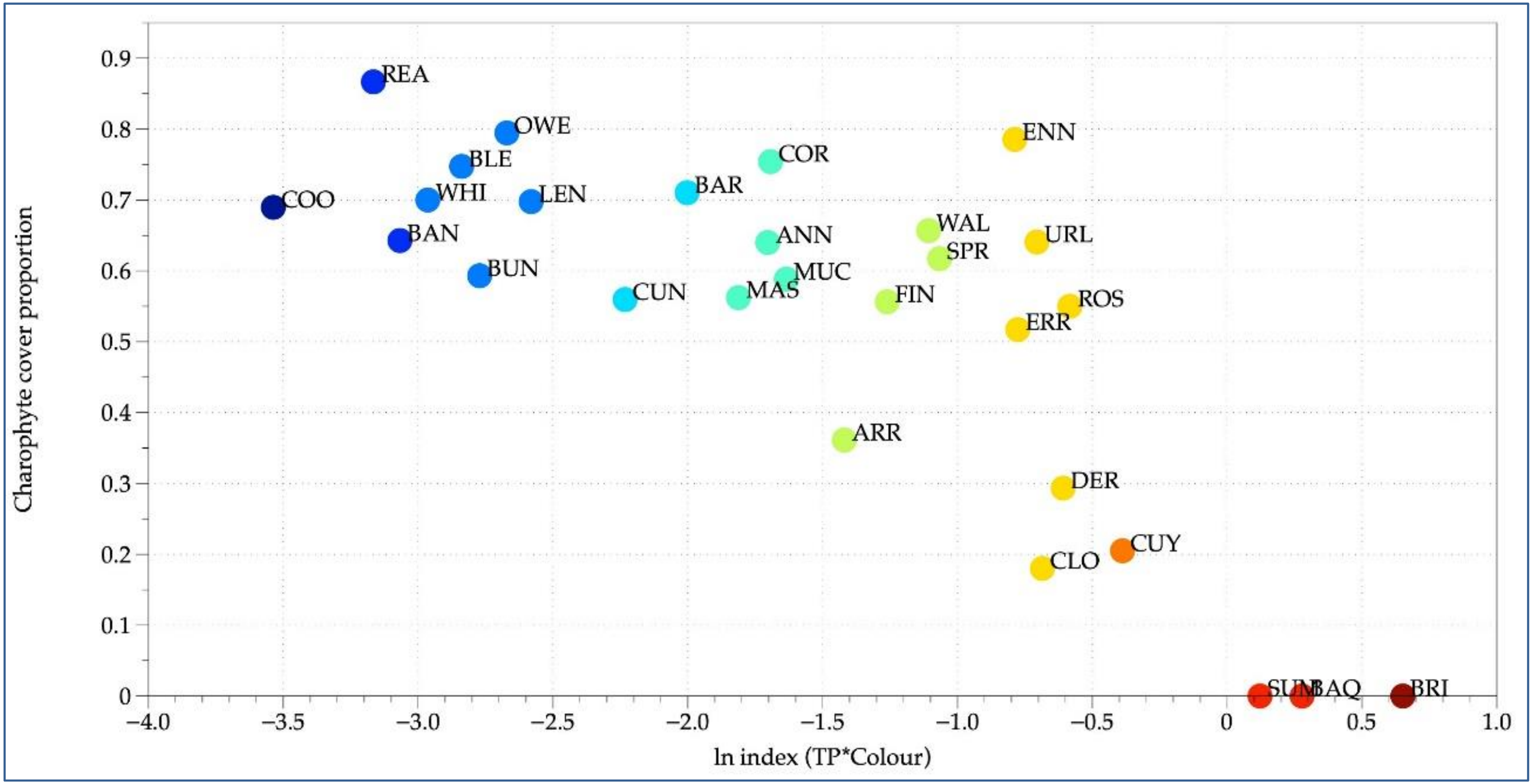

Figure 21 Charophyte cover, as a proportion, plotted against the log of the environmental quality index (TP × Colour). See Appendix I for key to the lake names used.

4 Discussion

4.1 Euphotic depth

There have been many studies of Irish marl lakes but the great majority have not used snorkel or scuba to make direct observations of the macrophyte flora. Previous snorkel/scuba surveys include Heuff (1984) and John *et al.* (1982). The studies described in this report, thus, provide new data on species colonisation and species composition as a function of depth in Irish marl lakes. The report also provides data that will help define marl lake reference conditions based on existing lakes, rather than inferring such conditions through palaeolimnological studies (*e.g.* Wiik *et al*., 2014), as is necessary in regions where eutrophication has damaged most existing sites and, consequently, lakes with large euphotic depths are rare.

The most striking finding is the great euphotic depth of some lakes, the best examples being Lough Rea and Cooloorta Lough where depths > 10 m were measured. Previous estimates, largely based on grapnel samples, appear to underestimate the euphotic depth of marl lakes (*e.g.* Free *et al*., 2006). However Spence (1967) records a euphotic depth for Loch Borralie (Scotland) of 12-15 m and Wiik *et al*. (2015a) infers a former euphotic depth for Cunswick Water (northwest England) of 10 m. As euphotic depth is used both to define lake type and Water Framework Directive 'Ecological Status', an underestimate of euphotic depth may result in misclassification and misunderstanding of a lake's ecological condition. There are two possible reasons for this underestimation: firstly, the inherent difficulty of estimating the parameter from the lake surface using a grapnel; and, secondly, an insufficient range of marl lakes may have been examined in previous studies. The most transparent lakes include several from the Burren karst region which are both small and only accessible on foot.

