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IUCN, International Union for Conservation of Nature, Switzerland
UOXF.AC, Oxford University, UK
UB, Universitat de Barcelona, Spain
UFZ, Helmholtz Zentrum für Umweltforschung, Germany
UCL, University College of London, UK
UCBL, Université Claude Bernard - Lyon 1, France
UPS, Université Paul Sabatier- Toulouse 3, France
ECOLOGIC, Ecologic GmbH Institut für Internationale und Europäische Umweltpolitik, Germany
EC-ERC, Commission of the European Communities - Directorate General Joint Research Centre, Italy
UD, University of Debrecin, Hungary
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BIOFRESH

Biodiversity of Freshwater Ecosystems: Status, Trends, Pressures, and Conservation Priorities

Project no. 226874

Large scale collaborative project

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Freshwater biodiversity: the temporal perspective

Deliverable for the EU BioFresh project WP4

Introduction

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Today there is increasing concern that biodiversity is being lost through human activity with respect especially to pollution and habitat disturbance, and that future global warming may cause rapid species migration and invasions on the one hand and range reductions and extinctions on the other, the consequences of which, in terms of ecosystem function and human livelihoods, are unknown. The starting point for most biodiversity research is the examination of present-day patterns and distributions.

However, contemporary biodiversity patterns are only a snapshot in time, the outcome of many processes acting and interacting dynamically on different time-scales. Understanding the present therefore also needs insights into the past. Our ability to track changes through time is compromised for many ecosystems by the rarity and brevity of long-term ecological records. For some ecosystems, on the other hand, it is possible to embrace the potential of palaeoecological techniques especially where they can be complemented by long-term observational records.

Palaeoecological methods continue to improve and can be used not only to record species occurences through time (for those taxa that leave a fossil record), but also to calculate rates of change, infer the causes of change and identify the ecological importance of biodiversity change in terms of habitat loss, community change and ecosystem functioning.

The approach is especially powerful for lake ecosystems as lake sediments contain an exceptionally rich fossil record and accumulate rapidly. Already the methodology is well developed as a means of reconstructing water quality change in response to human activity. In Europe we now have extensive palaeo data-sets for lakes that enable the extent of ecosystem change as a result of 19th and 20th century pollution to be assessed at the continental scale.

Palaeoecological methods now need further development to address more specifically questions of biodiversity rather than water quality relevance per se. The first challenge is to understand how the fossil record relates to the biodiversity of contemporary populations, with respect to:

- temporal perspective (dating, resolution issues)
- sampling design (core locations, core and sediment sample sizes, fossil concentrations)

- biased preservation (between and within fossil groups, within and between lake types)

Key questions that can be addressed using this approach are:

- what is the **history** (e.g. over the Holocene, over the Anthropocene etc) of taxa that are well preserved and identifiable?
- are trends in biodiversity between groups (e.g. diatoms, cladocera, chironomids) **congruent** in time?
- how useful are **diatoms** as indicators of biodiversity?
- can the fossil record be used to indicate changes in biodiversity of communities that do not leave remains?
- can the palaeoecological record be used to track changes in **genetic diversity**, e.g. from the analysis of diapausing bodies?
- what **processes** (natural climate change and variability, ecological succession, human activity e.g. related to soil erosion, eutrophication, acidification, salinisation, hydromorphology) have been responsible for biodiversity change through time.
- has human activity in the past caused a loss of biodiversity either at a site or amongst a population of sites on a landscape scale (**beta-diversity**) and do we see **convergence** of naturally diverse ecosystems towards more homogenous species-poor states?
- can we use palaeoecological records to identify the impact of different stresses on **ecosystem functioning** e.g. in terms of loss of resilience, early warning of approaching thresholds etc?
- can observations of biodiversity change amongst sites along environmental gradients (e.g. nutrients, acidity) in space be observed within a site in time and can **space and time** approaches be combined to develop better predictions of response to a pressure in future, e.g. in response to climate change?.
- with respect to **climate change** have there been changes in the past that we can use to evaluate threats for the future?
- how can the palaeoecological record be used to inform **nature conservation** and is there any evidence from the recent palaeoecological record that current restoration practices are leading to an increase in diversity or a return to good ecological status?
- how can we use sediment records to evaluate the role of other **drivers of biodiversity loss** to identify systems that are more **vulnerable to climate change** (especially relevant to shallow eutrophic lakes)?
- to what extent can palaeoecological data be up-scaled to address changes in biodiversity at the regional and global scales

In BioFresh we address some of these questions, focussing on both methodological issues relating to databases, coring methodology and taphonomy as well as substantive ones relating to the historical evidence for the impacts of acid deposition and nutrient enrichment on lake ecosystems.

Paper 1 is concerned with the building of a global meta-database, LakeCores, that will provide an inventory of lakes around the world for which published palaeoecological data are available.

Paper 2 describes a new sediment corer designed the obtain large volumes of sediment needed to detect macrofossils

Paper 3 and 4 are papers concerned with taphonomy, the extent to which fossil assemblages faithfully represent living plant and animal communities from which the fossils were derived. Paper 3 is a case study of a eutrophic lake, the Green Plantation Pond in England and is concerned with aquatic plants and their remains, whilst Paper 4 is a case study of an acidified lake, the Round Loch of Glenhead in Scotland, and is concerned with the representation of diatoms, aquatic plants, Cladocera and chironomids in surface sediments.

Papers 5 and 6 are concerned with diatom biodiversity and the use of diatoms as indicators of biodiversity change. Paper 5 examines the response of diatoms to the recovery of 11 lakes in the UK from a reduction in sulphur and nitrogen deposition. Paper 6 explores the use of different metrics in describing diatom diversity changes along nutrient and pH gradients.

Papers 7 and 8 are concerned with the use of lake sediment fossil records to track the recovery of lakes from eutrophication and acidification. Paper 7 describes how lake sediment records can be used to explain differences in contemporary biodiversity between lake districts, and paper 8 describes an analysis of the pre-acidification fossil record of an acidified lake in an attempt to identify species lost through acidification.

Paper 1

A palaeolimnological meta-database for assessing the ecological status of lakes

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LakeCores (www.lakecores.ucl.ac.uk) is a meta-database designed by Victoria Bauer, Gavin Simpson and Rick Battarbee to provide a global inventory of lakes from which sediment cores have been taken. Its original purpose, as part of the European project Euro-limpacs(“Global Change Impacts on European Freshwater Ecosystems”) , was to identify lakes in Europe where palaeolimnological methods had been used to reconstruct recent lake history associated with problems of eutrophication, acidification and other ecological pressures (see Battarbee *et al.* 2011).

It has now been modified as part of BioFresh. Its current purpose is to register cores that contain palaeolimnological records of any kind or age, allowing the user to identify rapidly the sites for which published palaeolimnological data are available throughout the world. It provides simple meta-data on lake name and location, principal characteristics of the lakes (size, altitude, depth) and the principal characteristics of the cores (length, age-span, analysis) (Table 1). It also links the core data to the publication or report where the primary analytical details can be found.

Table 1 Data types recorded in the LakeCores database. [1] Where no depth was indicated, coring depth was used on the (possibly dubious) assumption that the core was taken from the deepest point

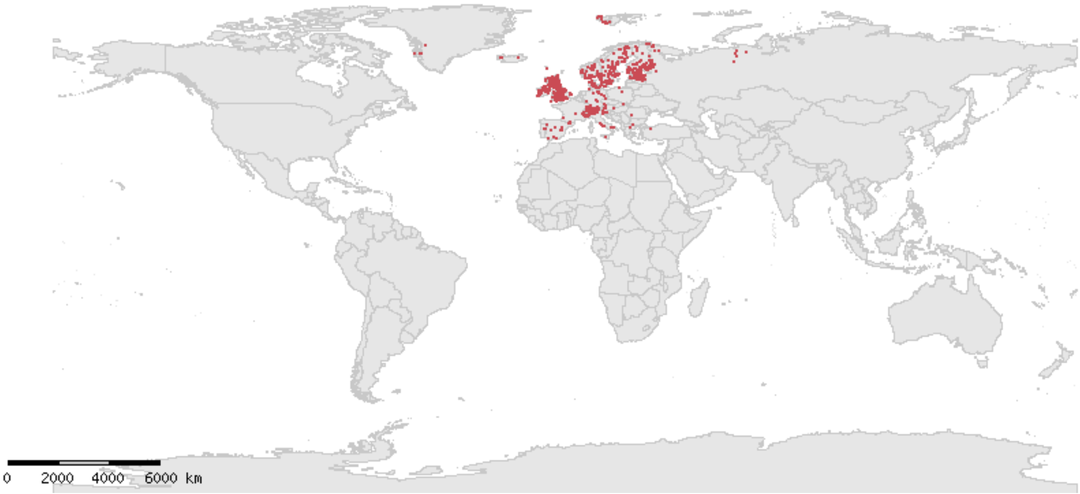
Geographical data	**Core data**
Site name	Corer type
Country	Core water depth (m)
Site latitude and longitude	Year of coring
Site altitude (m.a.s.l)	Length of core (cm)
Catchment area (km^2)	Sampling resolution (cm)
Catchment max. altitude (m.a.s.l)	Dating methods e.g. ^{210}Pb
Lake area (km^2)	Core analyses e.g. diatoms
Lake altitude (m.a.s.l)	Transfer function e.g. pH
Mean depth (m)	
Maximum depth (m)[1]	

We have so far only included sites where cores have been taken with an intact mud-water interface, have been dated and, ideally, extend in time back at least to the early nineteenth century. The database could be extended to hold data on longer and older cores.

The data themselves are held on a relational database management system (RDMS) using the open source database server software, MySQL, in a series of related tables. Access to the main data is provided by a dedicated website (www.ecrc.ucl.ac.uk/lakecores), which provides search and interactive mapping facilities.

The geographical data in the database rely upon the information contained in the papers from which the data were taken and these are listed in the database, although in some cases where essential information was missing other sources were also used.

In BioFresh we have re-designed the website and added a user interface to allow core data to be registered online. The objective is to build a globally comprehensive inventory, useful not only for other palaeo-scientists but also for lake managers concerned with changes in the water quality and biodiversity of lake ecosystems.



Reference

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Paper 2

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Big Ben: a new wide-bore piston corer for multi-proxy palaeolimnology

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Abstract

A large diameter, piston corer suitable for use in shallow lakes, is described. The design and operation of the corer along with an extruding framework are detailed. Finally we summarise recent experiences of deploying the corer and highlight its potential uses in the developing field of multi-proxy palaeolimnology.

Introduction

Over the last decade there has been an increasing tendency for multi-proxy studies in palaeolimnology. Using this approach sediment samples are analysed for several different fossil groups with the aim of reconstructing, among other aspects, past biodiversity patterns, trophic structure and the coherence and nature of biological changes over time (Brodersen et al. 2001; Birks & Birks 2006; Sayer et al. 2010a). With standard diameter cores (<8 cm), the multi-proxy approach typically requires that sediment is strictly rationed between different workers. This is problematic when sediments are analysed for plant macrofossils and remains of rarer, large-bodied animals such as invertebrates and fish as large quantities of sediment are required to achieve reliable results and good species representation (Davidson et al. 2003; Greenwood et al. 2006; Howard et al. 2009). One solution to the problem of limited sediment is to collect multiple parallel sediment cores which are cross-correlated using repeatable lithostratigraphic (e.g. geochemical and loss on ignition signals) and biostratigraphic features. However, this can be a time-consuming and expensive approach, which is also prone to error where it is not possible to establish stratigraphic matches between the collected cores. As a solution to these issues, we present a new wide-bore piston corer designed to collect short (<1.5 m) sediment sequences from generally shallow water. The corer has become known as “Big Ben”. In this paper, we detail the design of the corer and an associated extruding apparatus. We also describe the practical operation of the Big Ben coring system from setting up a coring platform, to collecting a core and extruding the sediment. Finally, we provide a brief summary of recent experiences relating to the operation and application of the corer.

Components of the Big Ben coring system

The design of the Big Ben corer is based on the principle of using metal rods to drive a core tube past a fixed piston into soft sediments (Livingstone 1955). For most gravity and piston corers, the diameter of the core tube (internally) is usually around 7-8 cm. If the diameter of a core tube is increased to obtain more sediment, core aspect ratios (core length/core diameter) have to be considered for gravity corers to avoid sediment slippage when the core is retrieved (Glew et al. 2001). For a piston corer the aspect ratio (which is usually high), is rarely a problem, but increasing a core tube's diameter and length means that the weight/effort required for sediment penetration increases.

Taking the aforementioned factors into account, Big Ben has a core tube length of approximately 1.5 m and an internal tube diameter of 14 cm. When full of sediment, the corer is often unwieldy due to its size and weight. Consequently a supporting system has been developed to permit the safe and accurate collection and extrusion of a core involving a raft (to act as a platform), a core catching device and a metal (Dexion™) framed extrusion rig. Core catchers are usually summarised as devices to prevent the loss of sediment from the bottom of the core tube during core retrieval (Glew et al. 2001) but here it is used to aid the support of the full core tube whilst on the raft.

Key components of the Big Ben coring and extrusion system are detailed in Table 1, which give dimensions for these components and suggestions for their construction and use. Given the simplicity of the corers design and the variable availability and specifications of materials in different parts of the world (e.g. plastic tubes), we are not suggesting that the coring system has to be built to the exact specifications presented here. Rather, we present a coring set up that works, which can be used as a basis for your individual situation.

Operation of the Big Ben corer

Collecting the core

A raft is formed from two lightweight inflatable Avon 'Redcrest' boats, strapped together with a wooden 'ladder' which holds the two boats side on. The ladder consists of two main spars and 4 cross spars of thinner wood, bolted together and fastened to the boats with straps. A wooden floor sits on top of the main spars affording a safe and appropriate working platform (Fig. 1a). The raft is fixed in position over the core site using anchors (3-4) positioned in a 'triangulated format' around the raft (Wright 1991). Anchors dropped close to the raft (<10 m) have been found to provide a less secure base for coring. A team of four people is ideal, two on each boat, each with a role.

Once over the coring site, the core catcher (Fig. 2a) is situated between the two boats and secured to the main spars of the raft frame. Coring takes place in the space between the core catcher and the boats (Fig. 1b). Firstly a piston is prepared (to act as an extrusion bung) for the core catcher by adjusting it so that it is held firm inside the core tube. Then a short length of rope is tied to the shaft of the piston (between the two adjustable portions), which is then placed in the slot cut into the core catcher plate so that the bottom of the piston is facing upwards. The piston and core catcher plate are then positioned in the bottom of the core catcher frame and the free end of the rope is loosely tied off (Fig. 2b). Another piston, held firm by friction, is positioned at the bottom of the core tube to which a piston rope is attached. The core tube is then filled with lake water by holding the core tube near horizontal just below the water surface. At this point the core tube becomes heavy, and is best partly supported by a person sitting on the raft, resting the core tube on the tops of their boots in the water. The corer head is then added to the core tube and secured using four eye bolts which subsequently afford a useful means of holding the core tube (Fig. 1b).

After measuring water depth at the core site, the core tube can be lowered in and coring rods added to the core head until a point (which can be marked by tape) where the base of the piston lies about 10-15 cm above the surface of the sediment. The piston rope is then secured. In shallow water, where the top of the corer is just below or above the water surface, it is best that the piston rope is looped round an oar shaft and held firmly by one person (Fig. 1b). This is because the piston needs to remain stationary above the corer head. Initially downwards pressure is gradually and smoothly applied to the metal rods by two people, one on either side of the raft. A gentle and even start to coring is important due to the potential for creating a downward pressure wave of water which can sometimes cause a disturbed and uneven sediment surface (Glew et al. 2001).

Once the core tube is well into the sediment, an extra person can be added to increase the downwards force (Fig. 1c). Even with secure anchoring, the raft may move a little when the metal rods are “driven down”. When this happens, the best approach is to let the raft re-position itself between each coring drive. Once the corer can be pushed no further, the piston rope is untied and held taut against the metal rods while the core is extracted. Some 2-3 people may be required to free the corer from the lake bed. Once the core tube has come out of the sediment, one person detaches the coring rods. When all the rods have been removed, the piston rope can be wrapped round the eye bolts to stop it from slipping. The corer can then be held fairly safely by supporting the corer head. Next the core tube needs lifting up by 2/3 people whilst the bottom of the tube is guided by another person (while still in the water) onto the piston situated in the bottom of the core catcher. This is best done with the person guiding the core tube lying on their front using their hands to feel the core into position. During this operation care and communication is needed taken to avoid injury to fingers, as the sediment filled corer is heavy. Once the core tube is sitting squarely on top of the piston it can be pushed down until it is resting on the core catcher plate (Fig. 2b). One person then holds the core tube, while the raft is brought to shore. Care must be taken as the raft approaches the shore, as the core catcher assembly is still in the water and can catch on the lake edge if it is shallow. The core tube and lower piston can be lifted out together from the core catcher aided by the rope attached to the piston. The core (Fig. 1d) is heavy and un-wieldy, and needs to be moved to the shore in carefully planned stages.

Extruding the core

Under normal circumstances the extrusion of a piston corer requires that the core tube is pushed over the piston (Verschuren 1993). In early trials the same method was applied to Big Ben but it was difficult to achieve evenly sliced intervals during extrusion. To overcome this, the extrusion process has been reversed by holding the tube stationary in a dedicated extrusion rig (Fig. 1e) and upward movement of the lower piston comes from a modified two ton car bottle jack (Fig. 1f). The modification of the car bottle jack consists of the addition of a circular metal plate at the top, so various lengths of 10 cm diameter drainage pipe (see below) can sit on it and act as packers as the lower piston gradually moves up during extrusion.

Before the extruding process commences, the extrusion rig is placed on top of a board (floor from raft) as this gives a flat platform in the field. Then the Dexion™ brace below the top plate is removed (Fig. 1e) so that the core tube can be easily lifted over and through the lower holder. The horizontal brace is then replaced and the upper holder is secured close to the core tube. The corer head is removed and the lower piston is fully inserted (by manually pushing down on the core tube and pulling on the piston rope simultaneously) so that both adjustable portions are inside the core tube. Subsequently the core tube/lower piston is placed on a section of 10 cm diameter drainpipe so that the top of the core tube is above the framework. The eye bolts are then threaded through the top plate and core tube holes until just short of flush with the inner wall of the core tube; otherwise the piston will be impeded later on. As the top plate is above the framework, two people standing opposite can use it as a lever to pull the top plate and core tube down into the framework. At the same time the piston is held stationary by keeping the rope tight - a pre-tied loop in the piston rope works well so a metal rod can be inserted and held by the other two people. This will move both pistons further up the core tube at the same rate. This procedure can be repeated by adding or replacing sections of 10 cm diameter pipe until the top piston is free from the core tube. We suggest that the car jack is not used at this stage, as it can cause the lower piston to move at a quicker rate than the top piston, resulting in water being compressed into the sediment thus disturbing the surface sediment.

With the top plate in place on top of the framework, two metal rods are placed through holes in opposite corners of the Dexion™, above the top plate. This stops the top plate/core tube rising out of the framework during extrusion. At this point the modified car jack can be placed under the drainage tube sections. Once ready to slice, a ring of the required thickness is placed on top of the core tube and the extrusion process can begin. The piston can be smoothly, accurately and evenly pushed upwards using the car jack. Once the jack has reached its full operating height, it can be removed and another section of 10 cm diameter pipe can be added. This is continued until the core is fully extruded.

Results and discussion

The Big Ben coring set-up has been in use since 2002. During this time we have successfully collected around 30 Big Ben sediment cores from several shallow UK lakes. For most sites we have cored in around 1 to 3 m of water. The deepest water in which we have successfully operated the corer is around 5 m and the shallowest around 0.5 m.

Due to the large volumes of wet sediment contained within a single 1 cm sediment slice (c. 153 cm^3), we have found Big Ben cores to be particularly useful for characterising assemblages of rarer sediment remains, especially of aquatic macrophytes, invertebrates and fishes (Sayer et al. 2010b; Wiik et al. 2011; Madgwick et al. 2011). Further, Big Ben has benefited on-going palaeo-genetic and palaeo-isotope studies that also demand large volumes of sediment to obtain sufficient fossil remains (TA. Davidson, A. Geerts, CD. Sayer, unpublished data).

The value of the Big Ben system for macrofossil analyses is illustrated by the construction of a yield-effort curve (Fig. 3) for core sediments collected from Ormesby Great Broad, Eastern England (52°40′47.55″N, 001°39′29.69″E). In Fig. 3 the cumulative number of identifiable remains from individual macrophyte taxa (e.g. *Zannichellia palustris* seeds, *Ceratophyllum demersum* leaf spines, *Potamogeton obtusifolius* leaf tips) are plotted against the sediment volume used. This shows that the number of represented aquatic plant species remains constant after c. 110-150 cm^3 of wet sediment has been analysed, indicating that this is the minimum volume necessary to reliably characterise species richness (Fig. 3). Thus, a typical 1 cm slice from a Big Ben core provides ample material for plant macrofossil analysis where reliable species representation is a key concern. Indeed, the advantage of analysing large volumes of mud for this purpose is illustrated by a study undertaken at Barton Broad, Eastern England where bulk basal core samples added a further 15 species not recorded in traditional Livingstone piston cores (Madgwick et al. 2011).

Big Ben allows multi-proxy paleolimnology to be undertaken from a single core, as opposed to multiple sediment cores. It is simple in design and relatively easy to operate in shallow lake settings by a small team. The construction of a wide bore corer like Big Ben is straightforward and does not involve the manufacture of any particularly complex components. The diameter of the core tube, materials and technical measurements used to manufacture its associated apparatus will be dependant on local supplies. Thus specifications given here are only a guide to demonstrate how and what we have developed in our research group and do not need to be exactly mimicked. If wide-diameter cores are required for a palaeolimnological study, Big Ben is ideal.

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Table. 1 Key components of the Big Ben coring system as used at UCL, including technical information regarding materials and design.