4.2 Vegetation structure – depth zonation

The report confirmed the well-established tendency for marl lake charophytes to form depth-specific bands (*e.g.* John *et al*., 1982; King & Champ 2000; Roden, 2002), and also demonstrated the near universal presence of a shallow cyanobacterial crust layer in marl lakes. The extent and probable ecological importance of this shallow-water crust in marl lakes is not perhaps fully appreciated, and it is rarely referred to by ecologists. Pentecost (2009) noted its existence in marl lakes, and referred to Austrian and German researchers who found a similar layer in alpine lakes. John *et al*. (1982) were ambiguous about the biological or physical origin of the marl in the shallows of Lough Owel. Kennedy (2012) gave an excellent description of the cyanobacterial crust layer. It also attracted the attention of Robert Lloyd Praeger who sent a sample from Lough Carra to the English phycologist William West (Praeger, 1906). West noted it contained a cyanobacterial flora dominated by *Dasygloea amorpha.* Modern researchers, *e.g.* Pentecost (2009) and Doddy *et al*. (2019a), have said the crust is dominated by *Schizothrix* sp. which resembles *Dasygloea* but has narrower trichomes (Komarek & Anagostidis, 2005). Praeger (1934) noted the very poor angiosperm flora of several marl lakes such as Lough Carra and Lough Corrib, perhaps showing that the lakes were dominated by cyanobacterial crust in shallow water. Free *et al*. (2016), suggested that the role of the *Schizothrix*-dominated marl crust of these lakes is underestimated. Roden (2002) and Roden & Murphy (2013), using snorkel survey, emphasised the extent and frequency of the cyanobacterial crust in Irish marl lakes. While it is mostly found on hard limestone rocks, it can, in some lakes, cover clay and gravel bottoms in shallow water. It can reach thicknesses of 50 cm (*e.g.* Lough Muckanagh) but in polluted areas is overgrown by mosses, green algae and even *Chara vulgaris* (Roden & Murphy, 2013, Doddy 2019a, b). The ecology of the cyanobacterial crust in Ireland has recently been investigated by Philip Doddy (Doddy *et al*., 2019 a, b).

This report has demonstrated the usefulness of snorkel/scuba survey in comprehensive recording of charophyte species present, as well as depth distribution data for characteristic species and zones

(Figures 6 to 9 in Chapter 3). In comparing these data to species records for the lakes made using other methods, it appears that, as well as underestimating euphotic depth, grapnel-based studies may underestimate species number. Species with short growth forms are especially unlikely to be sampled by grapnel or rakes.

It also appears that macrophyte distribution and zonation vary with varying euphotic depth. Thus, lakes with euphotic depths of less than 6 m are characterised by the growth of *Chara rudis* and angiosperms to the base of the lake's euphotic depth. In contrast, when euphotic depth exceeds 7 m, these species are replaced by *Chara virgata*, *Chara contraria* and *Chara denudata* at depth. In addition, angiosperms are uncommon or absent in lakes with euphotic depths > 7 m. An extreme example of this phenomenon is the small doline lakes of the Burren (Cooloorta and Ballyeighter 2 in this study) and Loughs Gealain, Travaun and Aughrim (Roden, 2001). Such lakes are dominated by macroalgae (charophytes) and microbial mats. Their existence is not widely noted in the literature (*e.g*. Moss, 2016) and they appear to deserve further study as a specific type of European lake.

Chara rudis is the most widespread of the charophyte species encountered, forming a mid-depth band in many lakes and occurring at all depths in lakes with low euphotic depth. However in a few high euphotic depth lakes it is scarce. This may indicate that the vertical zoning of charophytes observed in most of the lakes investigated does not occur in lakes with extreme water clarity and euphotic depth.

4.3 Replacement of charophytes with angiosperms as euphotic depth declines

Many of the recorded charophytes are confined to marl lakes and some, such as *Chara rudis*, *Chara denudata* and *Chara curta*, are otherwise scarce or unknown in Ireland (Stewart & Church, 1992). Similarly, the cyanobacterial crust is not otherwise recorded except perhaps in limestone springs or streams. Thus, the dominant flora of the marl lakes is rarely found in other habitats. In contrast the commoner angiosperm species appear to be more generalist or weed species. With the exception of *Myriophyllum verticilliatum*, all are listed by Free *et al*. (2006) as tolerant to total phosphorus and most have very widespread distributions in Irish aquatic habitats, or are introduced species such as *Elodea* (Preston & Croft, 1997). The observed increase of angiosperms with decreasing euphotic depth may be regarded as the displacement of a specialist marl lake flora by more generalist species. There is no evidence that these angiosperm-rich lakes with low euphotic depth contain specialised species not found elsewhere, which is in marked contrast to the high euphotic depth, algal-dominated lakes. Our data showing the predominance of vascular plants in low euphotic depth lakes can be interpreted as showing the invasion of a charophyte/cyanobacterial crust habitat by generalist angiosperms as euphotic depth decreases. This conclusion is supported by the experimental and observational work of Doddy *et al*. (2019a, b) on the replacement of the cyanobacterial crust with increasing concentrations of phosphorus and nitrogen. It is noticeable that the invasive Zebra Mussel is also confined lakes with lower euphotic depth.

These findings largely agree with those of Blindow (1992) who reported that in clear lakes charophytes grew at greater depths than angiosperms, but as lakes became more turbid, charophytes became confined to shallow water, while angiosperms could grow at comparatively greater depths.

Wiik *et al*. (2015b) reconstructed the vegetation history of a small kettle-hole marl lake, Hawes Water, on Carboniferous rock in north-west England, comparable in size and depth to Bleach Lough or Spring Lough. They demonstrated that since 1900 euphotic depth has decreased from 12 m to 4.5 m. In this period charophyte biodiversity declined from about seven widespread species (*Chara vulgaris*, *Chara rudis*, *Chara hispida*, *Chara aspera*, *Chara contraria*, *Chara aculeolata* and *Chara virgata*) to small, marginal populations of four (*Chara aspera*, *Chara .contraria*, *Chara aculeolata* and *Chara virgata*). In the same period, populations of angiosperms including *Nuphar lutea*, *Elodea canadensis*, *Utricularia* sp. and *Potamogeton lucens* increased. While cyanobacterial crust is not mentioned, it appears an open coarse sediment with *Littorella uniflora* has been replaced by dense reed-swamp with *Phragmites australis* and *Schoenoplectus lacustris*. These changes mirror the differences noted in this study between lakes with deep and shallow euphotic zone, and support our interpretation of charophyte/cyanobacterial crust replacement. Roden & Murphy (2020) noted a similar decline in charophyte abundance in Lough Arrow since 1984.

In a further study Wiik *et al*. (2015a) showed a now eutrophic lake, Cunswick Tarn, dominated by *Nuphar lutea*, *Elodea canadensis* and *Potamogeton berchtoldii* was formerly a charophyte lake with four *Chara* species.

4.4 Drivers of declining euphotic depth?

Factors that influence euphotic depth have been widely investigated (Free *et al*., 2006, 2016; Scheffer, 2004) and it is generally agreed that decreasing euphotic depth is driven by eutrophication, especially rising plant nutrient concentrations leading to increased phytoplankton and decreased light penetration. This interpretation is borne out by Figure 16 which shows lake total phosphorus increases as euphotic depth decreases in the surveyed lakes. A reasonable explanation of these results is that unmodified marl lakes are characterised by a vegetation of charophytes and cyanobacterial crust with few angiosperms, none of which are characteristic of such lakes. As eutrophication reduces euphotic depth and increases nutrient availability, angiosperm cover increases, while charophyte vertical zonation shallows and eventually breaks-down. The end point of this process includes lakes such as Summerhill or Cullaunyheeda with few if any charophytes and abundant generalist or tolerant species such as *Elodea canadensis*, *Nuphar lutea* and *Lemna trisulca*. Pentecost (1998) reports a change in Malham Tarn from *Chara* vegetation to *Chara/Elodea* vegetation. Figure 16 indicates that a euphotic depth > 6 m is associated with average total phosphorus of less than 0.01 mg/l.

Less often noted is the equally important relationship between water colour and euphotic depth, charophyte diversity and abundance. Our data (Figures 13, 14 and 15) suggest that lakes with euphotic depth greater than 6 m have colour less than 20 Hazen units and the two variables are strongly correlated. Given that increased colour directly reduces light penetration, this finding is not surprising but it does emphasise the role of water colour independent of nutrient enrichment. As large numbers of cut-over bogs in Ireland are near marl lakes, leaching of coloured water into marl lakes is an environmental problem. High water colour appears to explain the lack of deeper water vegetation in lakes such as Errit or Walshpool. In some studies, high water colour is associated with dystrophic or low-nutrient, acidic lakes (*e.g*. Free *et al*., 2006; Mackintosh *et al*., 2019). Here increased colour is positively correlated with total phosphorus, but is not correlated with alkalinity. The absence of lakes with high total phosphorus but low water colour may indicate that increasing total phosphorus in marl lakes also affects water colour. Vinogradoff & Oliver (2015) also reported a positive correlation between total phosphorus and lake colour for Scottish lakes on non-limestone bedrock.

As both factors may influence marl lake vegetation structure, it is useful to combine water colour and total phosphorus into a single index as is shown in in Figure 20. The highly significant regression coefficients indicate that the TP × colour index may offer a useful measure of marl lake ecological condition.

Doddy *et al*. (2019a, b) undertook a detailed analysis of the cyanobacterial crust in 12 of the lakes discussed in this report. Their main findings closely resemble the conclusions reached here. They reported that the best developed crust occurs in lakes with high euphotic depth and crust decays as euphotic depth decreases. A euphotic depth of 6 m is identified as the boundary between intact and damaged crust. Decay is exhibited by a decline in total cover, an increase in green algae relative to cyanobacteria and an accompanying increase in crust chlorophyll. Crust decay was shown to be caused by increasing concentrations of lake total phosphorus. These results strengthen our conclusions that near pristine marl lake vegetation is associated with very low levels of total phosphorus.

The suggestion, noted above, that the change from charophyte to vascular plant dominance may represent a shift in ecological stable states (Scheffer, 2004) with different nutrient cycles and food web structures, generates interesting testable hypotheses: Is nutrient cycling different in the two states?; does sediment phosphorus-saturation occur as ln index approaches -0.5?; does the disappearance of the cyanobacterial crust from extensive bare rock surfaces significantly decrease a marl lake's capacity to absorb phosphorus? Research to answer these questions will help define effective methods of marl lake restoration and allow a more comprehensive description of the features which separate marl from other lake types.