Component name	Dimensions	Comments
Corer		
Core tube	Approximately 150 cm long, 0.5 cm wall thickness	Perspex material, 0.5 cm wall thickness required to give some rigidity whilst coring and extruding
Core catcher	Wooden spars 97 cm long, 9 cm wide, 3 cm thick. Angle iron 2.5 cm wide	Angle iron part of core catcher has centre point 22 cm from one end of spar. Length of spars dependant on individual design of raft (Fig. 2a)
Core catcher plate	22 cm square, 4 cm thick. Notch 11 cm long and 2.5 cm wide. Steel plate 1 mm thick	Solid wood sandwiched between two plates of steel as this stops the wood from splitting, swelling or being too buoyant. Make sure plate is a loose fit in bottom of core catcher
Extrusion system		
Extruding framework	Total height approximately 180 cm. Leave approximately 30 cm below bottom of the core tube (once in framework) to allow easy insertion of the modified jack and drain pipe sections for extruding (see below)	Aluminium (Dexion™) framework. Addition of a pair of handles means frame and core can be carried over short distances (Fig. 1e)
Base plate	46 cm long, 30 cm wide, 4.5 cm thick	Solid wood, gives stability to framework and a level jacking point
Lower holder	46 cm long, 30 cm wide, 2 cm thick. Situated approximately 42 cm above base plate	Solid wood, has centrally mounted 15 cm diameter plastic tube, 7 cm deep
Upper holder	2 wooden spars 44 cm long, 4.5 cm wide, 4.5 cm thick. Situated approximately 90 cm above base plate	Centrally notched to match curvature of core tube
Top plate	47 cm long, 30 cm wide, 3 cm thick	Solid wood, has centrally mounted 15 cm diameter plastic tube, 7 cm deep. Has exterior flange to aid fixing to top plate. Rim of top plate needs to be thick to take threaded holes to support core tube (Fig. 1f).
Metal rods	34 cm long, 0.8 cm diameter	Threaded rod with nut on one end acts as a stop when rod is inserted into frame
Modified car bottle jack	23 cm tall (with circular plate fitted), maximum lift height 16 cm. Circular plate 13.5 cm diameter, 3.5 cm thick	Top circular plate has recess on top to accommodate rim of drain pipe section. Plate fixed to jack by being clamped to and bolted through circular plate and top of jack (Fig. 1f)
Drain pipe sections	10 cm diameter, varying lengths ranging from 15 cm to 50 cm. Pipe joiners 13 cm diameter, 13 cm long	Some lengths of pipe have pipe joiners (Fig. 1f) glued to them. Be sure that the pipe sections join/un-join easily to joiners to aid extrusion process

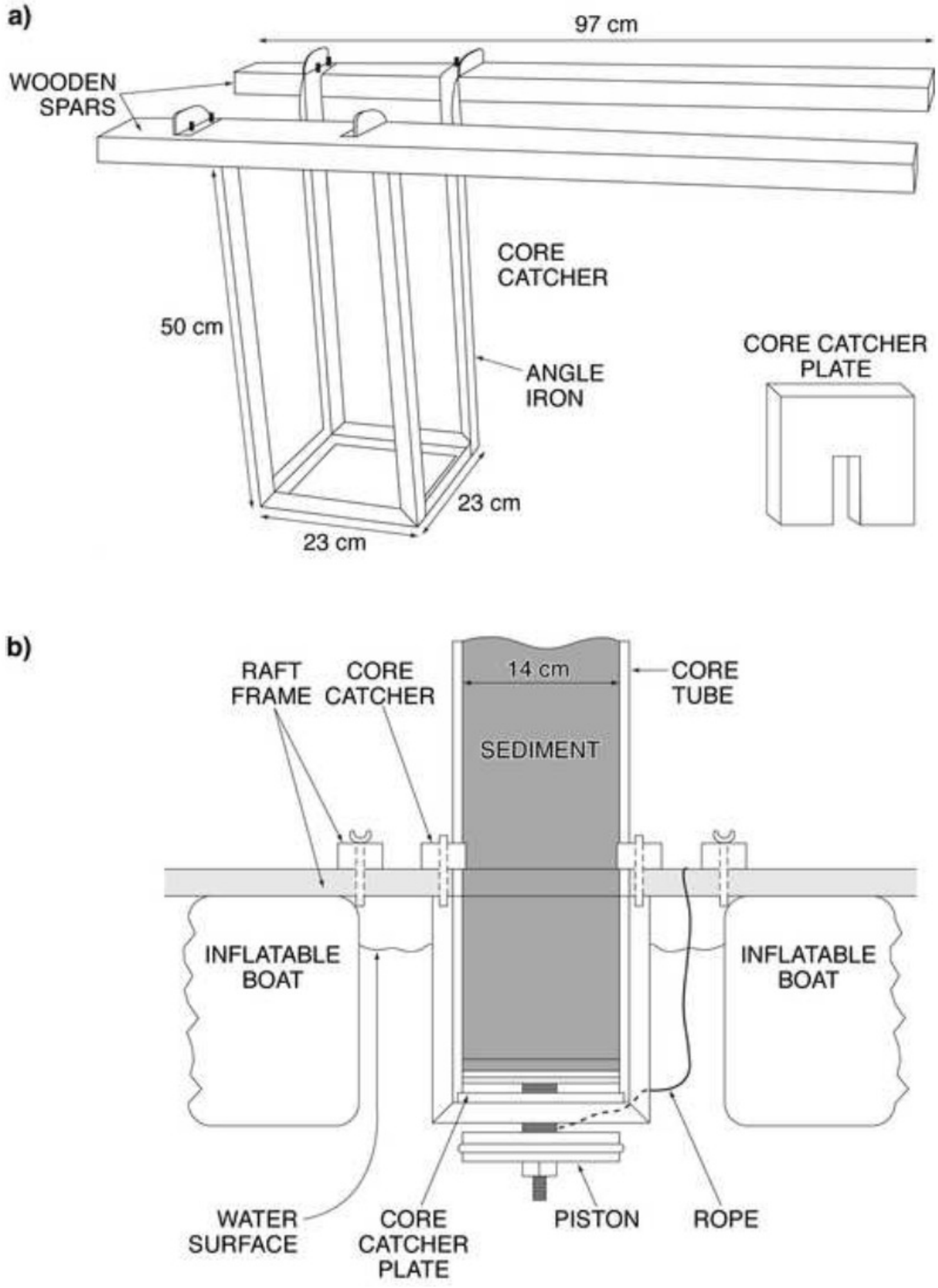
Figures

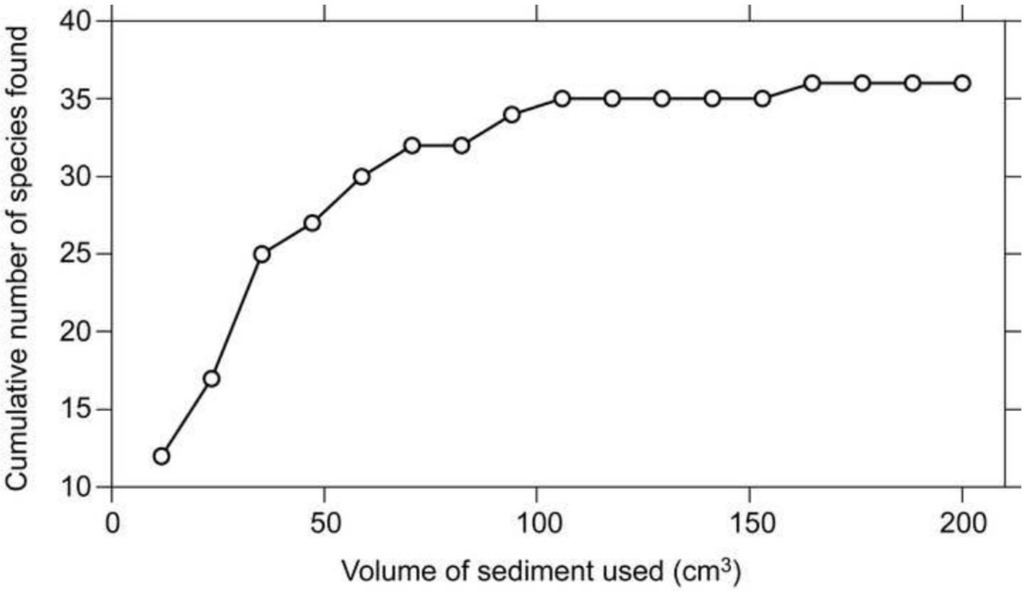
Fig. 1. Big Ben coring system: a) raft set up, b) coring set up, c) driving the corer, d) collected core, e) extrusion apparatus, f) modified bottle jack (left), attachment of core tube to extrusion top plate (middle), drainage pipe joiner for extrusion (top right), core head (bottom right).

Fig. 2. Core catcher device and its role in core collection. Drawings not to scale.

Fig. 3. Cumulative number of plant macrofossil remains found per volume of sediment for a sediment core sample collected from Ormesby Great Broad, a shallow lake in Norfolk, Eastern England.


a
b
c
d
CAMEL
e
f


a)
97 cm
WOODEN SPARS
CORE CATCHER
50 cm
ANGLE IRON
CORE CATCHER PLATE
23 cm
23 cm
b)
RAFT FRAME
CORE CATCHER
14 cm
CORE TUBE
SEDIMENT
INFLATABLE BOAT
INFLATABLE BOAT
WATER SURFACE
CORE CATCHER PLATE
PISTON
ROPE


Cumulative number of species found
40
35
30
25
20
15
10
0
50
100
150
200
Volume of sediment used (cm³)

Paper 3

Spatial and temporal representation of aquatic vegetation by plant macrofossils in a small, shallow freshwater lake

Gina H. Clarke, Carl D. Sayer, Simon Turner, Jorge Salgado, Sebastian Meis, Ian R. Patmore and Yan Zhao

Key words: Aquatic vegetation, plant macrofossils, shallow lake, taphonomy, dispersal, surface sediments

Introduction

Submerged macrophytes play a key role in the structure and function of lake ecosystems, influencing chemical and physical characteristics, whilst providing food, refugia and habitat for biota from multiple food web levels (Carpenter & Lodge, 1986; Jeppesen *et al.,* 1997; Jeppesen, 1998). They are also key components in conservation assessments for lakes Duigan *et al.,* 2007; +) and frequently underpin restoration initiatives, especially in shallow lakes (+). Aquatic plant communities are vulnerable to unwanted changes due to an array of human influences, not least eutrophication, acidification, hydrological manipulation and habitat disturbance (+). These changes frequently occur on decadal-centennial timescales and only rarely are such changes captured by historical records (e.g. Sand-Jensen, 2000; Davidson & Sayer, 2005; Madgwick *et al.,* 2011) and monitoring data (+;+), the latter of which seldom exceed 40 years.

Increasingly sedimentary macro-remains of aquatic plants (seeds, fruits, oospores, turions and various vegetative fragments) have been used to study past changes in the aquatic vegetation of lakes (e.g. Birks 2001, 2007; Birks & Birks 2000; Davidson *et al.,* 2005; Rasmussen & Anderson, 2005; Sayer *et al.,* 2010). In all of these studies workers have recognised the complex relationships which may exist between extant plant species and their fossil counterparts and in turn the need for further taphonomic studies on plant-fossil links (Madgwick *et al.,* 2011). The representation of plants by sedimentary macro-remains is controlled by numerous factors including lake morphology, macrophyte distribution and patchiness, the varying production of different plant fossils, transportation and re-distribution of fossils; persistence and preservation of fossil material and taxonomic issues (Dieffenbacher-Krall & Halteman, 2000; Zhao *et al.,* 2006; Dieffenbacher-Krall, 2007; Koff & Vandel 2008; Heggen *et al.,* 2012). All of these factors affect the degree to which macrofossils can be used to represent former aquatic plant communities and in turn interpretations that are made in palaeo-studies.

A number of studies have explored plant-fossil relations with a view to enhancing interpretations of sediment core sequences (+;+). The spatial representation of submerged macrophytes by macrofossils was studied by Zhao *et al.,* (2006) for Green Plantation Pond, a small, shallow lake in eastern England. By comparing macrophyte and macrofossil distributions for multiple, spatially-fixed survey points in 2000, several key observations were made. Overall, macro-remains were found to best represent local, ‘patch-scale’ vegetation within 20–30 m of the core site. Some species were significantly over-represented by macrofossils (e.g., *Chara* spp., *Nitella flexilis* agg., and *Zannichellia palustris*), while others were either under-represented (e.g. *Potamogeton* spp.), or not represented at all (e.g. *Lemna trisulca*). Nevertheless, the macro-remains effectively recorded the dominant plants in the lake with 63% of samples containing the three most abundant species and it was concluded that macrofossil analysis may be usefully employed to determine the dominant taxa in past aquatic plant communities of shallow, productive lakes.

The aquatic vegetation of Green Plantation Pond has undergone marked compositional change since 2000, with, among other lesser changes, a dramatic shift from a community dominated by *Elodea* spp., *Potamogeton pusillus* and *Chara* spp. to one dominated by *Ceratophyllum demersum*, *Ceratophyllum submersum* and *Chara* spp. after 2005. By comparing macrophyte and plant macrofossil distributions in Green Plantation Pond for 2000 and 2009, the present study sought to advance our understanding of macrophyte-macrofossil relations in both space and time, by assessing: (i) the degree to which major floristic changes in Green Plantation Pond were captured by accumulating sediments i.e. changes in macrofossil composition between 2000 and 2009, and; (ii) spatial representation of the changed macrophyte community by macrofossils. The implications of this study for paleolimnological research based on single sediment cores are discussed.

Study site selection

Green Plantation Pond (52^{o}55.29’N, 1^{o}05.48’E) is a small (1.6 hectares), shallow (mean water depth 165 cm, maximum depth of 330 cm), lake in North Norfolk, eastern England, that was excavated in the 1940s. It is an alkaline (141 mg $CaCO_3$ L^{-1} in 1999-2000), meso-eutrophic (29 μg total phosphorus L^{-1} and 4.1 μg chlorophyll-*a* L^{-1} in 1999-2000) lake which has two main basins and one small first-order inflow. Further site details are given in Zhao *et al.,* (2006). Similar to 2000, the site currently possesses a diverse macrophyte flora (>15 species) with a well developed depth-zonation of species (Table 1).

Materials and methods

Field sampling

Aquatic macrophyte surveys were undertaken in July 2000 and July 2008. In 2000 twelve transects were located at 10 m intervals using a Garmin 12XL® global positioning system (GPS) along the northern and southern banks of the lake. Then, at 10 m intervals along each transect, the submerged vegetation was recorded using the percentage volume infested (PVI) system (see Zhao *et al.,* 2006 for further details) assisted by use of a bathyscope and a double-headed rake. This resulted in a total of 108 open water survey points. In 2008 transects were established using the same system, but slight discrepancies meant that 18 transects were necessary to cover an equivalent area to 2000. This resulted in 121 open water sites (Figure 1).

To assess inter-annual variability of macrophyte communities in Green Plantation Pond, PVI surveys were undertaken over 1999-2009 with 30-40 points surveyed in each year. Points were not mapped using transects, but vegetation distribution was assessed using sketch maps. Species present in the lake were also recorded using the 1-5 (DAFOR) scale so that plants which were present, but nevertheless absent from PVI points could be incorporated in the surveys (Table 1). To help improve assessments of macrofossil representation of recently growing plants, data from previous years survey (1999 and 2007) have been utilised (Table 2). The 1999 data was based on 37 PVI points surveyed in August and the 2007 data was based on 37 points surveyed in July. The 1999 data were used to map the distribution of *Chara* spp. and *Zannichellia palustris* which were not recorded during the 2000 survey. Similarly, the 2007 data were used to map the distribution of *Z. palustris*, which was not recorded at the PVI points in 2008.

On 7th November 2000, after plant senescence, the upper 1.5 cm of lake surface sediment (probably representing less than 5 years of sediment accumulation) was collected using a Glew gravity corer (Glew, 1991) from 30 of the plant survey points located along the same transects and selected to evenly represent all areas of the lake. A repeat of this survey was undertaken on 24th April 2009 with surface sediment samples collected from 39 of the 2008 plant sample points coincident with positions that were also close to the 2000 sediment sampling locations. In both surveys sediment samples were stored at 4°C prior to further analysis.

Macrofossil analysis

Between 30-50 cm^3 of fresh sediment was used for macrofossil analysis, the exact volume being determined by water displacement. The samples were gently washed through meshes of 355 µm and 125 µm using a gentle jet of tap water. The 355 µm sample was examined in its entirety using a binocular dissecting microscope at 10-20x magnification and identifiable plant remains were enumerated. A sub-sample, approximately a quarter of the total sample, was analysed for the 125 µm fraction at a higher magnification of 20-40x. Identifications were made using an extensive reference collection of plant parts held at UCL, as well as seed atlases (Berggren 1964, 1981; Beijerinck 1976). All fossils are presented as numbers per 100 cm^3 of fresh sediment, the standard of macro-fossil data in palaeolimnological studies (Birks, 2001). Although macro-remains in surface sediments are not strictly macrofossils they are referred to as such here to simplify terminology.

The 2009 macrofossil samples included numerous thin leaf tips which could not be identified to species level but were attributed to either *Potamogeton pectinatus or Z. palustris,* were found. As so few *Z. palustris* plants were found in the lake for 2007/2008, it was assumed that these leaf tips belonged to *P. pectinatus*. For the 2009 macrofosssil samples *P. crispus* turion teeth were enumerated, whereas for the 2000 macrofossil samples turion fragments were counted as a unit. In order to compare the two years of data, turion teeth were converted to fragments by assuming 8 teeth per fragment based on an assessment of UCL reference material.

Data analysis

ArcView (v3.2) a geographical information systems (GIS) was used to manipulate and map all the lake survey data. The Topographic map of Green Plantation Pond (scale 1:10,000) was digitised using ArchInfo.

In order to compare the 2000 and 2008 macrophyte survey data and the two sets of macrofossil data Nonmetric Multi dimensional Scaling (NMDS) analysis (Minchin, 1987) was applied and plotted. Surface sediment samples were standardised prior to analysis using double Wisconsin and square-root transformations, while PVI data were only double Wisconsin transformed. Macrophyte community similarity was calculated using the Bray-Curtis dissimilarity index (Minchin, 1987). Statistical analyses were conducted in R (v.2.13; R Core Development Team 2) using the *vegan* library. Bray-Curtis dissimilarities were used to estimate variation in community composition: where sites are clustered together they have similar species composition, including abundances, while sites that are further apart have greater compositional dissimilarity.

Results

Vegetation survey comparison, PVI and spatial distribution 2000 and 2008 surveys

The number of species recorded over the past 10 years of surveys has fluctuated annually with the highest number of species recorded in 2007 and 2008 (Table 1). Inter-annual changes in species abundance were substantial with only *P. pusillus, Elodea* spp. and filamentous algae recorded in every year. *P. crispus, P. pectinatus, C. demersum, Ranunculus aquatilis* agg. and *Lemna trisulca* were relatively stable members of the community, with only a few absences from the record, but their abundances also fluctuated considerably.

Over the past decade the macrophyte community has shown marked changes (Table 1), mainly in the abundances of species present, with a shift from a community dominated by *Elodea* spp*.*, *Chara* spp., *P. pectinatus* and *P. pusillus* (<2001), to one dominated by *C. demersum, C. submersum, Chara* spp. and *P. crispus* (>2005). Abundances of charophytes show substantial inter-annual variation with years of absence often followed by years of high abundances. Large shifts in *Ceratophyllum* abundance are also particularly apparent. *C. demersum* started to increase in 2001 and peaked in 2003, but abundances remained high until 2005. In 2004 *C. submersum* started to dominate over *C. demersum* and this pattern continued until 2008. The increases in *Ceratophyllum* spp. coincided with elevated production of filamentous algae (Sayer pers comm.).

Spatial distribution and abundance changes between the macrophyte survey data in 2000 and 2008 are shown in Figure 2. Abundances of *P. crispus* increased substantially in 2008 in comparison to the 2000 survey, although it's location, remained relatively stable: dominating the deeper western basin, albeit spreading slightly eastwards in to shallower water during 2008. Likewise large changes are seen in the two *Ceratophyllum* species: *C. demersum* and C. submersum were rare and absent in 2000, while *C. submersum* was widely distributed in 2008. Increases in *Chara* spp. abundance are also evident between the two survey years and its location has shifted eastward to shallower water in 2008. *P. pusillus* was widespread in the western basin in 2000 and 2008, but absent from the PVI survey points in 2008 (although it was still present as a rare species in the lake). *Elodea* spp. which was present all over the lake in 2000 was much more localised in 2008, with a concentration of plants evident in the south-western part of the lake. The location and abundance of *Z. palustris* and *P. pectinatus* have remained relatively constant between the two survey years, with *Z. palustris* tending to occur in a small patch in shallow water close to the eastern inflow. *Lemna minor* was mainly found in the more wind-sheltered eastern arm of the lake and its abundance increased slightly in 2008. Although *M. spicatum* was absent from both the data sets it was known to be present within the lake in rare numbers at the time of sampling (Table 1).

Shifts in species composition between 2000 and 2008 are summarised by the NMDS plot (Figure 3) with all the 2008 macrophyte transects clustering together away from the 2000 transects. This separation is driven by the dominance of *P. pusillus* and, to a lesser extent, higher abundance of *Elodea* spp. and *N. flexilis* in 2000. The absence of *Lemna minor* and *C. submersum* in the 2000 data, and their presence in 2008 also contributes to the separation of the two data sets.

Macrofossil surface sample comparison 2000 and 2009 samples

A total of 7 and 10 submerged plants were represented by macrofossils in the sediments from 2000 and 2009 respectively (Table 2). In both datasets oospores of *Chara* spp. were the most abundant macrofossil occurring in all the sediment samples at concentrations ranging from 72 to 1604 per 100 cm^3 in 2000 and 10-1233 per 100 cm^3 in 2009.