4.5 Recognising near-pristine marl lakes

In this report, the correlation between decreasing euphotic depth and increasing angiosperm cover is interpreted as resulting from eutrophication and increased dissolved humic compounds. It follows from this interpretation that all marl lakes with euphotic depth less than about 6-7 m are to some extent altered by human influence and, consequently, could not be regarded as in good ecological condition. Given the rarity of such lakes with euphotic depths of greater than 6 m, even in Ireland and certainly in other western European countries (Langangen, 2007; Pentecost, 2009; Wiik *et al*., 2015a, b), this may appear to be a very restrictive view point. It is supported, however, by older reports of euphotic depth in lakes of several countries, *e.g*. 8 m in Foreso in Denmark (Olsen, 1944), 6.5 m in Cunswick Tarn and 12 m in Hawes Water in England (Pentecost, 2009; Wiik *et al*., 2015 a, b), while Corillion (1957) noted that in some French lakes in the Jura, only charophytes grow below 7 m. Even today, examples of such lakes continue to exist not only in Ireland but also in Scotland (Loch Boralie), Scandinavia, and the Alps. Langangen (2007) noted that angiosperms are rare in Scandinavian marl lakes, mirroring the Irish situation. It is our opinion that near pristine marl lakes over Carboniferous limestone are characterised by charophyte and cyanobacterial crust vegetation with few angiosperms and great euphotic depths, and that such lakes have low colour and low total phosphorus. Arguably, the existence of such lakes is not well known and their rapid decline has gone unnoticed by many limnologists (but see Pentecost, 2009).

While we propose that most Irish marl lakes can be placed on a gradient from deep to shallow euphotic depth reflecting increasing environmental pressure, certain charophyte-dominated lakes may be better regarded as being of different sub-types. Very small alkaline lakes or large, deep ponds have largely angiosperm and bryophyte cover, but they also have high euphotic depths. Brick Lough near Lough Rea is an example. Some coastal lakes on calcareous sea-sand are naturally shallow (< 5 m depth) and also have some distinctive angiosperm species, but their charophyte flora is comparable to inland limestone lakes. Fahy Lough or Aillebrack Loughs in Connemara are examples of these coastal marl lakes. It is probable that additional factors, such as extreme shelter leading to thermocline formation or increased salt content and wind-borne nutrients, influence vegetation development and species competition.

Other types of marl lake occur on the European mainland, *e.g*. Langangen (2007) suggests that another type of *Chara* lake occurs in Northern Sweden, a 'humic *Chara* lake' dominated by angiosperms and bryophytes and rich in humus, but it is unclear if types similar to Irish marl lakes occur elsewhere. Three charophyte species, *Chara curta*, *Chara rudis* and *Chara denudata*, which are characteristic of the lakes described here, are rare or absent in Britain and very localised mainland Europe. Nor are there many accounts of the typical cyanobacterial crust zone elsewhere, perhaps because it requires outcropping limestone bedrock and possibly an absence of ice formation in winter. It could be claimed that the alkaline, low nutrient lakes described here are as typical a feature of the Irish Carboniferous limestone, as the pavements of the Burren. Only a minority are now in near-pristine condition and many, such as Lough Arrow, Lough Carra and even Lough Corrib, show serious evidence of declining ecological quality. Their loss would be irreparable both for Ireland and Europe.

5 References

Blindow, I. (1992) Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. *Freshwater Biology* **28** (1), 15–27.

Corillion, R. (1957) *Les Charophycées de France et d'Europe occidentale*. Rennes Impr. Bretagne. pp. 449.

Bruinsma, J., Lansdown, R., Roden, C. & Van Der Wyer, K. (2009) *The botany and vegetation of the lakes of south east Clare*. Report to the Heritage Council.

Doddy, P., Roden, C.M. & Gammell, M.P. (2019a) Microbialite crusts in Irish limestone lakes reflect lake nutrient status. *Biology and Environment: Proceedings of the Royal Irish Academy* **119** (1), 1–11.

Doddy, P., Roden, C.M. & Gammell, M.P. (2019b) Nutrient-pollution degrades microbialites in Lough Carra, an Irish marl lake. *Aquatic Microbial Ecology* **83**, 203–209.

Free, G., Little, R., Tierney, D., Donnelly, K. & Coroni, R. (2006) *A reference-based typology and ecological assessment system for Irish lakes. Preliminary Investigations*. Final Report. Project 2000-FS-1-M1 Ecological Assessment of Lakes Pilot Study to Establish Monitoring Methodologies EU (WFD). EPA, Wexford.

Free, G., Tierney, D., Little, R., Kelly, F.L., Kennedy, B., Plant, C., Trodd, W., Wynne, C., Caroni, R. & Byrne, C. (2016) Lake ecological assessment metrics in Ireland: relationships with phosphorus and typology parameters and the implications for setting nutrient standards. *Biology and Environment: Proceedings of the Royal Irish Academy* **116**, 191–204.

Heuff, H. (1984) *The vegetation of Irish Lakes*. Unpublished report submitted to the Wildlife Service, Office of Public Works, Dublin.

John, D.M, Champ, W.S.T. & Moore, J.A. (1982) The changing status of Characeae in four marl lakes in the Irish Midlands. *Journal of Life Sciences, Royal Dublin Society* **4**, 47–71.

Kennedy, B., O'Grady, M. & Whitton, B.A. (2012) Cyanobacteria of Western Ireland. *Online supplement to:* Whitton, B.A. (Ed.) *Ecology of Cyanobacteria II* (Chap. 31). Springer, Dordrecht.

King, J.J. & Champ, W.S.T. (2000) Baseline water quality investigations on Lough Carra, western Ireland, with reference to water chemistry, phytoplankton and aquatic plants. *Biology and Environment: Proceedings of the Royal Irish Academy* **100B** (1), 13–25.

King, J.J. & Caffrey, J.M. (1998) Macrophytes in Irish lakes and rivers. *In:* Giller, P.S. (Ed.) *Studies in Irish Limnology*. Marine Institute, Dublin. pp 101–124.

Komárek J. & Anagnostidis K. (2005) Cyanoprokaryota -2. Teil/ 2nd Part: Oscillatoriales. *In*: Büdel B., Krienitz L., Gärtner G. & Schagerl M. (Eds), *Süsswasserflora von Mitteleuropa 19/2*. Elsevier/ Spektrum, Heidelberg. 759 pp.

Krause, W. & King, J.J. (1994) The ecological status of Lough Corrib, Ireland, as indicated by physiographic factors, water chemistry and macrophyte flora. *Vegetatio* **110**, 149–161.

Langangen, A. (2007) *Charophytes of the Nordic countries*. Saeculum ANS, Oslo.

Langangen, A. (2005) Charophytes collected in Cos Clare (H9) and south-east Galway (H15) in 2003. *Irish Naturalists' Journal* **28,** 151–158.

Moss, B. (2015) *Lakes, loughs and lochs*. Collins New Naturalist Library. Volume 128. HarperCollins UK.

National Parks & Wildlife Service (2008) *The Status of EU Protected Habitats and Species in Ireland. Conservation Status in Ireland of Habitats and Species listed in the European Council Directive on the Conservation of Habitats, Flora and Fauna 92/43/EEC*. Unpublished Report, the National Parks and Wildlife Service, Dublin.

Nelson, B., O Connor, Á., Foster, G.N., Doddy, P. & Roden, C. (2019) A review of *Ochthebius nilssoni* Hebauer (Coleoptera: Hydraenidae) in western Ireland including a first report from Lough Carra. *Irish Naturalists' Journal* **36** (2), 117–122.

O'Callaghan E, Foster, G.N., Bilton, D.T. & Reynolds J.D. (2009) *Ochthebius nilssoni* Hebauer new for Ireland (Coleoptera, Hydraenidae), including a key to Irish *Ochthebius* and *Enicocerus*. *Irish Naturalists' Journal* **30**, 19–23.

Olsen, S. (1944) Danish Charophyta. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* **3** (1), 1–240.

Pentecost, A. (1998) Phosphorus fractionation in the sediments of Malham Tarn, North Yorkshire. *Field Studies* **9**, 337– 342.

Pentecost, A. (2009) The marl lakes of the British Isles. *Freshwater Reviews* **2**, 167–197.

Praeger, R.L. (1906) On the botany of Lough Carra. *The Irish Naturalist* **15**, 207–214.

Praeger (1934) *The Botanist in Ireland*. Hodges Figgis & Co., Dublin.

Preston, C.D. & Croft, J.M. (1997) *Aquatic Plants in Britain and Ireland*. Harley Books, Colchester.

Reynolds, J.D. (1998) *Ireland's Freshwaters*. Marine Institute, Dublin.

Roden, C.M. (1999) *A survey of Irish machair Loughs*. Unpublished report submitted to the Heritage Council.

Roden, C.M. (2000) *A study of karstic algae growing in the west of Ireland*. Unpublished report submitted to the heritage Council.

Roden, C.M. (2001) *A report on the vegetation and algal plankton of base rich nutrient poor lakes in Clare and Mayo*. Unpublished report submitted to Heritage Council.

Roden, C. (2008) *The effect of excessive water abstraction on the vegetation and conservation status of Lough Bane, county Meath/ Westmeath. Special Area of Conservation no 002120*. Updated October 2008. Report to Meath County Council.

Roden, C. (2009) *The effect of excessive water abstraction on the vegetation and conservation status of Lough Bane, county Meath/ Westmeath. Results of monitoring programme. July 2008 -July 2009. 2nd Report (October 2009)*. Report to Meath County Council.

Roden, C. (2010) *The effect of excessive water abstraction on the vegetation and conservation status of Lough Bane, county Meath/ Westmeath. 3rd Report (December 2010).* Report to Meath County Council.

Roden, C. & Murphy, P. (2013) A survey of the benthic macrophytes of three hard-water lakes: Lough Bunny, Lough Carra and Lough Owel. *Irish Wildlife Manuals*, No. 70. National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Ireland.

Roden, C. & Murphy, P. (2020) *Sub littoral vegetation of Lough Arrow in 2019*. Report to the INTERREG VA CANN (Collaborative Action for the Natura Network) Project.

Roden, C., Murphy, P., Ryan, J. & Doddy, P. (2020) Marl Lake (Habitat 3140) Survey and Assessment Methods Manual. *Irish Wildlife Manuals*, No. 125. National Parks and Wildlife Service, Department of Housing, Local Government and Heritage, Ireland.

Scheffer, M. (2004) *Ecology of Shallow Lakes.* Population and Community Biology Series. Springer, Dordrecht.