Those species recorded prior to the 2000 survey (1998-2000), but not represented by macrofossils were *C. demersum, R. aquatilis* agg., *Ranunculus circinatus* , *L. trisulca*, and *Potamogeton natans*, all of which were rare in the lake. For 2009 the only species recorded in the previous two years of survey (2006-2008), but not present in the macrofossil samples was *Elodea* spp.

Macrophyte-macrofossil relationships

Comparisons between distribution and abundance patterns of the macrophytes and macrofossils are given in Table 2 and Figure 2. For both sets of macrofossil data oospores of *Chara* spp. are most abundant in the areas of the plant's growth in the southern shallows. The oospores have spread more widely eastwards in the 2009 macrofossil data, however, corresponding to the eastward spread of the plant in the 2008 PVI map. The widespread of oospores remains across the lake is also testament to their high production and ease of transportation (+;+). In 2000 *Elodea* spp. remains were most abundant in the central west basin, where the plant's growth was most concentrated. In line with the major decline of *Elodea* spp. in Green Plantation, remains were absent in the 2009 macrofossil samples, but this change may also reflect the influence of poor leaf preservation (see below). The macrofossil remains for 2009 also accurately reflect abundance increases for *Certophyllum* spp. (absent in 2000, but dominant in 2008) *L. trisulca*, *M. spicatum* and *P. crispus* between 2000 and 2008.

Remains of *P. pusillus* and *P. pectinatus* appear to be over-represented in the 2009 macrofossil record in comparison to %PVI data for 2008. This may be related to the difficulty of attributing a definitive species to the numerous leaf fragments derived from *Potamogeton,* or to the macrofossil sample reflecting the inter-annual variability of the macrophyte community (Table 1) and, in essence, representing macrophyte data from a number of years (see below). For both sets of macrofossil samples *Z. palustris* seeds were found in many more places than the recorded plants, with high numbers in the eastern and southern margins. The seeds seem to have spread considerably from the isolated bed of *Z. palustris* plants located close to the inflow in both the 1999 and 2008 surveys. In contrast despite the high abundance of *Ceratophyllum* spp. in the surveys reproductive remains in the macrofossil samples are sparse (Table 2, Figure 2). No *C. submersum* seeds were found in the macrofossils despite their presence on the plants during the surveys (Sayer pers comm.). *C. demersum* seeds were retrieved from the sediments, albeit in small numbers in comparison to their vegetative remains. The low retrieval of seeds is perhaps unsurprising, as *Ceratophyllum* plants are perennial, rarely fruit and rely on vegetative reproduction.

For both sets of macrofossil data reproductive remains (seeds and turions) of *Potamogetonaceae* were deposited primarily in the shallower lake margins with vegetative remains more widely and abundantly dispersed across the lake. *P. pectinatus* and *P. pusillus* both reproduce predominantly via vegetative means (Preston, 1995) so the relative lack of reproductive remains in the macrofossil record is unsurprising.

Relatively large numbers of *Nitella* spp oospores were found in the 2009 macrofossil samples but the plant was absent in 2008 and was only recorded over 1999-2002 (Table 1). *M. spicatum* was also present in the 2009 fossils and not present in the 2008 PVI data. The species was present as a rare species in 2008, however, and was recorded more abundantly in 2007 (Table 1).

Differences in the composition of the macrofossil surface samples are summarised in the NMDS analysis (Figure 4). The 2000 and 2009 data sets form distinctive clusters. The assemblages of the 2000 samples are mostly represented by *Elodea* spp., *P. crispus* and *P. pusillus,* while the 2009 samples are represented by *Ceratophyllum* spp. and *L. trisulca*. The macrofossil samples are thereby reflecting the shifts seen in the contemporary %PVI data (Figure 2).

Discussion

Species and community representation

Some 70% and 90% of the contemporary flora was recorded by macrofossil remains in the 2000 and 2009 sediment surveys, respectively. Typically it has been found that macrofossils often under-represent species diversity for aquatic plants (Davidson *et al.*, 2005, Koff and Vandel 2008; Salgado *et al.,* 2010; Madgwick *et al.,* 2011). Madgwick *et al.,* (2011) found 37% of historically recorded macrophyte taxa were recorded by the macrofossils records from Barton Broad. Salgado *et al*., (2010) reported that 81% of the species historically recorded for Loch Leven, Scotland, were present in the macro-remains. Whereas, Davidson *et al*., (2005) suggested that approximately 40% of historically-recorded aquatic macrophyte taxa were recorded by macro-remains for Groby Pool, a similar shallow, meso-eutrophic English lake. Thus macrofossil remains always likely under-estimate species-richness in the submerged vegetation of lakes. In particular those species reliant on vegetative parts for their reproduction may be especially under-represented due to their ability to readily decay (Koff and Vandal 2008). From a paleolimnological standpoint it is essential to understand which species are over- or under-unrepresented in the macrofossil record. Although in this study the macrofossils record species richness remarkable well (due to multiple samples), some species found in the contemporary surveys are not present in the macrofossil record, namely *C. demersum* in the 2000 macrofossils (although it was recorded by aquatic pollen during this survey – Zhao *et al.,* 2006) and *Elodea* spp. in the 2009 macrofossils.

Preservation is probably the key reason for the absence of *Elodea* spp. in the 2009 sediment samples despite its presence in the contemporary samples. For some species like *Elodea* with soft tissues, decomposition is often intensive and they are, therefore, unlikely to be preserved as fossils (Koff and Vandel, 2008, Davidson *et al*., 2005). *Elodea* spp. remains were, however, found in the sediments from 2000 possibly because *Elodea* spp. plants were significantly more abundant during 1999/2000 or a more plausible explanation for their presence is that the surface samples for the Zhao *et al*., (2006) study were taken in November, before the remains had a chance to degrade. The absence of *Elodea* spp. from a macrofossil record should not, therefore, be interpreted as a real absence from the lake.

In contrast some species absent from the contemporary record were recorded in the macrofossil samples. The charophyte *N. flexilis* was absent over 2003-2008. However, relatively high numbers of oospores were still present in the 2009 macrofossil samples. A possible explanation for this is that small numbers of plants were missed during the post-2003 surveys. The oospores of Charaeceare are light and easily transported (Birks, 1973, Dieffenbacher-Krall & Halteman, 2000) possibly accounting for their widespread distribution in the 2000 and 2009 macrofossils. Other studies have also found macro-remains of charophytes when they have not been found in the contemporary vegetation (Koff and Vandel 2008, Davidson *et al*., 2005). (Seed bank presence discussion- more to follow).

Z. palustris was also clearly over-represented in the macrofossil record due to the large number of seed remains found in comparison to the small number of plants recorded by contemporary surveys. *Z. palustris* is a pseudo-annual species and is known to be a prolific seed producer (Yeo, 1966; +) which predominantly relies on seed production for over wintering.

Increases in Lemnid (*L. trisulca and L. minor*) species occurred over the repeat sampling period and were recorded well by the macrofossils. *Lemna minor* first appeared in the DAFOR surveys in 2004 but was not present in the intensive PVI survey from 2008 possibly due to its amalgamation at the lake margins. Numbers of *Lemna trisulca* have also increased across the whole lake (Figure 2). These changes have been recorded in the macrofossil record with both *Lemna* species absent in the 2000 surface sediments but present, albeit in small quantities, in the 2009 sediments.

Do macrofossils reflect the dominant shift in aquatic plant communities?

- Shift from *Elodea/ Chara*/ fine leaf *Potamogeton* dominated to a *Ceratophyllum*/ *Myriophylllum* and *P. crispus* dominated community- do macrofossils record this? Yes - issues with *Elodea* spp. preservation (see above).
- It is likely that *Ceratophyllum* spp. were absent from the macrofossil samples in 2000 and not just missed during identification because although present the plant was still relatively rare in the lake. The macrofossil samples from 2008 record the rise in *Ceratophyllum* spp. after 2001 well.
- However, some issues with the use of surface sediments- Timing of core taken, how much time the surface samples represents. On the plus side- surface sediments eliminate the influence of annual seasonal variability of plant succession.
- *Z. palustris*/fine leaf *Potamogeton* leaves also may be affected by preservation and taxonomy - no way of distinguishing between the two when very little in the macros as just leaf tips. The reason they were fond in the 2000 macros may be because the material had not rotted down so much so the leaf stems and joints were present – implications for timing of sediment retrieval.
- Seeds from *P. pectinatus* are rare to find as the species has been present in the lake for the 15 years but no seed found in either macrofossil survey.

Implications for future macrophyte/macrofossil studies

Increasingly macrofossil analysis has been used to identify changes in the macrophyte community in reaction to catchment-scale disturbance, especially nutrient enrichment (+;+). For example, distinct phases of macrophyte development have been identified using palaeolimnology at Felbrigg Lake (Sayer *et al*., 2010) with a shift from *Myriophyllym-Chara-Potatmogeton* (c. pre-1900), to *Ceratophyllum- Chara Potamogeton* (c. 1900-1950) to dominance by *Z. palustris* and *Potamogeton* (c. post-1950) linked to progressive eutrophication. It is hard to know if the persistent increase of filamentous algae between 2001 and 2010 and the shift to dominance of *C. demersum* and *C. submersum* at Green Plantation over the past decade is indicative of nutrient-enrichment in the lake as evidenced in Felbrigg Lake and other studies (Mjelde & Faafeng, 1997; Preston *et al.,* 2002).

It is only through the continuation of the annual surveys at Green Plantation that phases of macrophyte development can be deciphered over and above the noise of the inter-annual plant variability, highlighting further the importance of long term vegetation monitoring in species-rich lake sites. Unfortunately, resources for such vegetation monitoring are often limited and in such circumstances it seems that palaeolimnology offers a creditable alternative, summarising whole lake community structure and changes in plant dominance often from only a single sediment core, at least in relatively small lakes (Davidson *et al.,* 2005; Sayer *et al.,* 2010; Heggen *et al.,* 2012) This study, however, has identified a few limitations when using single sediment macrofossil cores to represent changes in the submerged aquatic vegetation.

Firstly, it is well established that the location of the macrophyte core is paramount and this has been reiterated through this study. It has been shown that some plants disperse macrofossils widely across a lake and some are deposited close to where the plant is growing (Figure 3 and see Zhao *et al.,* 2006; Heggen *et al.,* 2012), that the deposition of a plant's reproductive remains are often more spatially discrete in contrast to the dispersal of it's corresponding vegetative parts (e.g. *P. pusillus, P. crispus*, Figure 3) and that the bottom topography of the lake can affect the distribution of macrofossils (Koff and Vandel, 2008 + other refs). As analysis of macro- remains is very time- consuming it is important to maximise research effort and take sediment core samples from a location that best represents the lake macrophyte community. Most studies suggest this to be from the littoral zone (Koff & Vandel, 2008, Davidson *et al*., 2005) but this study suggests that in shallow lakes, with relatively uniform lake bed topography, many areas are in fact suitable for macrofossil coring.

Secondly, caution is needed when significant and discrete plant zonation occurs within the macrophyte community. In such cases adoption of a multi- core approach may be more effective for summarising macrophyte community lake structure and understanding long-term vegetation change.

Thirdly, changes and advancement in the macrofossil technique over the last decade have highlighted new identification issues and provided extra information on the representivity of macrofossils for reconstructing aquatic vegetation. As the number of studies comparing macrofossil remains with contemporary vegetation surveys have increased recently so has our knowledge regarding the over- and under- representation of remains. Inevitably some species remains were possibly overlooked in the 2000 macrofossil analysis simply because they had not been encountered before and more work is still required to help distinguish between some species within the sediments particularly of the vegetative remains. In particular for this study a distinction between *C. submersum* and *C. demersum* leaf spines, and between the fine leaved *Potomogeton* species, would be advantageous. The use of multiple cores or an increase in the volume of sediment analysed may help provide further insights in to the abundances of these species as more reproductive remains of each species might be gathered. In addition repeat complimentary pollen analysis could also be undertaken at the site to maximise the numbers of species recovered (see Zhao *et al.,* 2006; Davidson *et al.,* 2005, Madgwick *et al.*, 2011).

Conclusions

Increasingly macrofossil records from cores are used to summarise lake vegetation community change in shallow lakes (Bradshaw *et al.,* 2005; Sayer *et al.,* 2010; ++). However, satisfactory interpretation of quantitative macrofossil data necessitates information concerning the modern representation and dispersal of individual macrofossil taxa and the representation of contemporary vegetation by macrofossil assemblages. It is only through spatially extensive macrofossil analysis and continuous annual survey work, of the like undertaken here, that such information will be gathered. Reassuringly, this study shows that macrofossils do provide a reliable indication of sub-decadal temporal change in the dominant components of the aquatic vegetation of small, shallow lakes.

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Table 1: Green Plantation Pond macrophyte surveys 1998-2012

Species	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
Myriophyllum spicatum	0	1	1	3	3	2	0	1	0	2	1
Potamogeton crispus	2	2	3	0	3	2	2	3	2	3	3
P. pectinatus	3	2	2	0	1	2	1	2	3	1	1
P. pusillus	3	2	3	2	2	1	2	1	2	2	1
P. natans	1	0	1	0	0	0	0	0	0	0	1
Ceratophyllum demersum	0	0	1	3	3	5	3	3	2	2	2
Ceratophyllum submersum	0	0	0	1	1	2	4	5	5	4	4
Elodea sp.†	1	5	5	2	3	3	2	3	2	2	3
Ranunculus circinatus	0	1	0	1	1	1	2	1	2	3	2
R. aquatilis/ peltatus	1	1	1	1	3	2	2	1	0	1	2
Zannichellia palustris	2	1	0	0	0	0	0	0	1	2	1
Lemna trisulca	0	0	1	2	2	1	1	1	1	1	2
Lemna minor	0	0	0	0	0	0	1	1	1	2	2
Alisma plantago-aquatica	1	0	0	0	0	0	0	0	0	1	1
Nitella flexilis agg.	0	1	1	2	2	0	0	0	0	0	0
Chara spp.	4	4	0	0	3	0	0	1	3	3	3
Chara vulgaris var. *papillata.*	X	X								X	X
Chara contraria var. *hispidula*	X								X		
Chara contraria					X			X		X	X
Chara globularis,										X	X
Total number of species	*10*	*10*	*10*	*9*	*12*	*10*	*10*	*12*	*11*	*16*	*17*

DAFOR (dominant (5), abundant (4), frequent (3), occasional (2), rare (1)) scores for submerged macrophyte species recorded 1998-2005. † dominantly *E. canadensis*, but some E. nutalli recorded. Charophyte species present marked with an X with identifications provided by Nick Stewart – the National Recorder

Table 2. Relationships between the dominant plants and their corresponding macrofossils.in 2000 and 2008 for Green Plantation

	1999/ 2000 macrophyte surveys and 2000 macrofossil samples			**2007/ 2008 macrophyte surveys and 2009 macrofossil samples**		
Species	**% of total PVI points with plant**	**% of total samples with reproductive remains**	**% of total samples with leaf remains**	**% of total PVI points with plant**	**% of total samples with reproductive remains**	**% of total samples with leaf remains**
Zannichellia palustris	3.6	37	-	2.7	53	- *
Potamogeton crispus	35.7	13	53	42.2	66	28.2
Potamogeton pusillus	45.2	30	40	2.7	2.5	33.3
Potamogeton pectinatus	8.4	20	-	1.6	-	43.5*
Chara spp.	16.7	100	-	22.91	100	-
Nitella flexilis agg.	4.8	27	-	-	64	-
Ceratophyllum demersum	0.9	-	-	11.5	5.1	- **
Ceratophyllum spp combined	1.8	-	-	59.4	-	100**
Myriophyllum spicatum	-	-	-	1.3	-	10.2
Elodea spp	72.6	-	67	8.7	-	-
Lemna trisulca	0.01	-	-	7.5	-	10.2
Lemna minor	-	-	-	8.1	-	5.1

PVI data is combined for the 1999 (37 survey points) and 2000 (108 survey points) surveys, and, the 2007 (37 survey points) and 2008 (update 121 survey points). Macrofossil remains were extracted from 30 samples for the 2000 data set and 39 samples for the 2009 data set. Reproductive remains include seeds, oospores and turions. PVI scores for plants not represented by macro- remains were: *Ranunculus circinatus* (present but not recorded in the points in 1999/2000 and 9.4% in 2007/ 2008), *Ranunculus aquatilis/ peltatus* (0.3% in 1999/2000 and 1.3% in 2007/2008). * The 2009 macrofossil samples contained several fine leaf tips which were identified as '*Z. palustris*/ fine leaf *Potamogeton* species' and occurred in 43.5% of points. These were too small to be identified to species level but were assumed to be *P. pectinatus* leaf fragments as *Zannichellia* plants were so rare within the lake. **The *Ceratophyllum* spp category combines *C. demersum* and *C. submersum* but the leaf spines in the macrofossil samples were not identified to species level (see discussion). No reproductive remains of *C. submersum* were found in the macrofossil samples.

Figure 1. Green Plantation Pond and immediate surroundings (a) and (b) site water depth map.

Not shown

Figure 2. Comparison of macrophyte % PVI for 2000 and 2008 and macrofossil densities for 2000 and 2009 surface sediments for key species. PVI for Chara spp. for 2000 macrophyte data are based on a detailed survey (n=37) undertaken in August 1999 and point locations for these are estimated subjectively beased on a field map (see text). The locations for Z. palustris for 2008 have been annotated based on observations in the field as no plants were prsent in the PVI survey points.

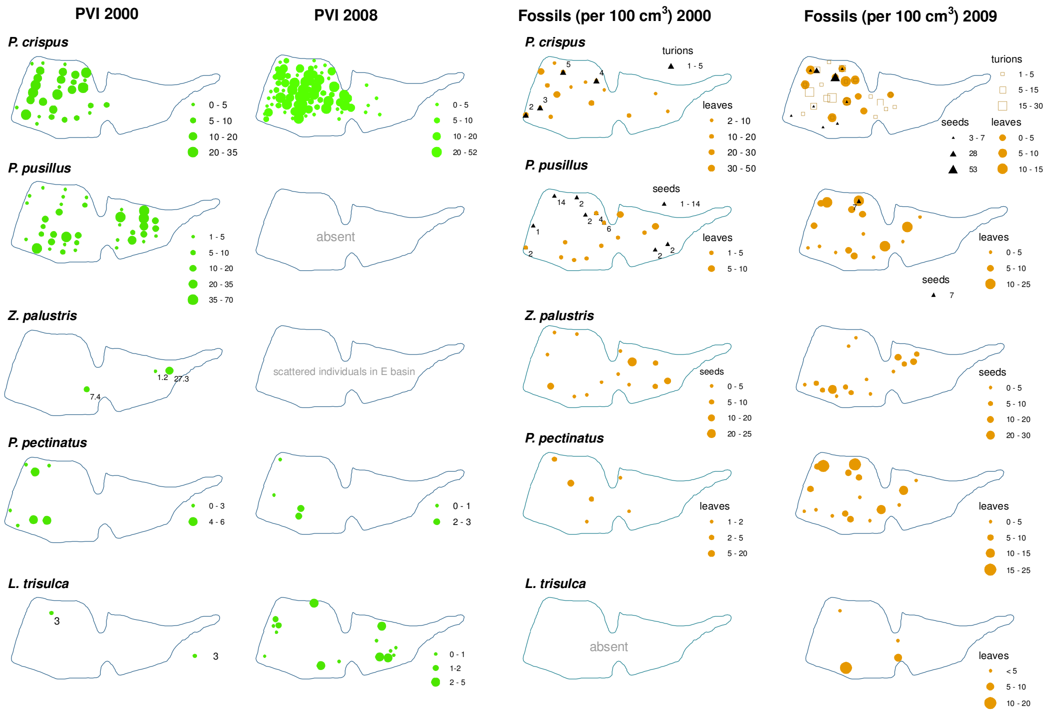


Figure2.Cont

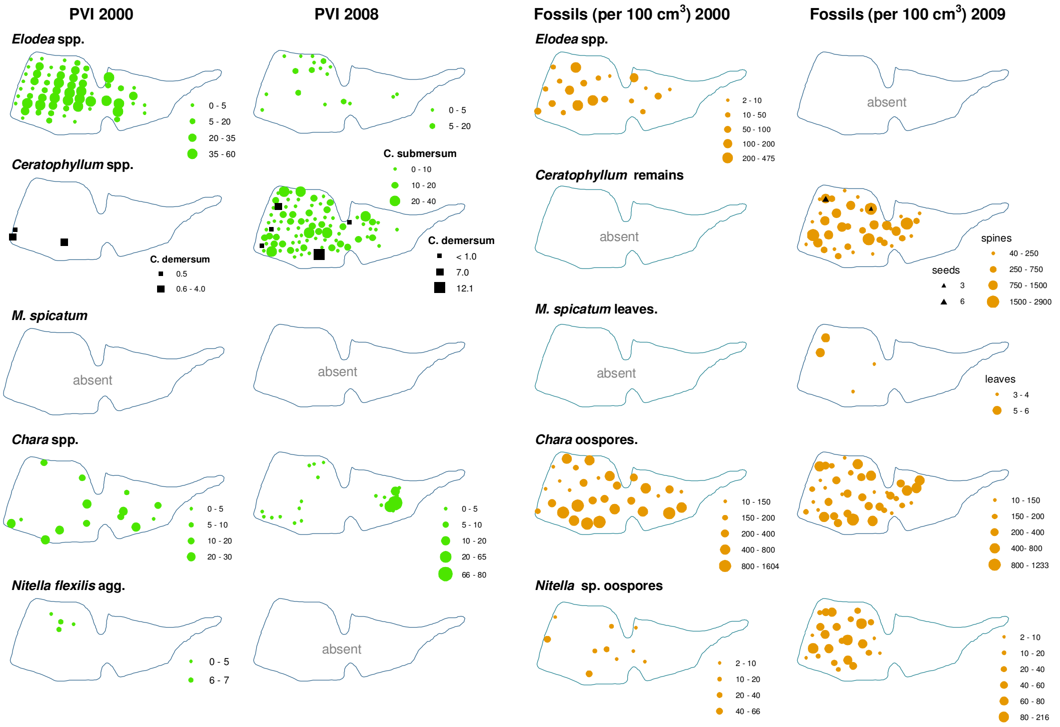


Figure 3. NMDS plot of the 2000 and 2008 % PVI data from Green Plantation pond (2000 data- filled circles, 2008 data- open circles)