Spence, D.H.N. (1967) Factors Controlling the Distribution of Freshwater Macrophytes with Particular Reference to the Lochs of Scotland. *Journal of Ecology* **55** (1), 147–170.

Stewart, N.F. & Church, J.M. (1992) *Red Data Books of Britain and Ireland, Charophytes*. Joint Nature Conservation Committee and Office of Public Works.

Vinogradoff, S. & Oliver, I. (2015) Should a Water Colour Parameter Be Included in Lake Total Phosphorus Prediction Models Used for the Water Framework Directive? *J. Environ. Manage.* **147**, 81–6.

Wiik, E., Bennion, H., Sayer, C.D. & Willby, N.J. (2014) Chemical and biological responses of marl lakes to eutrophication. *Freshwater Reviews* **6**, 35–62.

Wiik, E., Bennion, H., Sayer, C.D., Davidson, T.A., Clarke, S.J., McGowan, S., Prentice, S., Simpson, G.L. & Stone, L. (2015a) The coming and going of a marl lake: multi- indicator palaeolimnology reveals abrupt ecological change and alternative views of reference conditions. *Frontiers in Ecology and Evolution* **3**, 82. doi: 10.3389/fevo.2015.00082

Wiik, E., Bennion, H., Sayer, C.D., Davidson, T.A., McGowan, S. & Patmore, I. (2015b) Ecological sensitivity of marl lakes to nutrient enrichment: evidence from Hawes Water, UK. *Freshwater Biology* **60**, 2226–2247. doi: 10.1111/fwb.12650

Appendix I Summary vegetation and physico-chemical data

Summary data for lakes included in the analyses. Abbreviations are used in graphs in Chapter 3. Vegetation values are averaged across all transects. 2018 vegetation data were not included. 2010-2016 water chemistry data were provided by EPA for all lakes other than Cooloorta and Finn Loughs, and overall average values are given. 'Zones' is the number of vegetation zones. 'Charophyte species' is the number of charophyte species. 'Log colour' is to the base 10. For further information on all fields, see Chapters 2 and 3 and Roden *et al.* (2020).

Lake name	**Abbrev-iation**	**Survey**	**Zones**	**Charophyte species**	**Euphotic depth** (m)	**Charophyte cover**	**Vascular plant cover**	**Cyanophyte crust cover**	**C&K score**	**Colour** (mg/l PtCo)	**Log Colour**	**TP** (mg/l)	**Alkalinity** (mg/l $CaCO_3$)	**Index** (TP × Colour)
Annaghmore Lough	ANN	4	4	7	6.0	0.64	0.24	0.12	0.76	20	1.30	0.0091	159	0.182
Lough Arrow	ARR	4, 6	1	2	3.7	0.36	0.64	0.00	0.36	22.6	1.35	0.0107	120	0.242
Ballycuirke Lough	BAE	6	0	0	1.8	0.00		0.00	0.00	44	1.64	0.03	69	1.320
Ballyeighter Lough (1)	BAR	4	4	6	7.0	0.71	0.10	0.19	0.90	27	1.43	0.005	211	0.135
Lough Bane	BAN	1, 5	5	8	9.0	0.64	0.27	0.08	0.73	4.23	0.63	0.011	132	0.047
Bleach Lough	BLE	4	4	7	7.3	0.75	0.22	0.03	0.77	13	1.11	0.0045	193	0.059
Lough Bridget	BRI	2	0	0	3.0	0.00	1.00	0.00	0.00	41.7	1.62	0.046	218	1.918
Lough Bunny	BUN	3, 5, 6	4	6	8.4	0.59	0.32	0.09	0.68	10.6	1.03	0.0059	156	0.063
Clonlea Lough	CLO	2	1	5	5.1	0.18	0.82	0.00	0.18	42	1.62	0.012	230	0.504
Cooloorta Lough	COO	4, 5, 6	4	6	8.7	0.69	0.18	0.13	0.82	9.7	0.99	0.003	202	0.029
Lough Corrib	COR	4, 6	5	7	5.0	0.75	0.06	0.19	0.94	20.9	1.32	0.0088	92	0.184
Lough Cullaun	CUN	4	4	5	5.9	0.56	0.36	0.08	0.64	16.5	1.22	0.0065	172	0.107
Cullaunyheeda	CUY	4, 6	2	2	5.1	0.21	0.79	0.00	0.21	39.9	1.60	0.017	215	0.678
Lough Derravaragh	DER	4, 6	3	2	4.0	0.29	0.42	0.29	0.58	32.4	1.51	0.0168	213	0.544
Lough Ennell	ENN	4, 6	4	7	5.4	0.79	0.10	0.11	0.90	23.7	1.37	0.0192	188	0.455
Errit Lough	ERR	4	4	4	3.3	0.52	0.42	0.06	0.58	46	1.66	0.01	136	0.460
Finn Lough	FIN	4, 6	4	5	5.0	0.56	0.37	0.07	0.63	27	1.43	0.0105	162	0.284
Inchicronan	INC	2	0	4	1.5			0.00		20	1.30	0.022	149	0.440