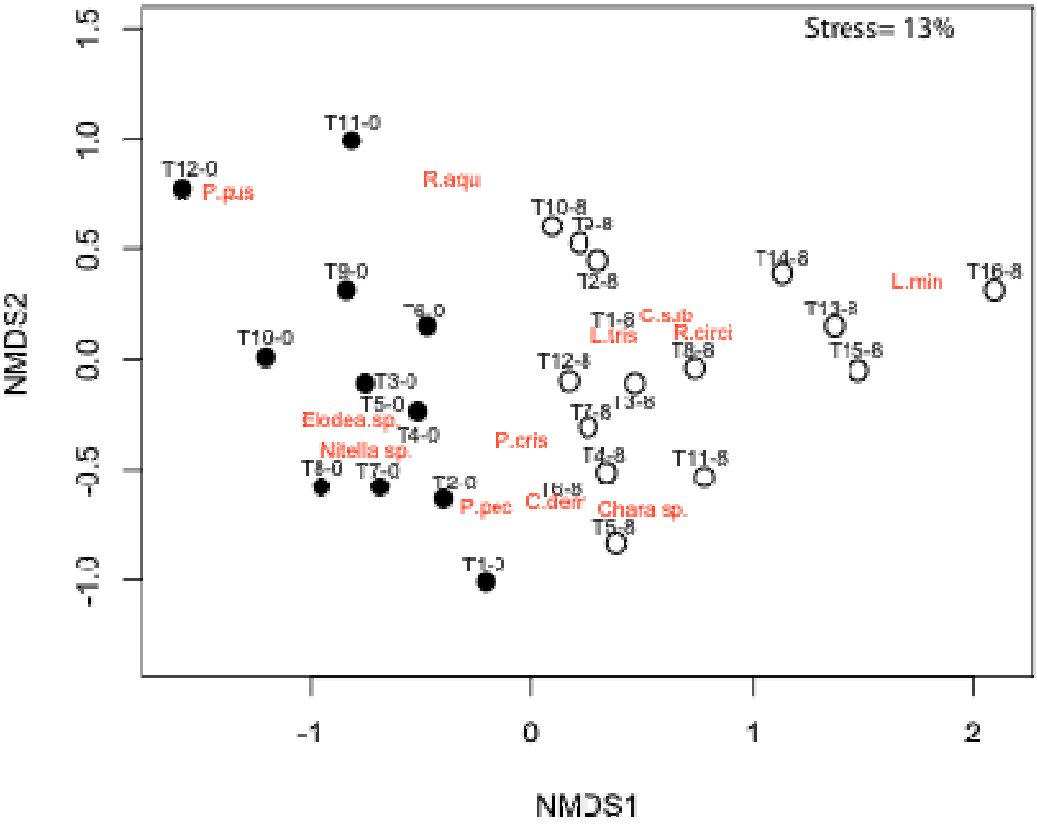
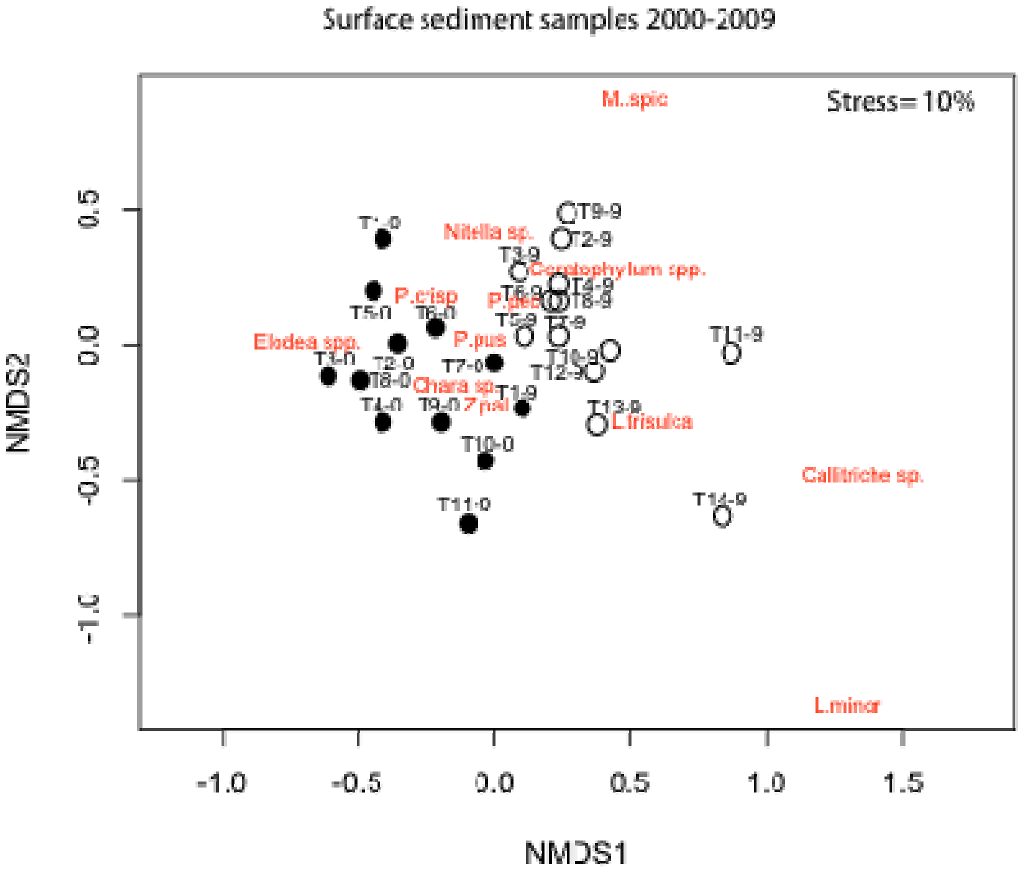


Figure 4. NMDS plot of the 2000 and 2009 Surface sediment macrofossil data from Green Plantation Pond (2000 data- filled circles, 2009 data- open circles)



Paper 4

A comparison between living populations of diatoms, aquatic plants, Cladocera and chironomids and their sub-fossil representation in the surface sediments of an acidified lake.

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Introduction

In assessing the value of palaeoecological methods to address questions of biodiversity relevance the main challenge is to understand how the fossil record relates to the biodiversity of contemporary populations. This relates not only to problems of preservation within and between fossil groups in different settings, but also to issues of taxonomic resolution and to methodological questions of sediment core locations, sediment core sample sizes etc.

Here we consider these questions with respect to surface water acidification, a major problem for low alkalinity surface waters in many, mainly upland regions of Europe, associated with acid deposition and its legacy over the last ca. 150 years. We restrict our study to those biological groups that are likely to leave a fossil record in acid waters and that are routinely used by palaeolimnologists in studies of freshwater ecosystem change. These include diatoms, aquatic plants, Cladocera, and chironomids. For each group we compare inventories of taxon presence and abundance from contemporary samples with their representation in the surface sediment using the Round Loch of Glenhead (Figure 1) as a case study.

The Round Loch of Glenhead is an acidified Scottish lake that has been extensively studied and is one of the main monitoring sites in the UK Acid Waters Monitoring Network (Shilland et al., 2012, http://awmn.defra.gov.uk/sites/site_07.php).

For diatoms we have used samples collected in August 2010 from littoral stone surfaces (the epilithon) and from sediment traps. Our hypothesis is that the sediment samples are richer than the epilithon normally used for monitoring as: (i) core material includes a mixture of diatoms from all habitats in the lake, not only the epilithon; and (ii) preservation of diatoms in the sediments of acid lakes is usually excellent.

For aquatic plants we have used data from: (i)the routine AWMN plant survey of August 2009; (ii) surface sediment samples collected in 2010 using an Ekman grab from a transect perpendicular to the east side of the island; and (iii) a surface sediment sample a deep water site adjacent to the Deep1 and Deep2 core locations (Figure 1). Our hypothesis is that *Isoetes lacustris* will be well represented at all water depths as megaspores but that other plants will be represented better in the littoral zone close to their living stands.

For Cladocera we have used data from three timed open-water sweeps of 2 minutes with a hand held 20 cm net (mesh size 100 µm) from the shore (Figure 1). The samples were preserved with Industrial Methylated Spirit (IMS). These have been compared with fossil material from the surface sediment samples collected along the transect (Figure 1) and from the top of the Deep1 core collected in July 2010. Our hypotheses were that: (i) the non-Cladoceran component of the plankton sweeps would not be preserved; (ii) *Daphnia* populations, if present, would be under-represented in the surface sediment samples; and (iii) the surface sediment samples would contain a richer assemblage than those contained in the contemporary samples.

To characterize the living Chironomidae larval community, three replicate samples at different depths were taken using either a kick sample (shallow water) or an Ekman grab along the depth transect (Figure 1) in July 2010. The samples were taken at 0.8, 3, 5 and 10 m depth (12 samples). Chironomidae pupal exuviae samples were also collected in the spring and summer of 2010 and 2011. The exuviae were mounted in Euparal® counted and identified to the required taxonomic level using a stereo microscope. Our hypotheses were that: (i) the Chironomidae species assemblages would differ along a depth transect, with the upper littoral being the most dissimilar from the 10 m depth ones; (ii) the exuviae samples would contain a richer assemblage at species level, but not at genus level, than those contained in contemporary larvae samples.

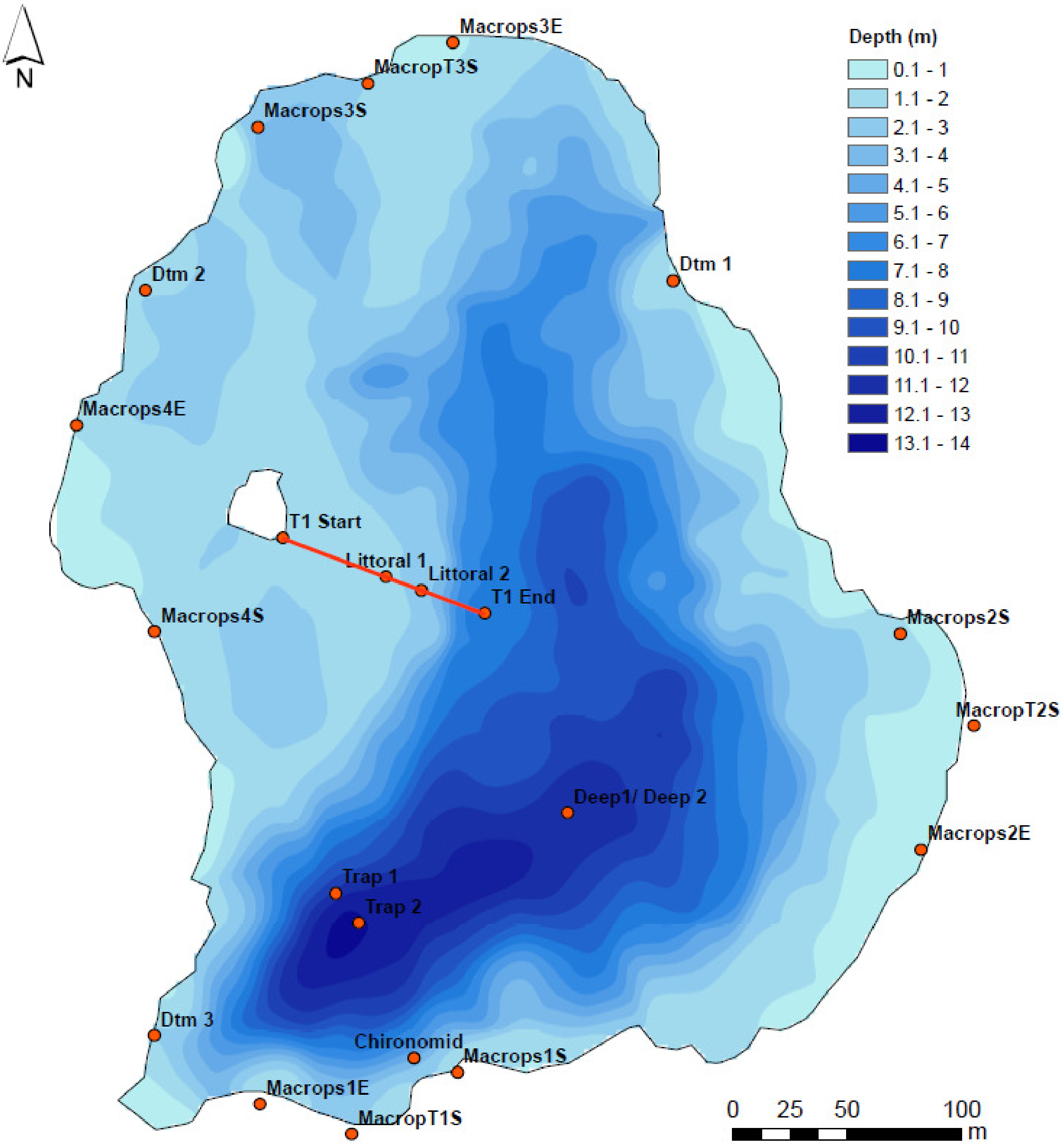

Figure 1 Map of the Round Loch of Glenhead showing water depth and sampling locations (courtesy of Simon Turner).

Results

Diatoms

Planktonic diatoms are usually absent from very acid lakes, but such lakes are good environments for benthic diatoms growing in a range of habitats including the epilithon, epipsammon, epiphyton and epipelon. In acid upland lakes in the UK the dominant habitat is the epilithicon and here we make a comparison between the diatom flora of the epilithon of the Round Loch of Glenhead, pooled from three sampling locations around the lake, and the composition of the diatom assemblage from a sediment trap exposed fro one year 1.5m above the sediment surface close to the deepest point in the lake (Table 1). The data are expressed as percentages of a ~300 total count in both cases.

The trap sample contains 47 species compared to 27 in the epilithon and the trap assemblage has a more even distribution of taxa by abundance. However, the four dominant taxa, *Navicula leptostriata*, *Eunotia incisa*, *Fustulia rhomboides* var. *saxonica* and *Brachysira brebissonii,* are the same in both. The main mismatches are *Peronia fibula* and *Tabellaria binalis* f. *elliptica* which are both much more abundant in the trap samples than the epilithon indicating that these taxa are common in the lake but occurring predominantly in non-epilithic habitats. Overall the sediment sample provides a more complete representation of diatoms growing in the lake than the living epilithic sample.

Table 1. Comparison between diatom assemblages from a sediment trap and from a pooled epilithic sample from the Round Loch of Glenhead.

Code	**Name**	**2010 Trap (%)**	**2010 Epilithon (%)**
AC013A	Achnanthes minutissima	0.2	0.0
AC022A	Achnanthes marginulata	1.3	0.1
AC9975	Achnanthes [altaica var. minor]	0.2	0.0
AU010A	Aulacoseira perglabra	1.3	0.0
AU010B	Aulacoseira perglabra var. floriniae	0.6	0.0
AU9999	Aulacoseira sp.	0.2	0.0
BR001A	Brachysira vitrea	0.6	0.0
BR003A	Brachysira serians	0.6	0.5
BR006A	Brachysira brebissonii	7.3	25.9
CM010A	Cymbella perpusilla	1.1	0.0
CM014A	Cymbella aequalis	0.4	0.0
CM017A	Cymbella hebridica	0.0	0.1
CM048A	Cymbella lunata	1.3	0.0
CM049A	CM049A	0.2	0.0
CY006A	Cyclotella kuetzingiana	0.2	0.0
EU002B	Eunotia pectinalis var. minor	0.2	0.0
EU003A	Eunotia praerupta	0.2	0.0
EU007A	Eunotia bidentula	0.0	0.7
EU009A	Eunotia exigua	1.9	0.1
EU011A	Eunotia rhomboidea	3.8	1.5
EU014A	Eunotia bactriana	0.4	0.2
EU015A	Eunotia denticulata	0.4	0.9
EU045A	Eunotia nymanniana	0.0	0.1
EU047A	Eunotia incisa	14.1	6.9
EU048A	Eunotia naegelii	4.4	1.4
EU049A	Eunotia curvata	1.7	0.0
EU051A	Eunotia vanheurckii	0.0	0.1
EU051B	Eunotia vanheurckii var. intermedia	0.2	0.0
EU057A	Eunotia exgracilis	0.2	0.0
EU9960	Eunotia [tenella/paludosa]	0.0	0.1
EU9961	Eunotia [vanheurckii var. 1]	0.0	1.1
EU9965	Eunotia [sp. 10 (minima)]	1.1	0.5
EU9999	Eunotia sp.	0.8	0.0
FR005D	Fragilaria virescens var. exigua	1.5	0.0
FU002B	Frustulia rhomboides var. saxonica	8.2	34.7
FU002F	Frustulia rhomboides var. viridula	2.5	0.0
GO004A	Gomphonema gracile	0.2	0.0

NA006A	Navicula mediocris	1.0	0.6
NA033A	Navicula subtilissima	3.4	1.9
NA044A	Navicula krasskei	0.4	0.0
NA046A	Navicula contenta	0.4	0.0
NA048A	Navicula soehrensis	0.2	0.0
NA156A	Navicula leptostriata	15.3	18.5
NA158A	Navicula cumbriensis	0.0	0.4
NA167A	Navicula hoefleri	1.7	0.1
NE004A	Neidium bisulcatum	0.4	0.0
PE002A	Peronia fibula	6.9	0.2
PI9999	Pinnularia sp.	0.6	0.0
SE001A	Semiorbis hemicyclus	0.4	0.0
SP002A	Stenopterobia sigmatella	0.4	0.0
TA001A	Tabellaria flocculosa	2.5	1.5
TA003A	Tabellaria binalis	0.4	0.1
TA003B	Tabellaria binalis f. elliptica	2.1	0.1
TA004A	Tabellaria quadriseptata	6.9	1.5
	TOTAL TAXA	**47**	**27**

Aquatic plants

The macrophyte flora of the Round Loch of Glenhead is species-poor, and characteristic of an upland oligotrophic loch with the dominant taxa being the acid-tolerant isoetid species, *Lobelia dortmanna* and *Isoetes lacustris* as well as *Juncus bulbosus* var. *fluitans* (Table 2). Surface sediments were collected along a transect in the loch (Figure 1) in order to asses how faithfully the extracted macrofossils represented the current aquatic flora of the site (Table 2).

Table 2 Comparison between the aquatic macrophyte flora of the Round Loch of Glenhead and macrofossils found in surface sediments. DAFOR is an index of abundance from rare (1) to abundant (5).

SiteCode	YEAR	Macrophyte Code	Scientific Name	DAFOR	Macrofossils found
RLGH	2009	ZZZ20	Batrachospermum sp.	3	
RLGH	2009	Elp	Eleocharis palustris	1	
RLGH	2009	Isl	Isoetes lacustris	4	Yes
RLGH	2009	Ja/Jac	Juncus articulatus/Juncus acutiflorus indet.	2	Juncus spp
RLGH	2009	Jba	Juncus bulbosus var. fluitans	4	Juncus spp
RLGH	2009	Jc	Juncus conglomeratus	1	Juncus spp
RLGH	2009	ZZZ50	Jungermannia sp.	2	
RLGH	2009	Lit	Littorella uniflora	3	
RLGH	2009	Lob	Lobelia dortmanna	5	Yes
RLGH	2009	Mal	Myriophyllum alterniflorum	2	
RLGH	2009	Ppol	Potamogeton polygonifolius	2	
RLGH	2009	Rfl	Ranunculus flammula	2	Seed fragment
RLGH	2009	Scapun	Scapania undulata	1	
RLGH	2009	Spa	Sparganium angustifolium	2	
RLGH	2009	Sphagaur	Sphagnum auriculatum	2	
RLGH	2009	ZZZZ1	Filamentous green algae	4	

The macrofossil record seems to represent the presence and abundance of the dominant plants, *Lobelia dormanna, Isoetes lacustris* and *Juncus* (at the genus level), fairly accurately. However the macrofossil record failed to register the presence of *Littorella uniflora, Potamogeton polygonifolius, Myriophyllum alterniflorum* and several other less abundant taxa. It is known that *Littorella uniflora* leaves few macrofossil remains. The absence of *Potamogeton polygonifolius* and *Myriophyllum alterniflorum* may be due to the relatively low abundance of these species in the lake (Table 2) and/or to the patchiness of macrofossil deposition in the sediment. This might be overcome by increasing sampling effort or increasing the volume of mud analysed per sample.

In general it appears that macrofossils can be used to record the dominant macrophytes in the lake, but not the full range of the flora. Future work will examine the pollen content of the sediments to assess whether additional taxa can be identified.

Cladocera

To characterise the contemporary Cladoceran fauna of the RLGH, three open water samples (Figure 1) were collected, one in spring 2010 and two in spring and summer respectively of 2011. The results are presented in Table 3 and Figure 2. For comparison the Cladocera remains from two littoral surface sediments from the loch are presented in Table 3 and Figure 3. The surface sediment sample from a deep water core (Deep 1) has still to be analysed.

Table 3 Cladocera species present in the contemporary water column samples and the littoral surface sediments from the RLGH

Species	**Cont 02/05/2011**	**Cont 24/07/2011**	**Cont 04/05/2010**	**Litt 1, 0-1cm**	**Litt 2, 0-1cm**
Units	*No. per L*	*No. per L*	*No. per L*	*Relative % abundance*	*Relative % abundance*
Acroperus harpae	0	0	142.8	5.2	4.7
Alona spp	0	0	476.1	3	1.3
Alona affinis	52.6	0	95.2	3	4.1
Alona c.f. elegans	0	0	142.8	0	0
Alona guttata	157.8	285.7	809.5	5.5	1.9
Alona intermedia	0	0	0	0	0.2
Alona rustica	0	0	0	1.5	6
Alonella excisa	0	0	0	7.5	5.9
Alonella nana	894.7	2000	2142.8	12.2	9.1
Alonopsis elongata	157.8	428.5	1714.2	3	2.6
Bosmina longispina	3263.1	14285.7	3238	31.5	43.6
Copepod nauplius	11263.1	3428.5	8000	0	0
Cyclopoid (Cyclops)	526.3	0	5714.2	0	0
Cyclopid (Calonoid)	789.4	6285.7	1809.5	0	0
Diaphanosoma brachyurum	1368.4	6571.4	4761.9	1.2	1.9
Daphnia longispina	0	3000	0	0.5	0.4
Eurycercus spp	105.2	0	0	3	6
Graptoleberis testudinaria	0	0	0	0.5	1.3
Holopedium gibberum	631.5	1428.5	0	1	0.5
Monospilus dispar	157.8	0	0	19.5	9.6
Polyphemus pediculus	1473.6	1428.5	476.1	1.5	0

Several species present in the surface samples were not found in the contemporary samples. These include *Sida crystallina, Bythotrephes longimanus, Alona costata, Alona intermedia, Alona rustica, Alonella excisa* and *Graptoleberis testudinaria*.

The only species present in the contemporary sample and not in the sediment sample were the copepods whose exoskeletal parts do not preserve in lake sediments. *Daphnia longispina* is also poorly represented.

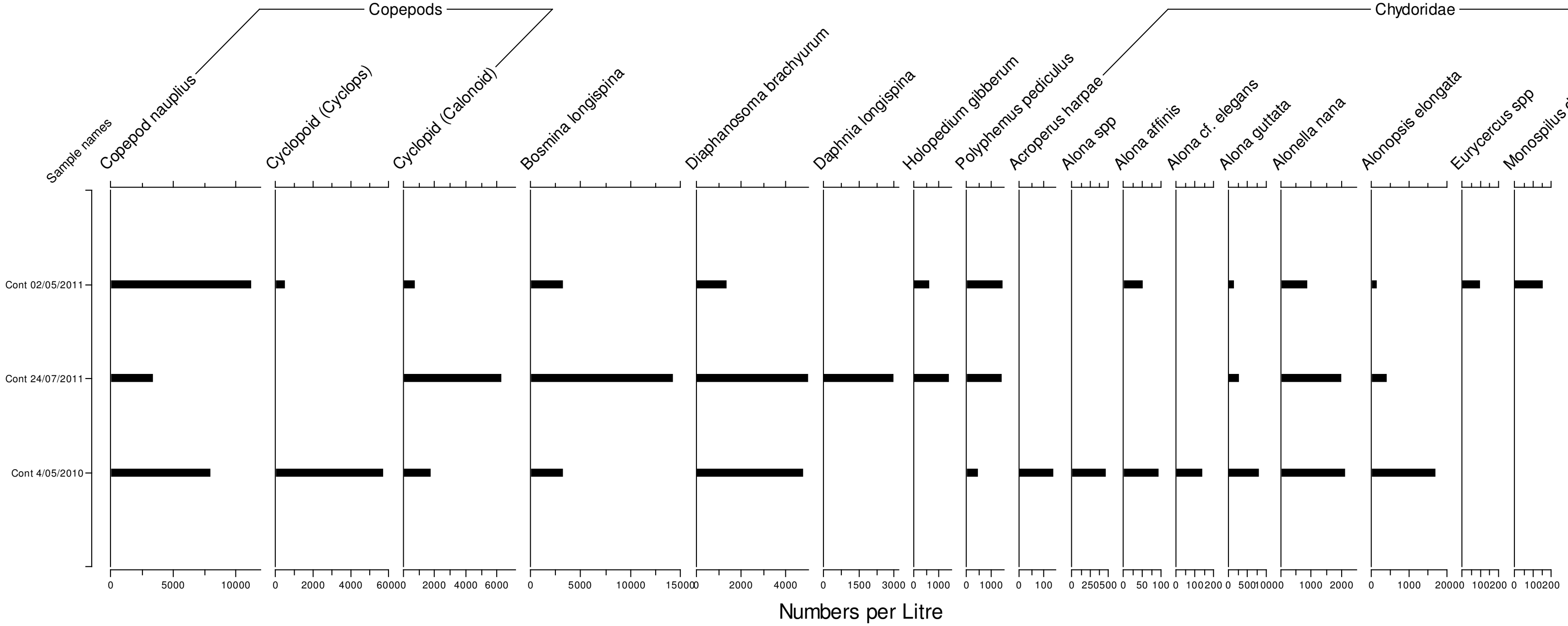

Figure 2. Composition of three Cladoceran samples collected from the open water of the Round Loch of Glenhead in 2010 and 2011.

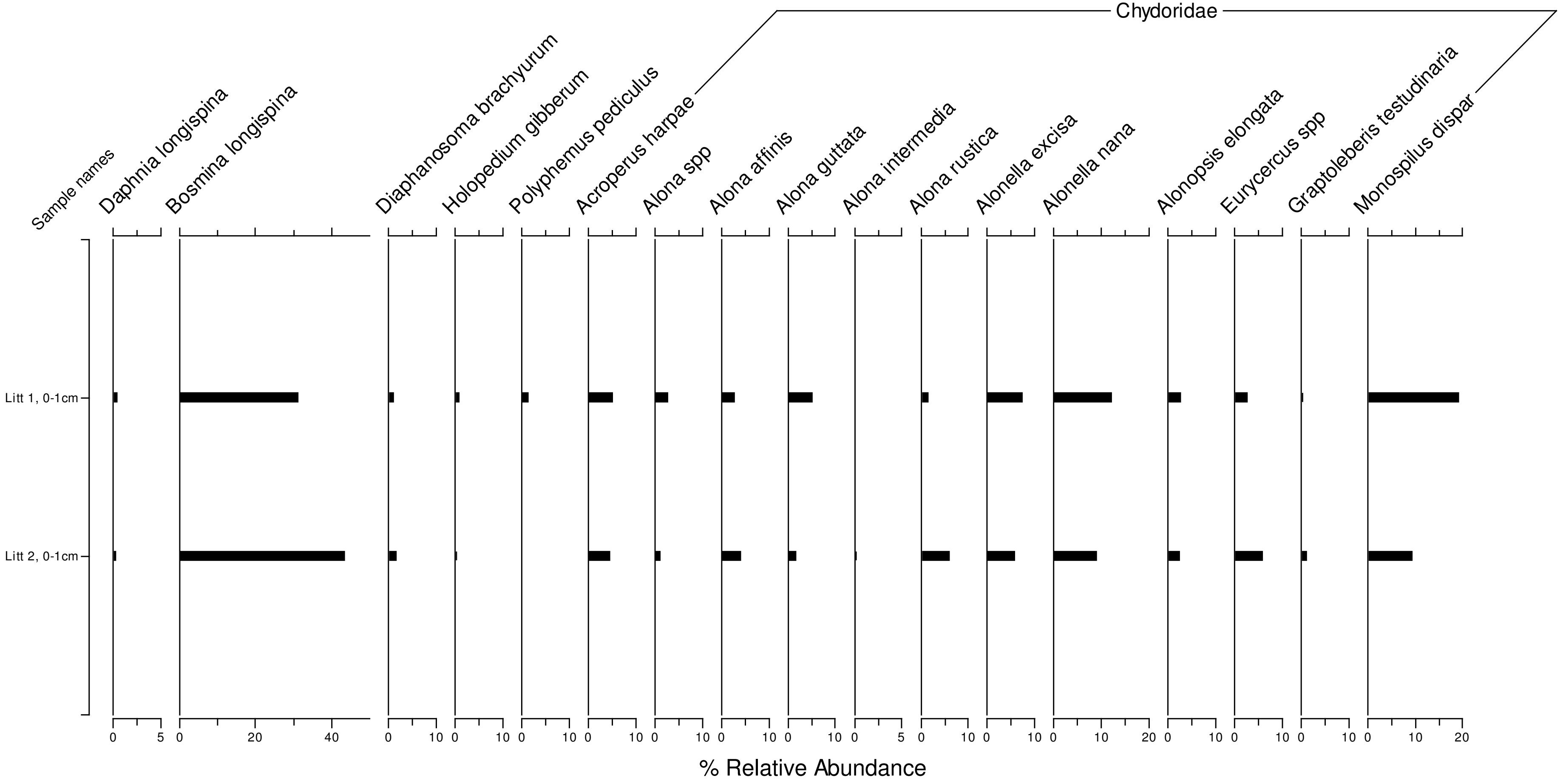

Figure 3 Composition of two Cladoceran assemblages from surface sediment samples collected in the littoral zone of the Round Loch of Glenhead.

Chironomids

Although Chironomidae dominate the contemporary invertebrate fauna of RLGH until now there has been no attempt to identify taxa to genus and species level. We have analysed benthic samples along a depth transect from the stony littoral zone to the muds in deep water. A total of 913 Chironomidae larvae were dissected and mounted and 23 taxa were identified (Table 4).

Table 4 Round Loch of Glenhead Chironomidae totla taxa presence and species relative abundances in the contemporary littoral and mud samples collected along a depth transect (T1) in July 2010 (three replicates pooled), and in the exuviae collections from spring and summer 2010 and 2011. Taxon codes follow CEH coding.

	%	Contemporary 07-2010	samples			Exuviae samples			
CEH Code		RLGH-T1-0.8m	RLGH-T1-3m	RLGH-T1-5m	RLGH-T1-10m	spring/ 2010	07/ 2010	05/ 2011	07/ 2011
50420801	*Ablabesmyia longistyla*	1.1	1.4	0.0	0.0	0.0	0.0	0.0	0.0
50420802	*Ablabesmyia monilis*	0.5	0.0	0.0	0.0	0.0	3.1	0.0	16.3
50420800	*Ablabesmyia*	0.6	4.1	0.0	0.0	0.0	2.7	0.0	38.0
50420902	*Arctopelopia griseipennis*	2.9	5.5	0.0	0.0	0.3	0.0	19.2	0.0
50420400	*Macropelopia*	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
50420515	*Procladius (H.) signatus*	0.0	1.4	0.0	0.9	1.5	0.0	0.0	0.0
50440100	*Protanypus*	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
50463401	*Acamptocladius submontanus*	1.1	0.0	0.0	0.0	0.0	1.1	0.0	0.3
50463800	*Corynoneura spp.*	1.7	4.8	0.0	0.0	1.7	0.8	0.0	31.3
5046051H	*Cricotopus (C.) ? curtus*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
50460540	*Cricotopus (Isocladius)*	0.2	0.0	0.0	0.0	0.0	0.0	3.8	0.0
50461201	*Heterotanytarsus apicalis*	0.0	0.7	0.0	0.0	89.3	0.0	19.2	0.0
50461301	*Heterotrissocladius grimshawi*	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
50461302	*Heterotrissocladius marcidus-type*	0.0	4.1	16.7	0.0	0.0	0.0	0.0	0.0
50464701	*Parakiefferiella bathophila*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	3.0
50464703	*Parakiefferiella fennica*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
50462720	*Psectrocladius (Allopsectr.)*	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0
50462710	*Psectrocladius (Monop.) septemtrionalis-*type	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0
50462746	*Psectrocladius oligosetus*	90.5	49.3	0.0	2.7	7.0	40.8	50.0	1.3
50462740	*Psectrocladius Pe*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0

	sp.A Langton 1980								
50460000	*Orthocladiinae indet.*	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
50470900	*Dicrotendipes modestus*	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0
50471902	*Microtendipes chloris*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3
50472201	*Pagastiella orophila*	0.2	3.4	50.0	0.0	0.0	0.2	0.0	0.0
50472801	*Phaenopsectra flavipes*	0.0	7.5	0.0	0.0	0.0	0.5	0.0	3.7
50472900	*Polypedilum* indet.	0.0	3.4	16.7	0.0	0.0	0.3	0.0	4.0
50473000	*Sergentia*	0.0	1.4	0.0	41.8	0.0	0.0	0.0	0.0
50473200	*Stictochironomus rosenschoeldi-type*	0.0	0.7	0.0	53.6	0.0	0.0	0.0	0.0
50470000	*Chironomini indet.*	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0
50490933	*Tanytarsus signatus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
50490900	*Tanytarsus smolandicus*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.7
50490Z00	*Tanytarsus striatulus/Pe 11/pseudolestagei*	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
50490Z00	*Tanytarsus* indet.	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0
	total abundance (ind/sample)	**651**	**146**	**6**	**110**	**776**	**1332**	**26**	**300**
	Total Taxa	**11**	**17**	**4**	**5**	**7**	**16**	**5**	**11**

The results show clearly differentiated larval assemblages along the depth gradient (Figure 4). In the rocky shores down to 1m depth, *Psectrocladius oligosetus* is highly dominant, accompanied by the tanipod *Arctopelopia griseipennis* and other less abundant taxa (*Acamptocladius submontanus*, *Macropelopia, Ablabesmyia* spp.). The muddy sediments from the sublittoral zone contained a rich community including, in addition to the former taxa, chironomini (*Phaenopsectra flavipes*, *Dicrotendipes modestus*, *Pagastiella orophila*, *Polypedilum*), tanytarsini (*Tanytarsus*), some orthoclads (*Heterotrissocladius*, *Heterotanytarsus*) and the tanypod, *Procladius signatus*. The deepest zone has its own simpler assemblage of *Stictochironous rosenschoeldi*-type, *Sergentia* and *Protanypus*.

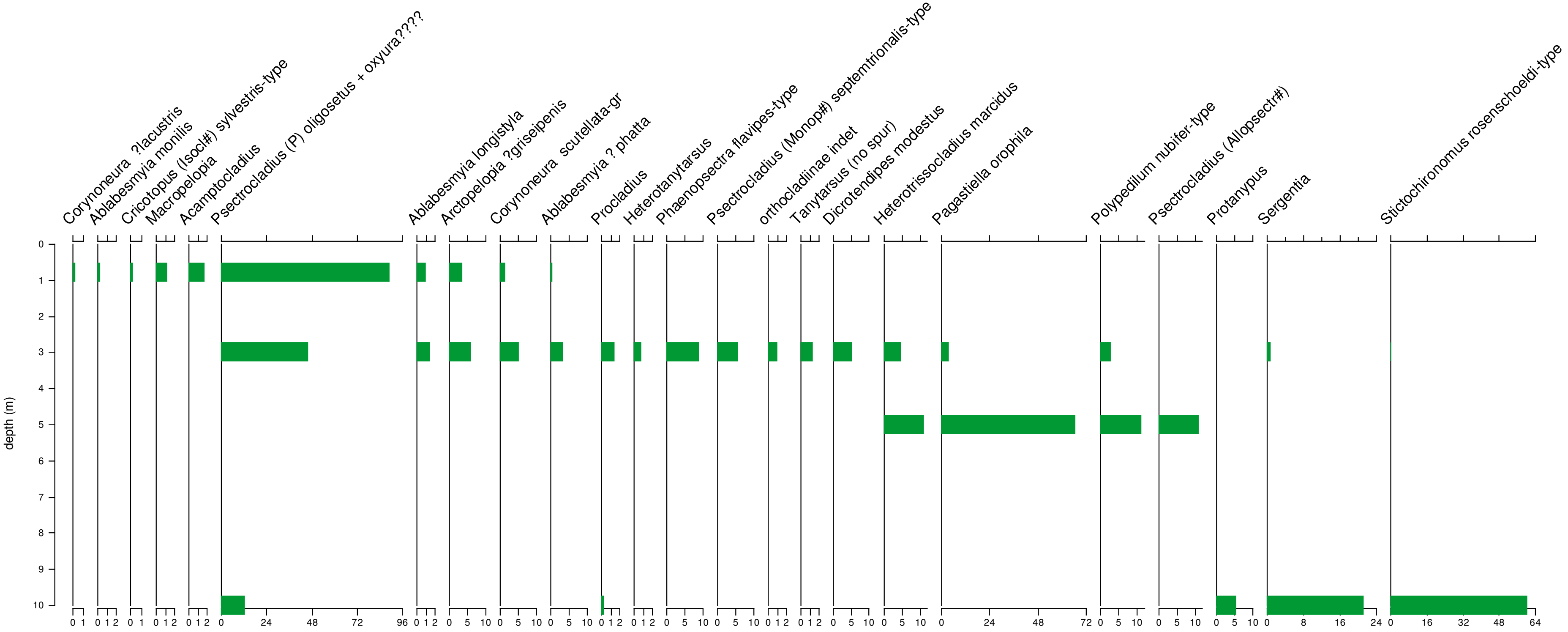

Figure 4. Chironomid larval assemblages along a depth transect in the Round Loch of Glenhead.

In addition to the larval material we also collected chironomid pupal exuviae on four occasions. Altogether 2434 exuviae were identified from the RLGH representing 24 taxa (Table 4). This information together with living larvae and pupae collected in habitat specific samples enlarge the global contemporary Chironomidae biodiversity of RLGH to around 30 taxa. Disagreements between living larvae and exuviae samples can be related to either the timing of emergence or the timing of sampling. Taxa present as exuviae but without habitat assignment (absent in the contemporary samples) include *Microtendipes chloris*, *Parakiefferiella* species and *Heterotrissocladius grimshawi*. Others, such as *Psectrocladius sp A* and *P. oxyura* (only found as pupae in 1990 samples, not included in Table 4) are rare compared to the very dominant *Psectrocladius oligosetus.*

We cannot assign a species name to *Sergentia* and *Stictochironomus rosenschoeldi*-type as these profundal taxa were not present in the exuviae samples. Neither were *Dicrotendipes modestus*, *Psectrocladius (Allopsectrocladius)*, *P. (Monopsectrocladius), Protanypus, Macropelopia* and *Ablabesmyia longistyla*. *Tanytarsus* was present in low numbers and only one type of larvae was identified in the 3m deep samples, while up to three species could be recognized as pupal exuviae.
Finally, some species can be over-represented in the pupal exuviae collections in respect to their abundances and distribution in the lake, as *Heterotanytarsus apicalis*, which presented high emergence peaks in spring (in both 2010 and 2011). Similarly, another spring emerging species is *Arctopelopia griseipennis*.

So far no surface sediments have been analysed for comparison. The intention is to examine surface sediments from the two littoral cores (Litt1 and Litt2, Figure 1) and from a deep water core (Deep1, Figure 1).

Reference

Shilland, E. M., Irvine, L., Malcolm, I. A., Marazzi, L., Panizzo, V. N. & Salgado, J. (2012) The United Kingdom Acid Waters Monitoring Network Data Report for 2010-2011 (year 23). Report to the Department for Environment, Food and Rural Affairs (Contract EPG 1/3/160). 239pp. ENSIS Ltd., Environmental Change Research Centre, University College London, London.

Paper 5
(in press *Ecological Indicators*)

Recovery of UK lakes from acidification: an assessment using combined palaeoecological and contemporary diatom assemblage data

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Abstract

We assess the recovery of UK lakes from acidification using the combined data from sediment cores and sediment traps to track changes in diatom assemblages in 11 UK upland lakes from pre-acidification times (prior to ca. 1850 AD) to the present (2008 AD). We projected the data into a Principal Component Analysis (PCA) of diatom assemblage data from 121 low-alkalinity lakes in the UK to show how the floristic composition of the core and trap diatom assemblages for each site has changed through time. The results show that the degree of recovery from acidification varies amongst sites but in all cases its extent is limited when compared with the pre-acidification reference. In most cases the recovery, although usually slight, is characterized by a decline in acid tolerant taxa and a return towards taxa that occurred previously at each respective site. In a few cases, however, the floristic composition of recent samples is different from those that occurred during and before the acidification phase. The reasons for this are not yet clear but it is possible that nutrient enrichment from atmospheric N deposition and/or climate change is beginning to play a role in driving water quality as acidity decreases. More generally the results show that annually recovered samples from sediment traps can be successfully combined with sediment core data to provide a continuous record of environmental change in lake systems, and that diatoms collected in sediment traps can be used to provide a very powerful lake monitoring tool.

1. Introduction

Surface water acidification became a major environmental issue in Europe after Odén (1968) and Almer et al. (1974) attributed the loss of salmonid populations in southern Swedish rivers and lakes to acidification caused by sulphur deposition from fossil fuel combustion ("acid rain"). Similar losses of fish populations in Norway (Jensen and Snekvik, 1972) and Canada (Beamish and Harvey, 1972) were also ascribed to acid deposition. Although alternative hypotheses were advanced to explain the acidification of surface waters (Krug and Frink, 1983; Pennington, 1984; Rosenqvist, 1978), major multinational research programmes both in Europe and North America (Mason, 1990; NRC, 1984) concluded that the primary cause of acidification was indeed acid deposition from fossil fuel combustion.

Following the introduction of legislation to reduce emissions of sulphur and nitrogen gases from fossil fuel combustion sources, acid deposition has declined markedly in Europe including the UK (RoTAP, 2012; Vestreng et al., 2007), and there is increasing evidence that acidified lakes and streams are beginning to recover, both chemically and biologically (Driscoll et al., 2007; Forsius et al., 2003; Nierzwicki-Bauer et al., 2010; Skjelkvåle et al., 2005).

Over the last 20 years in the UK data from the Acid Waters Monitoring Network (AWMN) show that there has been significant reductions in the concentrations of non-marine sulphate and concomitant increases in pH, acid neutralising capacity (ANC) and dissolved organic carbon (DOC) along with a significant decrease in the concentration of toxic labile aluminium at the most acidified sites (Monteith, this issue).