Lake name	**Abbreviation**	**Survey**	**Zones**	**Charophyte species**	**Euphotic depth** (m)	**Charophyte cover**	**Vascular plant cover**	**Cyanophyte crust cover**	**C&K score**	**Colour** (mg/l PtCo)	**Log Colour**	**TP** (mg/l)	**Alkalinity** (mg/l $CaCO_3$)	**Index** (TP × Colour)
Lough Lene	LEN	1, 4, 6	4	7	6.5	0.70	0.25	0.06	0.75	6.82	0.83	0.0111	104	0.076
Lough Mask	MAS	4, 6	1	2	5.5	0.56	0.35	0.09	0.65	23	1.36	0.0071	107	0.163
Muckanagh Lough	MUC	4, 5, 6	4	6	6.5	0.59	0.15	0.27	0.85	25	1.40	0.0078	208	0.195
Lough Owel	OWE	3, 5, 6	4	8	6.4	0.79	0.12	0.09	0.88	6.85	0.84	0.0101	109	0.069
Lough Rea	REA	4, 5, 6	4	7	11.0	0.87	0.06	0.07	0.94	5.7	0.76	0.0074	128	0.042
Rosroe Lough	ROS	2	2	5	4.7	0.55	0.45	0.00	0.56	18	1.26	0.031	199	0.558
Spring Lough	SPR	4	4	7	7.0	0.62	0.36	0.02	0.64	25.5	1.41	0.0135	150	0.344
Summerhill Lough	SUM	4	0	0	1.5	0.00	1.00	0.00	0.00	46.1	1.66	0.0245	158	1.129
Urlaur Lough	URL	4	3	5	1.8	0.64	0.23	0.13	0.77	41.5	1.62	0.0119	148	0.494
Walshpool Lough	WAL	4, 6	4	6	3.3	0.66	0.18	0.17	0.82	34.8	1.54	0.0095	178	0.331
White Lough	WHI	1, 5	4	6	7.5	0.70	0.30	0.00	0.70	8.6	0.93	0.006	188	0.052

Appendix II Indicator Species Analyses

The tables below present the results of cluster and indicator species analysis on vegetation data from 2012 and 2018. Vegetation units (groups of relevés), distinguished using cluster analysis at the 50% similarity level, are presented in the columns. The constituent, characteristic species of each group were distinguished using indicator species analysis. Indicator species for each relevé group are grouped in the rows in the table. Numbers in each column are indicator/index values. Significant indicator values are emboldened and corresponding p-values are given in the first column.

Dufrêne and Legendre indicator species analysis values for 2012 survey

	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	number of relevés	18	61	6	69	5	49	4	2	99	27	11	2	5	2	2	2
**	*Potamogeton perfoliatus*	**54**	.	.	.	.	1	.	.	.	.	.	.	.	5	.	.
	Myriophyllum spicatum	**35**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Potamogeton praelongus	**13**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
***	*Chara rudis*	.	**51**	4	1	2	2	.	.	.	3	.	.	.	.	.	.
	Nuphar lutea	.	**10**	.	.	.	.	.	.	.	9	.	.	.	.	.	.
	Potamogeton natans	.	**10**	.	.	.	.	.	.	.	.	.	.	.	.	.	.
***	*Chara aspera*	.	.	**88**	.	.	.	1	1	.	.	.	.	.	.	.	.
	P. x *nitens*	.	.	**23**	.	.	2	.	.	.	.	.	.	.	.	.	.
***	Cyanobacterial crust	.	.	.	**81**	.	.	.	.	.	.	.	3	.	.	.	.
	Chara virgata var. *annulata*	.	.	.	**22**	.	.	.	.	.	1	.	.	.	.	.	.
	Littorella uniflora	.	.	.	**17**	.	.	.	.	.	1	.	.	.	.	.	.
	Ophrydium versatile	.	.	.	**10**	.	.	.	.	.	.	.	.	.	.	.	.
***	Red cyanophyte	.	.	.	.	**87**	1	.	.	.	.	.	.	.	.	.	3
***	*Chara virgata*	1	.	2	.	.	**68**	.	.	.	1	2	.	.	.	.	.
***	*Schoenoplectus lacustris*	.	1	.	.	.	.	**87**	.	.	.	.	.	.	.	.	.
	Phragmites australis	.	.	.	3	.	.	**12**	.	.	1	.	.	.	.	.	.
*	*Potamogeton crispus*	.	.	.	.	.	.	.	**50**	.	.	.	.	.	.	.	.
	Potamogeton lucens	.	2	.	.	.	.	.	**11**	.	1	.	.	.	.	.	.
*	*Chara contraria*	1	.	.	.	.	.	3	.	**42**	.	.	.	.	.	.	.
**	*Chara curta*	.	.	2	6	.	.	2	3	**41**	.	.	.	.	.	.	.
	Chara aculeolata	.	2	.	3	.	.	6	.	**10**	.	.	.	.	.	.	.
**	*Lemna trisulca*	1	.	.	.	.	.	.	.	.	**58**	.	.	.	.	4	.
*	*Elodea canadensis*	2	.	.	.	.	2	.	.	.	**47**	3	.	.	1	.	.
***	*Chara denudata*	.	.	.	.	.	.	.	.	.	.	**98**	.	.	.	.	.
	Tolypella glomerata	.	.	.	.	.	.	.	.	.	.	**27**	.	.	.	.	.
*	Lichen	.	.	.	.	.	.	.	.	.	.	.	**50**	.	.	.	.
***	*Ceratophyllum demersum*	.	.	.	.	.	.	.	.	.	.	.	.	**97**	.	.	.
	Cladium mariscus	.	.	.	1	.	.	.	.	.	.	.	.	.	**33**	.	.
	Potamogeton friesii	.	.	.	.	.	1	.	.	.	4	.	.	3	.	.	.
	Potamogeton berchtoldii	.	.	.	.	.	1	.	.	.	3	1	.	.	.	.	.
	Fontinalis antipyretica	2	.	.	.	.	8	.	.	.	2	.	.	.	.	.	.
	Cladophora sp.	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Nymphaea alba	.	3	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Potamogeton gramineus	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.
Hippuris vulgaris	.	8	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Myriophyllum alterniflorum	.	.	.	1	.	1	.	.	2	.	.	.	.	.	.	.
Potamogeton sp.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.
Potamogeton filiformis	.	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.
Juncus bulbosus	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
Chara hispida	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
Utricularia vulgaris	.	2	.	.	.	2	.	.	1	.	.	.	.	.	.	.
Chara tomentosa	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.
Equisetum fluviatile	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.
Juncus articulatus	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Callitriche sp.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Nitella tenuissima	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Utricularia sp.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.
Potamogeton pectinatus	6	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Utricularia intermedia	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus baudotii	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus flammula	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Bryophytes	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Baldellia ranunculoides	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Chara vulgaris	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Mentha aquatica	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oenanthe aquatica	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Persicaria amphibia	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eleocharis palustris	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus sp.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nitella flexilis	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Dufrêne and Legendre indicator species analysis values for 2018 survey