Biological recovery is most clearly seen by trends in benthic diatom populations (Kernan et al., 2010), by the appearance of new aquatic plant species in seven of the lake sites and four of the stream sites (Kernan et al., 2010) and by significant changes in invertebrate populations at about half of the 22 AWMN sites (Murphy et al., this issue). In addition new populations of brown trout (*Salmo trutta*) have appeared at a number of the most acidified sites (Malcolm, this issue). All changes are consistent with chemical trends towards less acidic conditions.

Key questions now concern the extent of recovery, whether there are barriers to continued recovery, whether a complete recovery can be achieved or whether other pressures and processes will lead to the emergence of novel ecosystems that differ in their structure and function from those in the past (Hobbs et al., 2009).

Answers to these questions require an understanding of pre-acidification conditions that can be used to assess both the extent of acidification and the extent of recovery. As no direct observations of the chemistry and biology of upland waters are available for the relevant periods in the past, pre-acidification conditions need to be inferred using either space-for-time substitution techniques (Simpson et al., 2005) or palaeoecological techniques (Battarbee et al., 2005). Palaeoecological methods have been used to assess the effectiveness of liming as a restoration measure for acidification (Flower et al., 1990; Guhren et al., 2007; Norberg et al., 2008) and to evaluate the response of acidified lakes to the reduction in acid emissions (Arseneau et al., 2011; Ek and Korsman, 2001; Juggins et al., 1996).

One of the problems of using palaeoecological techniques to track the response of lakes to the reduction in acid deposition is the low rate of sediment accumulation (often < 1 mm/yr) that is characteristic of many upland lakes. Surface sediments can also undergo bioturbation from benthic invertebrates and can be mixed as a result of wind-induced sediment resuspension. Consequently, samples, even from very finely sliced sediment cores (e.g. 0.25 cm) are likely to contain material representing several years of deposition, and the mixing of sediment upwards and downwards by bioturbation and resuspension tends to smooth out signals. For example, in a multi-core study of the Round Loch of Glenhead, Allott et al. (1992) demonstrated that diatom evidence of recovery was only registered in cores that had an accumulation rate greater than 0.7mm/yr.

The limited evidence of recovery indicated by an earlier study of sediment cores from the lakes in the AWMN (Juggins et al., 1996) was partly due to the relatively short time that had elapsed between the beginning of significant efforts to reduce acid emissions in the UK and the date of sediment coring, but also due to such time-averaging and sediment mixing processes. In this present study, not only has more time now elapsed but we also have data from annually emptied sediment traps that have been deployed in the AWMN lakes since 1991. They are designed to collect an integrated sample of diatoms from all lake habitats in a way that closely mimics the formation of accumulating sediments but that also provides a discrete sediment sample representing a fixed time period. They are invaluable in tracking recovery on annual time-steps and the time-series data can be combined with the sediment core data to generate long-term records that uniquely track both the acidification and recovery trajectories at each site.

Here, approximately ten years after our first evaluation of the recovery of the lakes in the AWMN (Juggins et al., 1996) we use these combined sediment trap-sediment core datasets from the 11 lakes to assess the extent of recovery from acidification that has now occurred relative to the pre-acidification reference state. We also consider whether additional influences such as nitrogen deposition leading to nutrient enrichment or climate change may be confounding recovery or might lead to the emergence of new communities and new ecosystem functions.

2 Sites

The primary sites used in this study are the 11 lakes in the AWMN (Table 1, Figure 1). The AWMN has been operating continuously since 1988 (Monteith and Evans, 2005) and now provides a multi-decadal time-series for key chemical and biological variables (Kernan et al., 2010). Sediment trap data, however, are only available from 1991. Detailed site descriptions and data assembled so far for all the AWMN sites can be found on the AWMN website (http://awmn.defra.gov.uk/). Table 1 summarises the key data for the sites monitored.

In the data analysis we have used a data-set of diatom assemblages from 121 lakes that has been compiled over the last 30 years (Figure 1). These data have been used in a Principal Components Analysis into which the sediment core and sediment trap data from the 11 AWMN sites have been entered passively. The dataset has been previously described by Battarbee et al. (2011). It has been compiled from the results of many different projects on many sites over a period of years. Consequently the sites are neither a random sample of all possible sites that could have been included nor are they evenly ordered along any specific geographical or chemical gradient, but they do include sites representative of the full range of low alkalinity lake found in the UK today with respect to e.g. size, altitude, marine proximity (sea-salt influence), base cation concentration, dissolved organic carbon (DOC) concentration and degree of acidification. As such the diatom assemblages in the 121 lake data-set are likely to include the full range of diatom taxa found in UK low alkalinity waters today and in the past and are thereby assumed to form a suitable training set for comparison with the AWMN core and sediment trap data. It allows the temporal change in diatom assemblages indicated by the core and trap data to be compared with analogous contemporary samples that span a gradient of pH from sites across the UK (Fig. 1).

3 Methods

3.1 Laboratory and field methods

Although the diatom data used here were generated by different analysts at different times the slides were prepared according to the same standard techniques (Battarbee et al., 2001). The slides were counted using x 100 oil immersion objectives in either phase contrast, differential interference contrast or brightfield. The taxonomy and nomenclature used have been consistent throughout the programme, following the protocol developed for the SWAP project (Stevenson et al., 1991). Observations for all taxa, expressed as proportions of the total sample count, were used in the data analysis.

The sediment cores used for the diatom analysis presented here were taken between 1989 and 1992 using either a Mackereth mini-corer (Mackereth, 1969), or a small gravity corer (Glew et al., 2001). The summary data were published in Juggins et al. (1996). All were dated using ^{210}Pb measurements, and in each case good chronologies were obtained. The calculated sediment accumulation rates derived from the chronologies indicated that the acidification period, since approximately the mid-nineteenth century, is confined to the uppermost 10 – 20 cm of the sediment record. With a sampling interval of 0.25 or 0.5 cm for the uppermost 5 cm the core records have a sub-decadal resolution for the last 20 years and a decadal-scale record or better for the last 200 years.

Sediment trap samples have been collected on an annual basis from all sites using a standard cylinder trap array. Two arrays of cylindrical sediment traps with high aspect ratios (height : diameter) are anchored and buoyed about one metre above the sediment surface at locations close to the deepest point at each lake site. Each trap array contains three individual sediment traps, each having a height of 33 cm and an aspect ratio of 6.47. The traps are serviced and the accumulated sediment recovered on an annual basis in August.

Sampling began at Coire nan Arr, Lochnagar, Loch Chon, Loch Tinker, Round Loch of Glenhead, Scoat Tarn and Llyn Cwm Mynach in 1991, at Burnmoor Tarn and Blue Lough in 1992 and at Loch Grannoch and Llyn Llagi in 1993 (Table 1). The record is complete for all sites except for Loch Chon in 1993, Loch Coire nan Arr in 2000 and Lochnagar in 1992 and 2005, occasions when trap arrays were either removed by members of the public or destroyed by rafting ice.

Cores used to derive the data for the 121 lake data-set were taken at different times since 1980. Diatom assemblage data from the surface sediments and the pre-1800 AD basal sediments were used in the PCA described below.

3.2 Numerical techniques

3.2.1 Trend tests of trap data-sets

Trend tests based on PCA axis 1 scores were used to assess whether changes in the trap diatom assemblages were significant over the period of monitoring. The Hellinger transformed species data were ordinated for each site using PCA and the primary direction of variation was retained (PCA axis 1) as a time series of change. An additive model was applied to each of these series in turn, with a thin-plate spline of the variable sample year used as the sole predictor variable

$$y_i = \beta_0 + s(Year_i) + \varepsilon_i, \quad \varepsilon \sim N(0, \sigma^2 \Lambda)$$

where y_i is the PCA axis one score in the ith observation, β_0 is a constant term, $s(Year_i)$ is the value of the spline of sample year for the ith observation (i.e. the estimate of the trend). The residuals ε are assumed to be mean zero identically distributed Gaussian random variables with variance σ^2. The correlation matrix **Λ** indicates the degree of autocorrelation in the model residuals. We assume a continuous time first-order autoregressive process, CAR(1), for **Λ**, which has the effect of modelling an exponentially decreasing correlation with increasing temporal separation of residuals. This model allows for the possibility of non-linear trends in the PCA axis one scores.

3.2.2 PCAs of combined core and trap data-sets

The modern diatom training set percentage data were subjected to a Hellinger transformation (Legendre and Gallagher, 2001) prior to subsequent analysis. Principal component analysis (PCA) of the centred, Hellinger-transformed diatom data was used as the base ordination within which the sediment core and trap diatom data could be projected. Details of the PCA are available in greater detail in Battarbee et al. (2011).

The sediment core and trap samples were projected into the base ordination described above by computation of site scores on PCA axes 1 and 2 for each core and trap sample. The ith predicted sample score for each axis $\hat{x}_i$ is given by:

$$\hat{x}_i = \lambda^{\alpha-1} \sum_{k=1}^{m} w_k y_{ik} \hat{b}_k / \sum_{k=1}^{m} w_k$$

where λ is the eigenvalue of PCA axis, $\alpha = 1$, such that the sample score is a weighted sum of the species scores, $\hat{b}_k$ is the fitted species score on the current axis for the kth species, y_{ik} is the observed species data for the kth species in the ith sample where the species data for the core and trap samples was subjected to the same transformation as the training set data. w_k is the user-supplied weight for the kth species, which was 1 for all species in our analyses (Ter Braak and Šmilauer, 2002).

All analyses were performed using R (version 2.14.1; R CORE Team, 2011) and the vegan (version 2.0-1; Oksanen et al., 2011), mgcv (version 1.7-19, Wood, 2004, 2006a, b) and analogue (version 0.9-10; Simpson, 2007; Simpson and Oksanen, 2011) packages.

4. Results

4.1. Trend tests of sediment trap data

Acid deposition in the UK has declined significantly over the last few decades (RoTAP 2012) and the alkalinity of acidified surface waters has increased (Monteith, this issue). The composition of diatom assemblages collected annually by the sediment traps over the last 20 years would thereby be expected to change in response to the change in water chemistry. Consequently the individual sediment trap data-sets from the 11 lakes were analysed as described above to test for the presence of significant trends. The results are shown in Table 2 and Figure 2.

The site plots in Figure 2 are ordered by year and the variance in the diatom data explained by the first PC is given in Table 2 along with the Eigenvalue. The complexity of the fitted smooth (df = degrees of freedom) plus test statistic and p-value (F and p respectively) in Table 2 indicate the presence of a significant trend at all sites except Loch Grannoch, with somewhat weaker evidence at Loch Coire nan Arr and Scoat Tarn. The lack of a trend at Loch Grannoch site might be an artefact of the statistical test used. Here the diatom data (Fig. 3k) show that there was an abrupt change in 1997/8 which is reflected by the PCA axis 1 scores (Fig. 2). The model, however, is designed to pick up smooth changes in the mean values and in this case has treated the step change in assemblage composition as auto-correlation. At Corrie nan Arr (Fig. 2), a trend is detected but the confidence intervals are very high (and therefore not plotted) suggesting weak support for the presence of a trend. As this site is only very slightly acidified and is treated in the AWMN as a reference site, this result is not unexpected (cf Fig. 3a).

Overall the first PCA axis explains between 20 and 50% of variance in the data. Although this is high for diatom data these may still be underestimates as, in these cases where there may be a single dominant gradient, PCA splits the variation into two or more axes (e.g.Swan, 1970) to maintain the geometric representation of dissimilarities. In addition, PCA focuses on linear gradients and may fail to represent adequately non-linear trends. Other techniques, such as principal curves (De'ath, 1999; Simpson and Birks, 2012) may offer a better solution.

4.2 Diatom assemblage change: sediment core (ca. 1800 – 1990 AD) and sediment trap (1991-2008 AD) data for AWMN sites

Figure 3a-k shows changes in diatom composition for the 11 sites combining sediment core and sediment trap data and Figure 4a-k shows the PCA analysis for the 121 diatom assemblages in the UK low alkalinity lake data-set with the combined core and trap data for each AWMN loch inserted passively. Only the dominant taxa are shown in Figure 3 although all taxa are used in the ordination analysis (Fig. 4).

The sediment trap arrays were installed in the respective lakes one or two years after the cores were taken in 1989. The trap record, therefore, follows on from the core record, indicated in Figure 3 by the break in the x axis. Dates for the cores are based on ^{210}Pb dating whereas dates for the trap samples are calendar years. The temporal spacing of the core samples is therefore variable, depending on the rate of sediment accumulation, but the trap samples are annually and therefore equally spaced in time.

In Figure 4 the core and trap diatom data from each AWMN site are constrained by the range of variability of the diatom assemblages in the overall UK training set of 121 sites. The time trajectory for each site runs from its pre-1850 reference towards the present day and shows the extent to which the composition of the assemblage has changed during the acidification phase from approximately 1850 to 1989 (the core data) and the recovery phase (the trap data) from 1990 to the present (2008).

The data for the AWMN sites shown in Figure 4 shows the trajectories of the core samples and the trap samples for each site through time. The floristic difference between the present day flora and the pre-acidification reference flora at each site is indicated by the difference in the position of the 2008 trap sample (arrowed) and the basal core sample (closed circle). Except for the case of Llyn Cwm Mynach, where the data are problematic (see below), the gap represents the degree of recovery in diatom floras that has taken place.

The position and direction of the individual trajectories differ from site to site according to their sensitivity to acidification, indicated by their base cation status, their historical exposure to acid deposition, and by their response to the reduction in acid deposition that has taken place over the last two decades (Table 1). Using these criteria, the sites can be divided into several groups ranging from Loch Coire nan Arr, a sensitive control site in a low deposition region, where there has been little acidification, to Burnmoor Tarn, a less sensitive site in a formerly high acid deposition region, where there also has been little acidification.

4.2.1 Loch Coire nan Arr

Loch Coire nan Arr (Fig. 3a, 4a) acts as a control site in the AWMN. It is a very sensitive site but remains relatively unaffected by acid deposition as it is situated in the north-west of Scotland, one of the regions in the UK with the lowest acid deposition (RoTAP, 2012). Diatom analysis of a core obtained earlier from this site (Juggins et al., 1996) showed that the flora has been dominated by *Achnanthes minutissima*, *Brachysira vitrea* and *Tabellaria flocculosa* almost unchanged for at least the last 200 years (Fig. 3a). The trap sequence (Fig. 3a) shows a change towards an increasing abundance of *A. minutissima* but the difference between the trap and the core flora is minor confirming the status of the site as a good control for acidified lakes elsewhere in the UK.

4.2.2 Blue Lough

Of the acidified sites in other regions the most sensitive is Blue Lough, a naturally acidic site in the Mourne Mts. of Northern Ireland but one that has become even more acidic as a result of acid deposition. The pre-acidification assemblage (Fig. 3b) is dominated by the acidophilous benthic taxa *Eunotia incisa*, *Frustulia rhomboides* var. *saxonica* and *Cymbella perpusilla*. *Tabellaria quadriseptata*, perhaps the diatom most tolerant of acidic conditions and found in abundance at many acidified sites, is present throughout the pre-acidification period.

The acidification period at Blue Lough began in the late 19th century marked by an increase in *T. quadriseptata*. As the lough became more acidified after WWII *Navicula hoefleri* and *Melosira arentii* (not shown) appeared and became increasingly abundant. During the recovery phase over the last few decades, although pH has not increased greatly, there have been very significant decreases in sulphate concentration and in labile aluminium concentration (Monteith, this issue) indicating a clear chemical response to the reduction in acid deposition in eastern Northern Ireland. At the same time there has been a marked change in the diatom flora recorded by the sediment traps with a decline in *T. quadriseptata* and an increase in *Semiorbis hemicyclus* (Fig. 3b), a diatom that has not been previously recorded in the lake and one that is relatively rare in the UK. The combined core and trap sequences shown in Figure 4b, therefore, track the acidification and recovery phases but the recovery is characterised by the appearance of *S. hemicyclus* rather than the re-emergence of *Cymbella perpusilla*, *E. incisa* and *F. rhomboides* var. *saxonica,* the pre-acidification dominants.

4.2.3 The Round Loch of Glenhead, Llyn Llagi and Scoat Tarn (Figs. 3c,d,e; 4c,d,e)

These sites represent lakes that are somewhat less sensitive than Blue Lough but nevertheless have a naturally low base status (Table 1) with a pre-acidification chemistry probably very similar to that of Loch Corrie nan Arr, the control site (see above). However, these three sites are situated in areas where acid deposition has been very high in the past. All three became strongly acidified by the middle of the 20th century (Battarbee et al., 1988; Flower and Battarbee, 1983; Haworth et al., 1988).

The Round Loch of Glenhead is one of the most well-studied sites in the AWMN (Allott et al., 1992; Battarbee et al., 2005; Flower and Battarbee, 1983). It is situated in Galloway, southwest Scotland at an altitude of 298 masl. The core data (Fig 3c) show changes in the composition of diatom assemblages from the early 19th century to the present day. In the pre-acidification period the dominant taxon was *Brachysira vitrea*, a very common diatom found in low alkalinity lakes sensitive to the effects of acidification. Its decline in the mid-nineteenth century together with the increase in the relative abundance of *Eunotia incisa* provides the first evidence of decreasing pH in the loch. The later expansion of *Tabellaria quadriseptata* and decrease in *Peronia fibula* (not shown) and *Tabellaria flocculosa* indicates continuing acidification during the 20th century reaching the most acidic state by the 1970s, the time at which the first direct measurements of lake water pH were taken. The pH of 4.7 inferred from the diatom-pH transfer function (Birks et al., 1990) for the surface sediment diatom sample is in very close agreement with direct measurements.

In the Round Loch the trap data (Fig. 3c) show little change for the first few years of monitoring but after approximately 1995 there is a gradual reduction in the relative abundance of the acid tolerant taxon *Tabellaria quadriseptata* and an increase in *Navicula leptostriata* reflecting the increase in pH and the slight recovery from acidification that has taken place at this site over the last 15 years (Monteith, this issue).

When the core and trap data are entered passively into the PCA of all samples, a clear acidification trajectory followed by a partial recovery can be seen (Fig. 4c). The difference in composition of the present day assemblage, with its dominance by *N. leptostriata,* from previous assemblages (Fig. 3c) is illustrated by the difference in the orientation of the recovery from the acidification trajectory, and the limited extent of the recovery is illustrated by the considerable distance between the position of the present day and pre-acidification assemblages in ordination space.

Llyn Llagi is situated in North Wales at an altitude of 375 m. It’s pre-acidification diatom flora (Fig. 3d) was dominated by *A. minutissima*, *B. vitrea* and *E. incisa*, similar to the contemporary flora of Corrie nan Arr (Battarbee et al., 1988). Unlike Corrie nan Arr, however, these taxa decreased during the 20th century and were eventually replaced by *T. quadriseptata* as the lake acidified. Following the reduction in acid deposition over the last 30 years there has been a very marked change in the lake’s chemistry, with a major decrease in sulphate and increase in pH and a concomitant change in the diatom flora. *T. quadriseptata* declined rapidly and *B. vitrea* and *E incisa*, two of the dominant pre-acidification taxa, increased. The recovery process, however, has still some way to go as there is no indication as yet of any increase in the population of *A. minutissima,* the most sensitive of the pre-acidification dominants. The extent of the acidification and subsequent recovery is seen by the assemblage trajectory shown in Figure 4d. It is the site in the AWMN that shows the greatest recovery to date although the recent increase in *T. flocculosa* suggests that the recovery may not be a simple reversal of the acidification phase.

Scoat Tarn is situated in the Cumbrian Lake District at an altitude of 598 m. It is one a cluster of small sensitive acidified tarns in the Wasdale region (Haworth et al., 1988). Scoat Tarn itself is one of the first lakes in the UK to have become acidified. The sediment core data show that in the early 19th century the lake not only contained populations of sensitive benthic taxa such as *A. minutissima* and *B. vitrea* (not shown), but also the planktonic taxon *Cyclotella kuetzingiana* (Fig. 3e). By the middle of the 19th century *C. kuetzingiana* had disappeared and the relative abundance of *A. minutissima* and *B. vitrea* had begun to decline, being replaced by the acidophilous *Achnanthes marginulata* which became the dominant taxon in the first part of the 20th century. The tarn became increasingly acidic and during the latter part of the 20th century, *A. marginulata* declined and *Navicula krasskei* (not shown), *Aulacoseira distans* var. *nivalis*, *A. tethera* (not shown) and *Tabellaria binalis* appeared and increased in abundance, reflecting an almost complete species turnover in the diatom flora between approximately 1850 and 1990 AD. Following measures to reduce acid emissions over the last 20 years there has been a significant decrease in sulphate concentration as at other sites, but only a relatively small increase in pH. Consequently, except for a small reduction in the relative abundance of *T. binalis* there has been little change in the overall composition of the diatom flora in the lake, and this is reflected by the position of the sediment trap diatom samples in ordination space in Figure 4e showing that very little biological recovery has taken place at this site.

4.2.4 Lochnagar (Fig. 3f, 4f)

Lochnagar has a similar sensitivity to acidification as the previous sites, but differs because of its high elevation (788m). It is an alpine corrie loch situated in the Scottish Highlands (Fig. 1) in the Cairngorm-Lochnagar Mts. It is a very well studied site (Rose, 2007). Diatom evidence for its acidification, beginning in the 19th century, was described by Jones et al. (1993) and by Juggins et al. (1996). The acidification trajectory is shown in Figure 4f. It is driven principally by a decline in *A. minutissima*, *A. scotica* and *Fragilaria virescens* var. *exigua* and an increase in the relative abundance of *A. marginulata* and *Aulacoseira distans* var. *nivalis* (Fig. 3f). During the last 20 years although there has been a significant decrease in sulphate concentration at Lochnagar, as at other sites, there has been little obvious biological recovery according to diatom evidence. The contemporary flora remains significantly different from the pre-acidification flora (Fig. 4f).

4.2.5 Loch Chon and Loch Tinker (Figs. 3g,h; 4g,h)

Loch Chon and Loch Tinker are less sensitive than the sites described above (Table 1), but nevertheless both have been acidified (Juggins et al., 1996). They have a relatively high calcium concentration (Table 1) and both supported planktonic diatom populations prior to acidification (Battarbee et al., 2011). L. Tinker is at a higher altitude than L. Chon (Table 1) but they are situated close to each other in the same region of Scotland and therefore will have experienced a more or less identical history of acid deposition. The catchment of L. Chon, however, has been partially afforested, a feature of the lake that caused Kreiser et al. (1990) to argue that L. Chon has experienced a more intense acidification than L. Tinker owing to the "forest effect" (Harriman and Morrison, 1982). For both sites the main evidence of their acidification was the strong decline in *A. minutissima* populations. In L. Chon it was replaced by the acidophilous taxa *N. leptostriata* and *E. incisa* (Fig. 3g), and in L. Tinker by *B. vitrea*, *F. virescens* var. *exigua* and *F. rhomboides* (Fig. 3h). Over the last two decades, there has been some evidence of recovery in L. Chon with the decline of *N. leptostriata,* but the extent of recovery is very slight, judging by a comparison of the present and pre-acidification floras (Fig. 4g). For L. Tinker there has been some decrease in the abundance of *F. virescens* var. *exigua* (Fig. 3h) in recent years but this also represents only a limited recovery (Fig. 4h).

4.2.6 Burnmoor Tarn (Figs. 3i, 4i)

Burnmoor Tarn is the least sensitive of the AWMN sites, with a calcium concentration of 1.89 mg/l in 1989 (Table 1). Although the lake has a highly elevated sulphate concentration reflecting its location in one of the highest acid deposition regions historically in the UK, only very minor diatom changes have taken place there over the last 200 years (Fig. 3i). Planktonic *Cyclotella* taxa and the benthic *A. minutissima* and *B. vitrea* have been the dominant taxa throughout the period. They are still abundant in Burnmoor Tarn whereas they have been replaced by more acid tolerant taxa at more sensitive sites in the region. Only the loss of *C. atomus* (not shown) and the slight increase in abundance of a small number of acidophilous benthic taxa since the mid-19th century are changes that are indicative of acidification. In the last twenty years, during the period of monitoring, there has been little change in the dominants, although *C. kuetzingiana* var. *minor* has becoming increasingly abundant, possibly due to the increase in alkalinity at the site or also possibly related to increased water temperature (cf. Ruhland et al., 2008).

4.2.7 Loch Grannoch and Llyn Cwm Mynach (Figs. 3j,k; 4j,k)

Finally there are two sites in the Network, Loch Grannoch and Llyn Cwm Mynach, that were similar to the others at the time of initial acidification in the 19th century and became further acidified through the 20th century. However, the chemistry and biology of the lakes have been influenced not only by acid deposition over the last 50 years but also by catchment afforestation. There is evidence that afforestation also affected Loch Chon (see above) but not to the same extent. At Loch Grannoch the sediment core data show that afforestation probably exacerbated acidification, creating extremely acidic conditions not only with low pH but also with high Al (Monteith, this issue). Afforestation was also probably responsible for the sudden appearance of the planktonic taxon *Asterionella ralfsii* as a response to the inwash of nutrients following the application of fertilisers to the catchment forest. Although *A ralfsii* subsequently disappeared as the nutrient effect was lost, the trend in the overall diatom composition shown by the trap material shows no evidence of diatom recovery (Fig. 3j). The diatom flora remains one characteristic of very acid waters, dominated by *T. quadriseptata* and *E. incisa* (Fig. 3j) despite the reduction in sulphate concentration. This is consistent with the lack of a significant increase in pH at the site over the last 20 years (Monteith, this issue). Figure 4j shows how far the current diatom assemblage composition is in ordination space from that prior to acidification when *B. vitrea* and *T. flocculosa* were dominant.

In Llyn Cwm Mynach (Fig. 4k) it is more difficult to connect the core and trap data, as noted above. The core data show only a slight acidification from a reduction in the abundance of *B. vitrea*, *F. virescens* var. *exigua* and *A. minutissima* to increases in *E. incisa* and *Peronia fibula* (Fig. 3k). The trap data, however, are significantly different from the core data, being dominated by *E. incisa*, *P. fibula* and *E. denticulata* (not shown) a taxon that is not evident in the sediment core assemblage. A probable explanation for the difference, as suggested above, is that the uppermost sediment is missing from the core top. Consequently the data presented here are of little value in assessing acidification recovery at this site.

In summary many of the acidified sites show some evidence of recovery but, with the exception of Llyn Llagi, the extent of recovery over the last 20 years appears quite limited. The gap between the composition of the present-day diatom assemblages and the pre-acidification reference assemblages remains substantial at most sites.

Where there is evidence of recovery the direction of assemblage change is, in some cases (e.g. Lochs Chon and Tinker, Fig. 4g,h) back towards the pre-acidification reference flora. In other cases (Blue Lough, Llyn Llagi and Lochnagar, Fig. 4b,d,f), however, the back (or recovery) trajectory is different from the forward (acidification) trajectory, indicating that the current diatom assemblage comprises different taxa or a different relative abundance of taxa than during the acidifying stages. The core data (Fig. 3) show that for Llyn Llagi, *Tabellaria flocculosa* is now more abundant than in the past, for Lochnagar there has been a major increase in *Aulacoseria distans* var. *nivalis*, a taxon that was formerly rare in the lake, and in Blue Lough, *Semiorbis hemicyclus* has become the dominant diatom in the lake over the last 10 years, although it also was very rare in the past. For the Round Loch of Glenhead (Fig.4c) it is unclear whether the reverse trajectory is being followed. *Navicula leptostriata* has increased strongly in recent years to values not seen in the core material (Fig. 3c), but in the latest trap sample its abundance is much reduced and the overall composition of the assemblage is not very different from earlier assemblages during the acidification phase.

5. Discussion

5.1 Sediment traps and water quality monitoring

The core and the trap data are almost perfectly compatible. At most sites the composition of the diatom assemblages in the earliest trap samples (the 1991 samples) match closely the composition of the respective surface sediment assemblages (the uppermost core sample) from each site. The similarity is illustrated by the small distance between the two samples in ordination space (Fig. 4). There are only two sites, Loch Grannoch and Llyn Cwm Mynach where the compositional difference is significant as indicated by the space between the last core and first trap samples (Fig. 4). For Loch Grannoch the difference is relatively minor: the traps have a significantly higher abundance of *Eunotia incisa* than the sediments. For Llyn Cwm Mynach, however, there is a major mismatch. The trap assemblages are dominated by *Peronia fibula*, *Navicula leptostriata*, and *Eunotia incisa* all of which are either not present or rare in the uppermost level of the core, whereas the core top samples are dominated by *Brachysira vitrea* and *Fragilaria virescens* var. *exigua*, taxa associated with less acidic conditions than those observed in the lake over the last 20 years. As the trap assemblage closely matches the diatom assemblage found in the epilithon of Llyn Cwm Mynach (Shilland et al., 2011) the mismatch suggests that the sediment core may have been truncated with sediment representing the last few decades missing. Further work is needed to resolve this question.

The similarity between the core top and trap samples is not due to the sediment traps being contaminated by resuspended surface sediments, as might be the case in large shallow lakes (Flower, 1991). Cameron (1995) showed that sediment traps of the same design and deployed in a lake similar to those described here faithfully recorded the changes in benthic diatom populations that occurred following a lake liming project, and, at the same time, they did not contain any measurable amounts of the acid tolerant diatoms that characterised the surface sediments. Moreover in all the sites included here, where planktonic diatom populations were largely absent, the changes in trap diatom assemblages over the last 20 years closely follow the trends in epilithon (Shilland et al., 2011).

In consequence for the kind of lakes described here, diatoms collected annually in sediment traps can provide excellent material for water quality monitoring. As they have almost identical characteristics to naturally accumulating sediments, sediment trap time-series can be combined with sediment core data to generate a continuous and highly resolved record from the distant past through to the present day. No other technique yet available can be used so powerfully, and, in terms of acidification recovery it provides the only means of evaluating the success of mitigation strategies as the method enables direct comparisons to be made between pre-acidification conditions and the present day.

5.2 Evidence of recovery: chemical and biological monitoring

Both chemical and biological data from over 20 years of monitoring acidified lakes and streams in the UK show that significant improvements in water quality have occurred (Kernan et al., 2010). Non-marine sulphate concentrations have decreased markedly at all sites and there has been an overall increase in alkalinity, rising pH, falling Al concentrations and rising dissolved organic carbon concentrations (Monteith, this issue), all changes consistent with recovery from acidification and similar to changes observed in other lake systems recovering from acidification (Driscoll et al., 2007; Skjelkvåle et al., 2005). These chemical changes have been accompanied by changes in epilithic diatom communities towards less acid-tolerant taxa (Kernan et al., 2010). Changes in aquatic macrophyte (Kernan et al., 2010) and macro-invertebrate populations (Murphy et al., this issue) have also taken place over the last 20 years that are also consistent with recovery.

5.3 The extent of recovery: diatom data from sediment traps and sediment cores

As described above, diatom data from the sediment trap samples collected over the same time period as the diatom epilithic samples are floristically similar at most sites and follow similar trends, reflecting the dominance of stone surfaces as the dominant habitat for diatoms in these low alkalinity upland lakes. Burnmoor Tarn is the single exception. It is a richer, somewhat more alkaline site and supports a planktonic diatom community as well as benthic communities. The trap sediments from Burnmoor Tarn therefore contain a mixture of planktonic and benthic diatoms with the planktonic component, mainly comprising *Cyclotella* taxa, being dominant.

Although the epilithic diatom data show that significant changes have taken place over the monitoring period following the improvements in water quality across the Network noted above, the core and sediment trap diatom data show that the overall improvement in water quality is, so far, very limited. There remain very significant differences between the composition of the contemporary diatom assemblages (latest trap sample) and the pre-acidification assemblages recorded by the sediment cores (core bottom sample) at all sites except for Blue Lough and Coire nan Arr. For Coire nan Arr this lack of dissimilarity is expected as the site has experienced very little acidification and acts as a control site within the network. Blue Lough, on the other hand, is a strongly acidified site. However, it is also a naturally acidic site, so the pre-acidification flora is composed of acid-tolerant taxa and the floristic difference between the basal core samples and the present-day trap samples is much less than for other acidified sites. Of these only Llyn Llagi (Fig. 4d) has started to regain some of the acid-sensitive taxa, such as *Brachysira vitrea*, that were dominant in pre-acidification times. At other sites there has been a reduction in the most acid tolerant taxa, for example *Tabellaria quadriseptata* at the Round Loch of Glenhead (Fig. 3c) but little evidence yet of the re-appearance in any abundance of the acid-sensitive flora that characterised the lake in the early 19th century and before (Fig. 3c).

The reasons for the limited scale of recovery are probably varied. There is strong empirical evidence that diatoms are very sensitive to shifts in water pH and, because of their very short generation time, track secular changes in pH with little time delay (Battarbee et al., 2008; Cameron, 1995). Consequently it is likely that the limited recovery in acid sensitive diatom populations is due to the, as yet, limited increase in pH, relative to the pre-acidification pH, rather than a lag in biological response. Although there has been a major decrease in acid anion concentration, especially sulphate, at all sites (Monteith, this issue), there have been balancing changes in base cations, especially Ca^{2+} concentration, DOC and labile Al^{3+}, as well as by H^+ . It is probable therefore, that the pH increase seen so far is modest compared to pre-acidification pH levels and that a much greater reduction in the acid anion concentration is needed for pH values to rise to pre-acidification levels and allow a fuller biological recovery to occur.

Further reduction in acid anion concentrations depends principally on whether S and N compounds reaching lake waters will be reduced. As sulphur emissions and deposition have reached very low levels following successful mitigation strategies to reduce emissions across Europe the proximate cause of continuing elevated acid anion concentrations may be the continued release of S from catchment soils coupled with N leaching at some sites (Curtis et al., 2005). Although many studies have shown that S acts conservatively in catchment soils and that reductions in deposition are rapidly followed by concomitant reductions in sulphate flux to surface waters (Cooper, 2005; Davies et al., 2005), there is also evidence that stored 'legacy' S may continue to be released through time even after deposition is reduced to negligible levels, especially at sites with organic soils, through both oxidation and erosion processes (Daniels et al., 2008). Sulphate levels at many of the AWMN sites do indeed remain high compared to expected background values typical of those at Coire nan Arr, the AWMN control site in the North-west of Scotland (Fig. 1, Table 1). Nitrate concentrations are generally low relative to sulphate at most sites but at a small number of sites in the Network (e.g. The Round Loch of Glenhead and Loch Chon) nitrate concentrations have risen, offsetting some of the effects of reduced sulphate concentrations, and at other sites (e.g. Scoat Tarn, Lochnagar) nitrate levels remain at much higher levels than the expected background values of <5 μeq l^{-1} found in "control" sites in the far north-west of Scotland.

5.4 Factors confounding recovery

Whereas acid deposition, especially S deposition, has been the dominant control on the chemistry and biology of acidified upland surface waters over recent decades, upland waters have also been subject to other influences, most notably N deposition and climate change, over the same time period. N deposition can result in an increase in nitrate concentration that not only acts as an acidic anion, as described above, but also as a nutrient (Curtis et al., 2005; Maberly et al., 2002). Where the productivity of upland waters is limited by the availability of nitrogen, rather than phosphorus, N deposition can be a cause of eutrophication (Elser et al., 2007).

Although the main impact may be in the future if and when N saturation of catchment soils becomes more extensive and climate change accelerates N leaching (Curtis et al., 2005), N enrichment may already be having an effect at some sites in the AWMN and be responsible for some of the diatom changes observed from the sediment trap record. This possibility is supported by *in situ* bioassays of periphyton (Maberly et al., 2002) and phytoplankton (Curtis and Simpson, 2007) in UK upland lakes. Across the 43 lakes studied, growth and productivity were limited almost as frequently by N availability as by P, but joint- or co-limitation of growth by both N and P together was the most common status. Consequently N- nutrient enrichment might be one of the factors explaining the difference between the composition of diatom assemblages on the recovery trajectory as compared to the acidification trajectory at sites such as the Round Loch of Glenhead and Lochnagar. Both sites have experienced elevated nitrate concentrations over the last 20 years and the significant increase in the relative abundance of *Aulacoseira distans* var. *nivalis*, a taxon thought to be planktonic, in Lochnagar may especially indicate nutrient enrichment. For the Round L. of Glenhead, a system more dominated by benthic algae, the response to enrichment may be different. At this site, the diatom that has increased in abundance is the epipelic *Navicula leptostriata*. A recent study of epipelic diatoms in the Round Loch of Glenhead (Yang and Flower, 2012; Yang et al., 2009) has shown that this taxon is not only abundant on the surface of the muds within the photic zone of the lake but is also common in the epilithic biofilms. We hypothesise at this site, therefore, that increasing N concentrations may have led to higher primary production on stone surfaces and the development of a rich biofilm within which the motile *N. leptostriata* has been able to flourish. The diatom response in this case may have been a result of habitat modification rather than through a direct nutrient stimulus. For Loch Chon, a third site in the network where N concentrations have increased, no special effect of N has been detected, as changes in the composition of the diatom assemblages in the trap samples during the recovery phase largely mirror the changes that occurred during the acidification phase. In this case, either N is not limiting or increased primary production that may be occurring is not reflected by any significant shift in the composition of the lake diatom flora.

N enrichment is not the only factor that may explain these structural changes in the composition of the diatom assemblages during recovery as most sites have also experienced a change in climate over the monitoring period. Based on evidence for Lochnagar (Agusti-Paraneda and Thompson, 2002), surface waters of lakes across the Network are now likely to be up to 1° C warmer than in the early 19th century, potentially influencing both the thermal structure of the water column and the rate of important biogeochemical and ecological processes in the lakes and their catchments.

Although site specific long-term precipitation data are lacking climate change is predicted to increase the intensity and frequency of precipitation in the uplands (Murphy et al., 2009). Evans et al. (2008) have shown that storm events can have a significant impact on runoff chemistry, including pH and acid neutralising capacity. Sites close to the west coast of Britain especially can receive substantial amounts of sea-salt deposition that can exacerbate the acidity of runoff from soils already depleted in base cations due to acid rain (Kernan et al., 2010). Analysis of the 20-year water chemistry record from the Network shows a strong negative relationship between ANC and the state of the Arctic Oscillation (AO), a mode of climate variability in the Northern Hemisphere associated with wet, relatively warm winters in Western Europe, and one which has intensified over recent decades.

The extent to which climate change is responsible for the observed change in diatom assemblages in the AWMN lakes over the last 20 years is unknown and it is difficult to disentangle the warming effects of climate change from the effects of N enrichment as both pressures are likely to cause symptoms of eutrophication (Moss et al., 2011). However, at sites such as Lochnagar and Burnmoor Tarn where planktonic diatoms are now more abundant than in the pre-acidification period, increasing surface-water temperature may be playing a role. The increase in *Cyclotella* taxa at Burnmoor Tarn is indeed consistent with changes that have taken place at other sites where climate change is believed to be responsible (Catalan et al., 2002; Ruhland et al., 2008).

Overall, some of these confounding influences, such as increased storminess or increased nitrate leaching, may simply delay the recovery process by providing a secondary source of acid anions that offset the reduction in sulphate concentration. Other factors, on the other hand, such as increased temperature and the influence of nitrate as a nutrient might lead to the development of entirely new ecosystems where communities in future are characterised by less acid-tolerant flora and fauna as acidity decreases, not necessarily by a faithful progression towards the return of pre-acidification taxa. Such a return may also be inhibited by modifications to within-lake habitat structures and food-webs that have taken place during the acidification process that are not only difficult to reverse but are also likely to be further modified by external pressures if water temperatures continue to rise.

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Tables

Table 1. AWMN lake sites including location, altitude, calcium concentration (mg L^{-1}), pH, sulphur deposition (kg S $ha^{-1}yr^{-1}$) and the code of the sediment core used for the diatom data in Figure 4). Data are mainly from Kernan et al. (2010). S deposition for 1990 is 10km Institute of Terrestrial Ecology data (1989-91) and Centre for Ecology and Hydrology CBED data (2006-2008). Coire nan Arr ceased to be an AWMN site in 2007 so data from 2009 are not available (na). For Blue Lough, Ca and pH 1989 data are for 1991. CBED = Concentration Based Estimated Deposition.

	Lat long	*alt (m)*	*Ca 1989*	*Ca 2009*	*pH 1989*	*pH 2009*	*S dep 1990*	*S dep 2007*	*Core code*
Coire nan Arr	N57°24.99', W005°39.08	125	1.04	na	6.36	na	12.5	3.8	ARR5
Blue Lough	N54°9.53', W005°58.13	340	1.10	0.44	4.63	5.03	13.1	5.6	BLUE5
Round L of Glenhead	N55°5.62', W004°25.84	298	0.76	0.45	4.88	5.14	21.4	7.6	RLGHK5
Llyn Llagi	N53°0.86', W004°0.92'	375	1.06	0.80	5.20	5.59	24.4	6.1	LAG3
Scoat Tarn	N54°28.9', W003°17.95	598	0.66	0.43	5.00	5.25	21.4	7.7	SKT1
Lochnagar	N56°57.54', W003°13.88	788	0.70	0.38	5.40	5.58	10.3	7.2	NAG6
Loch Chon	N56°12.87', W004°32.91	92	1.72	1.36	5.25	6.01	18.7	7.0	CHON11
Loch Tinker	N56°13.65', W004°30.51	418	1.80	1.23	5.88	6.03	18.7	7.1	TIN5
Burnmoor Tarn	N54°25.7', W003°15.58	253	1.89	1.49	6.62	6.51	21.4	6.6	BURN1
Loch Grannoch	N55°0.14', W004°16.85	214	1.22	0.58	4.71	4.71	19.9	6.3	GRAN89/1
Llyn Cwm Mynach	N52°47.76', W003°57.63	287	1.63	1.00	5.47	5.07	18.8	6.0	MYN6

Table 2. Analysis of trends in sediment trap diatom assemblages using PCA and additive modelling. PC1 = Eigenvalue for principal component axis 1; % VarExpl = % variance explained; df = degrees of freedom; F = test statistic.

Site	PC1	% VarExpl	df	*F*	*p* value
Coire nan Arr	0.032	19.94	5.64	11.12	0.0127
Blue Lough	0.084	51.5	4.16	52.68	<0.001
Round L of Glenhead	0.035	25.04	1	41.51	<0.001
Llyn Llagi	0.086	44.17	3.02	29.52	<0.001
Scoat Tarn	0.041	21.59	1	6.03	0.0256
Lochnagar	0.031	19.95	4.94	13.37	<0.001
Loch Chon	0.016	20.75	2.66	19.14	<0.001
Loch Tinker	0.03	21.19	3.57	51.37	<0.001
Burnmoor Tarn	0.033	25.32	2.74	15.75	<0.001
Loch Grannoch	0.069	39.71	1.89	2.07	0.1645
Llyn Cwm Mynach	0.025	17.63	1	23.09	<0.001

Figure captions

Figure 1 Map showing location of AWMN lake sites and secondary sites used for sediment coring and the compilation of a dataset of diatom assemblages from UK low alkalinity lakes using in Figure 4. Site numbering follows the scheme used for AWMN sites.

Figure 2 Trend tests using general additive modelling of PC axis 1 scores for the 11 AWMN lake sites: (a) Corrie nan Arr; (b) Blue Lough; (c) Round Loch of Glenhead; (d) Llyn Llagi; (e) Lochnagar; (f) Loch Chon; (g) Loch Tinker; (h) Burnmoor Tarn; (i) Loch Grannoch; (j) Llyn Cwm Mynach.

Figure 3. Sediment core (1790-1990) and sediment trap (1991-2009) diatom data for 11 AWMN sites: (a) Corrie nan Arr; (b) Blue Lough; (c) Round Loch of Glenhead; (d) Llyn Llagi; (e) Lochnagar; (f) Loch Chon; (g) Loch Tinker; (h) Burnmoor Tarn; (i) Loch Grannoch; (j) Llyn Cwm Mynach. Only selected taxa are shown.