	Group	1	2	3	4	5	6	13	12	11	7	8	9	10
	number of relevés	34	42	36	21	8	8	13	9	3	3	2	3	3
***	Cyanobacterial crust	**84**	1	.	.	.	.	.	3	.	.	.	.	.
	Utricularia intermedia	9	1	.	.	.	.	.	.	.	.	.	.	.
***	*Chara curta*	5	**61**	.	.	.	.	5	6	.	.	.	.	.
***	*Chara aculeolata*	1	**13**	.	.	2	4	.	.	47	.	.	.	.
***	*Chara rudis*	.	3	**55**	.	6	.	1	.	.	.	.	.	3
	Nuphar lutea	.	.	**10**	.	.	.	.	2	1	.	.	.	**12**
***	*Chara virgata*	.	.	2	**57**	6	.	.	.	3	2	.	.	.
***	*Elodea canadensis*	.	.	.	.	**77**	1	2	.	.	.	.	.	.
	Bryophytes	.	.	.	.	**23**	.	.	.	.	.	.	.	.
	Hippuris vulgaris	.	.	2	.	**20**	.	.	.	.	.	.	.	.
	Lemna trisulca	.	.	.	.	**13**	.	.	.	.	.	.	.	.
***	*Chara denudata*	.	.	.	.	.	**100**	.	.	.	.	.	.	.
	P. x *angustifolius*	.	.	.	.	.	**25**	.	.	.	.	.	.	.
	Nitella flexilis	.	.	.	.	.	**13**	.	.	.	.	.	.	.
***	*Chara contraria*	.	2	.	7	2	.	**63**	.	.	.	.	.	.
**	*Myriophyllum spicatum*	.	.	.	.	1	.	**36**	.	.	.	.	.	.
	Potamogeton pectinatus	.	.	.	.	.	.	**15**	.	.	.	.	.	.
	Littorella uniflora	2	.	.	.	.	.	**12**	.	.	.	.	.	.
***	*Chara tomentosa*	.	.	1	1	.	.	4	**64**	.	.	.	.	3
**	*Myriophyllum verticillatum*	.	.	.	.	4	.	.	**42**	.	.	.	.	.
	Schoenoplectus lacustris	2	1	2	.	.	.	.	**22**	.	.	.	.	.
**	*Utricularia vulgaris*	2	1	.	.	.	.	.	8	**39**	.	.	3	6
	Potamogeton lucens	.	.	1	.	.	.	1		**23**	.	.	.	.
**	*Sparganium minimum*	.	.	.	.	.	.	.	.	**32**	.	.	.	.
	Phragmites australis	.	6	.	.	.	.		7	.	.	.	.	.
	Potamogeton filiformis	.	.	.	.	.	.	1	5	.	.	.	**21**	.
	Chara virgata var. *annulata*	6	.	.	.	.	.	.	2	.	.	**18**	**15**	.
**	*Potamogeton gramineus*	.	.	.	.	.	.	1	.	7	.	.	**64**	.
**	*Potamogeton perfoliatus*	.	.	2	1	8	2	.	.	.	2	.	.	**60**
	Myriophyllum alterniflorum	2	1	.	.	4	.	6	.	.	.	.	.	.
	Fontinalis antipyretica	2	.	.	.	6	.	3	.	.	.	.	.	3
	Ranunculus sp.	5	.	.	.	.	.	3	.	.	.	.	.	.
	Chara aspera	.	.	.	4	.	.	1	.	.	.	.	.	.
	Red cyanophyte	.	.	.	2	.	6	.	.	.	.	.	.	.
	Potamogeton praelongus	.	.	6	.	.	.	.	.	.	.	.	.	.
	Potamogeton friesii	.	.	3	.	.	.	.	.	.	.	.	.	.
	Juncus articulatus	.	.	3	.	.	.	.	.	.	.	.	.	.
	Ophrydium versatile	.	6	1	.	.	.	.	.	.	.	.	.	.
	Chara hispida	6	.	.	.	.	.	.	.	.	.	.	.	.