Figure 4. Acidification and recovery trajectories for diatom assemblages at 11 AWMN lakes using data from sediment cores (light line) and sediment traps (bold line). The basal sample used for reference at each site is represented by a closed circle and the most recent sample (2008) for each site is indicated by an arrow head: (a) Corrie nan Arr; (b) Blue Lough; (c) Round Loch of Glenhead; (d) Llyn Llagi; (e) Lochnagar; (f) Loch Chon; (g) Loch Tinker; (h) Burnmoor Tarn; (i) Loch Grannoch; (j) Llyn Cwm Mynach.

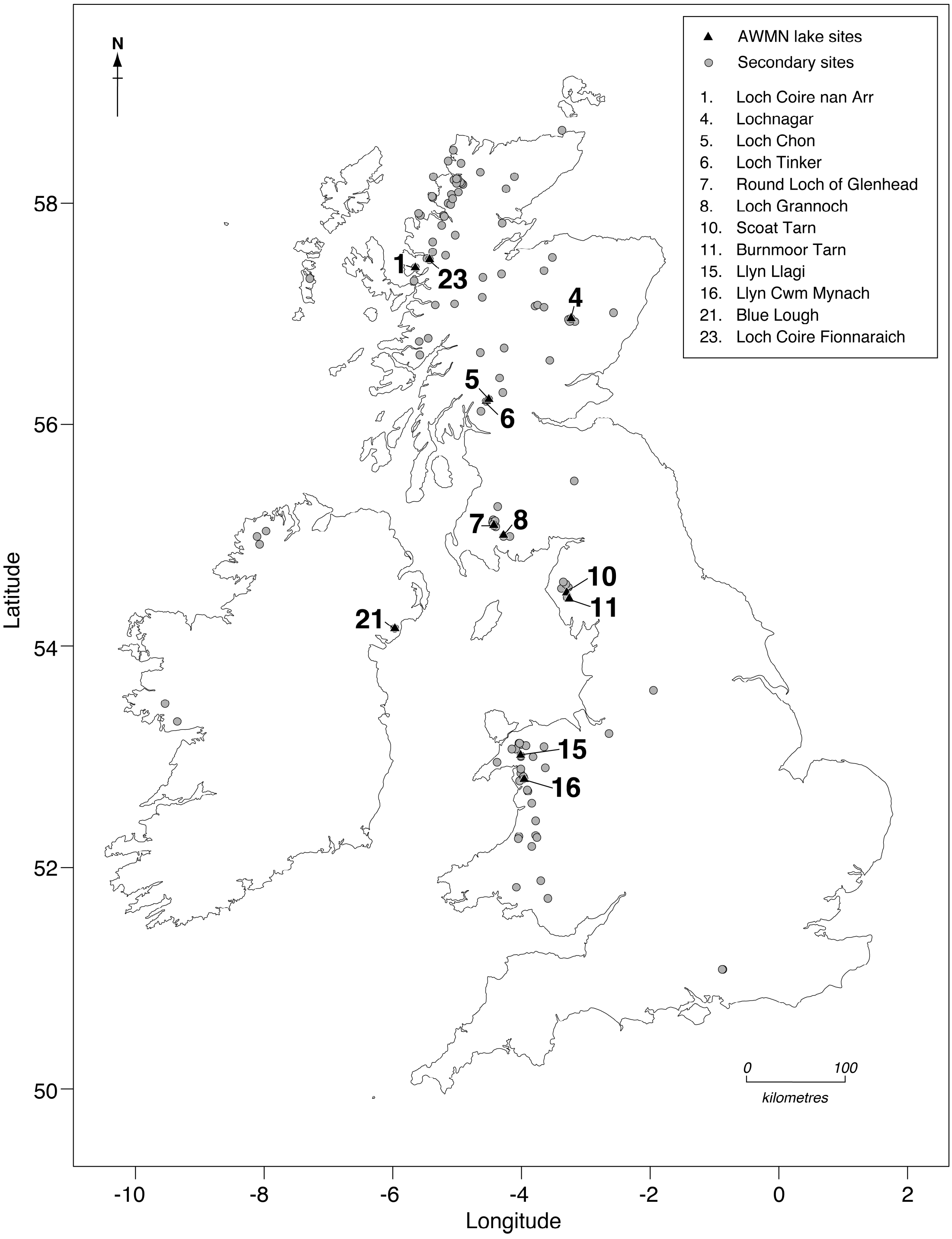

N
▲ AWMN lake sites
● Secondary sites
1. Loch Coire nan Arr
4. Lochnagar
5. Loch Chon
6. Loch Tinker
7. Round Loch of Glenhead
8. Loch Grannoch
10. Scoat Tarn
11. Burnmoor Tarn
15. Llyn Llagi
16. Llyn Cwm Mynach
21. Blue Lough
23. Loch Coire Fionnaraich
1
23
4
5
6
7
8
10
11
21
15
16
58
56
54
52
50
Latitude
-10
-8
-6
-4
-2
0
2
Longitude
0
100
kilometres

Figure 1

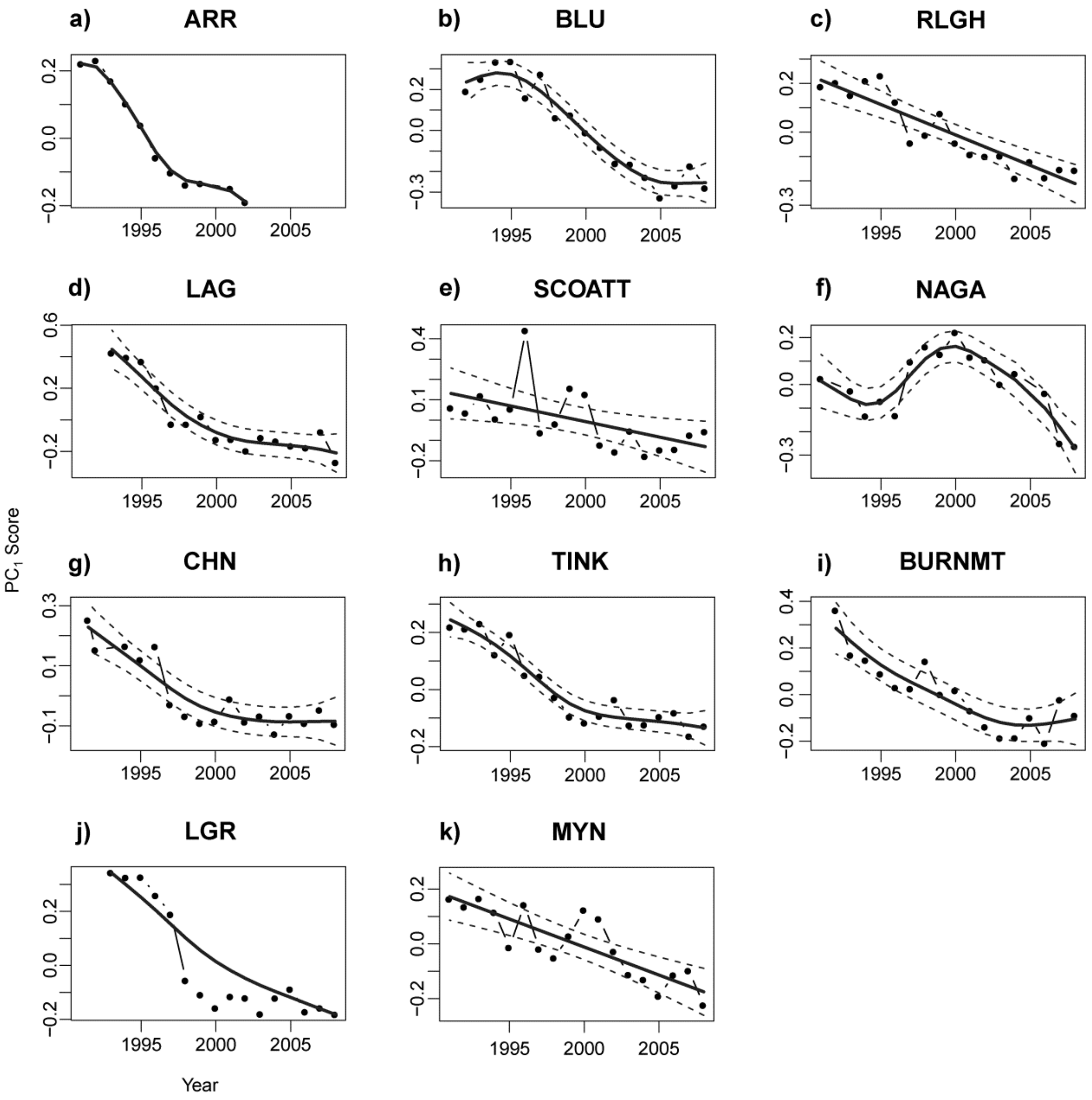
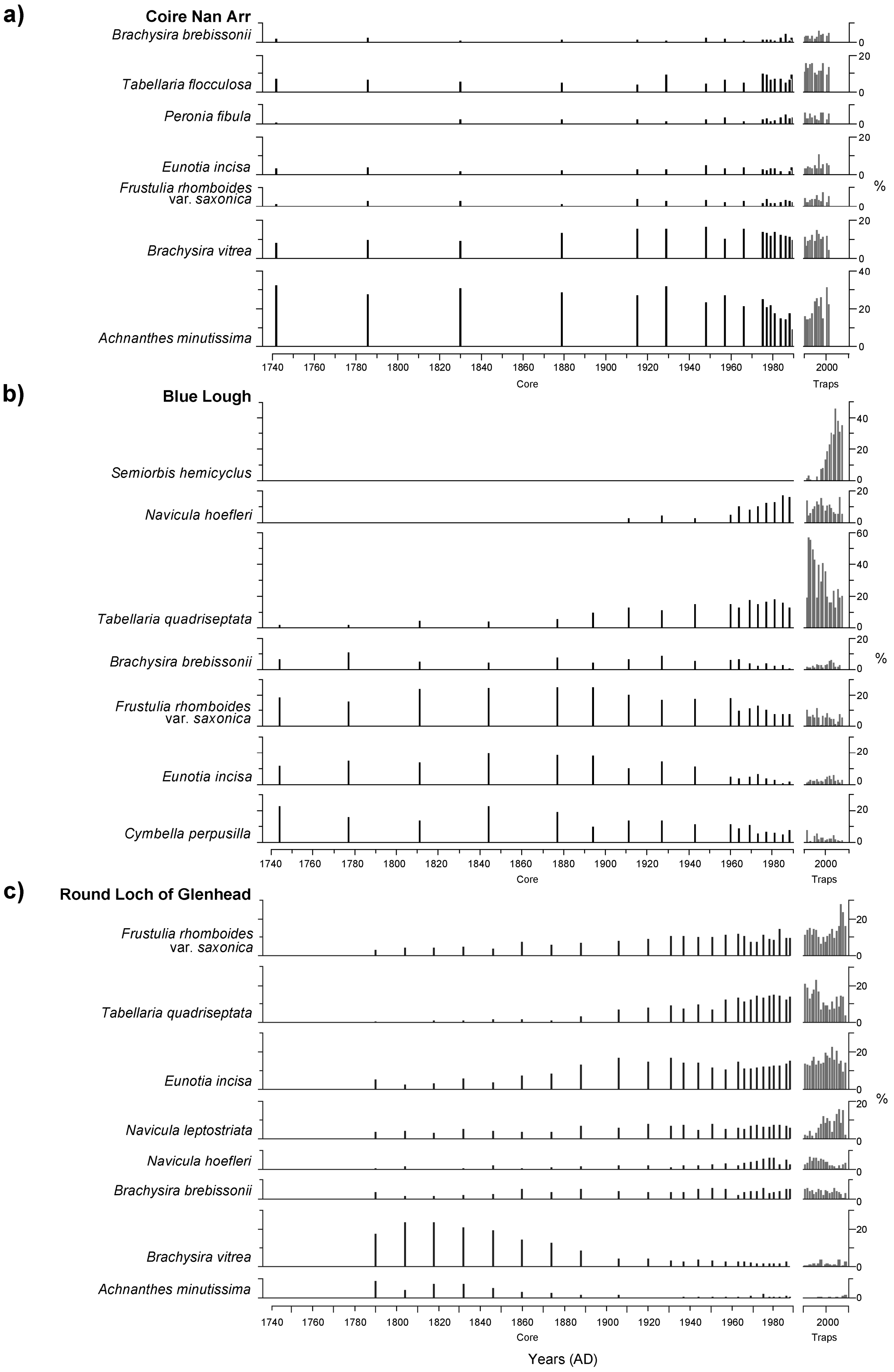
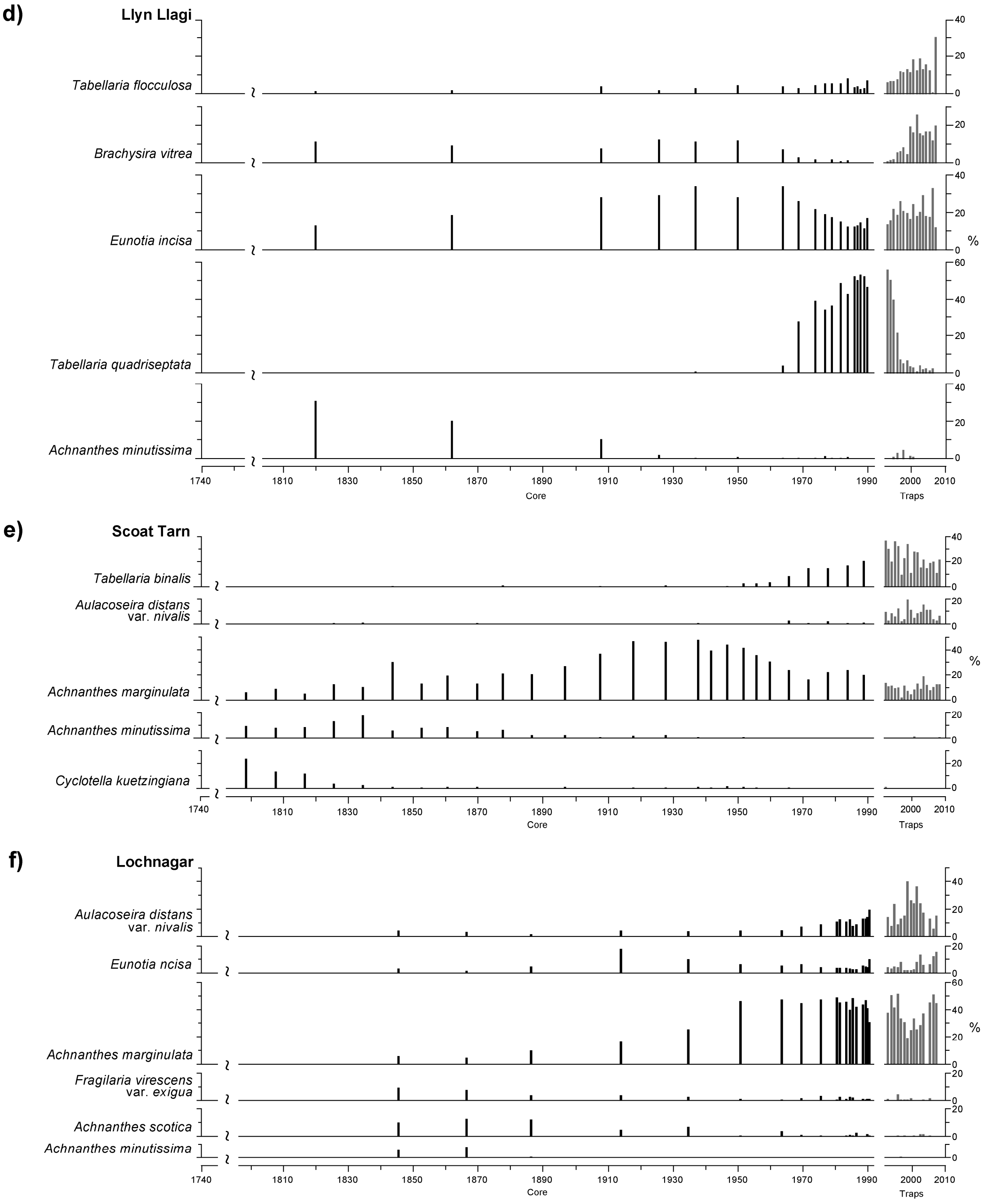

a) ARR
b) BLU
c) RLGH
d) LAG
e) SCOATT
f) NAGA
g) CHN
h) TINK
i) BURNMT
j) LGR
k) MYN
PC1 Score
Year
1995
2000
2005

Figure 2


a)
Coire Nan Arr
Brachysira brebissonii
Tabellaria flocculosa
Peronia fibula
Eunotia incisa
Frustulia rhomboides var. saxonica
Brachysira vitrea
Achnanthes minutissima
0
20
40
%
1740
1760
1780
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
Core
2000
Traps
b)
Blue Lough
Semiorbis hemicyclus
Navicula hoefleri
Tabellaria quadriseptata
Brachysira brebissonii
Frustulia rhomboides var. saxonica
Eunotia incisa
Cymbella perpusilla
60
c)
Round Loch of Glenhead
Frustulia rhomboides var. saxonica
Tabellaria quadriseptata
Eunotia incisa
Navicula leptostriata
Navicula hoefleri
Brachysira brebissonii
Brachysira vitrea
Achnanthes minutissima
Years (AD)


d)
Llyn Llagi
Tabellaria flocculosa
Brachysira vitrea
Eunotia incisa
Tabellaria quadriseptata
Achnanthes minutissima
%
0
20
40
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1810
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1910
1930
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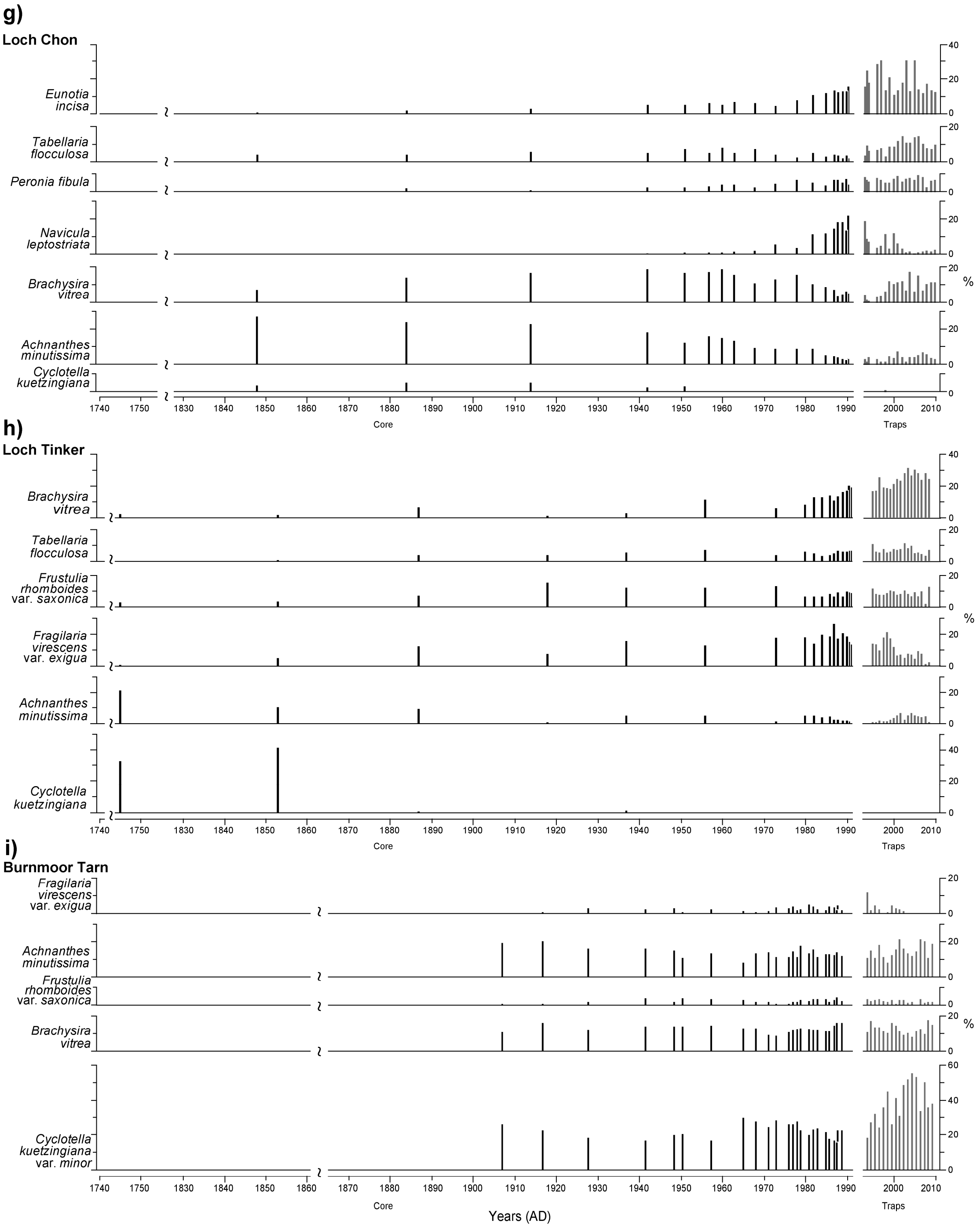
1970
1990
2000
2010
Core
Traps
e)
Scoat Tarn
Tabellaria binalis
Aulacoseira distans var. nivalis
Achnanthes marginulata
Achnanthes minutissima
Cyclotella kuetzingiana
f)
Lochnagar
Aulacoseira distans var. nivalis
Eunotia ncisa
Achnanthes marginulata
Fragilaria virescens var. exigua
Achnanthes scotica
Achnanthes minutissima


g)
Loch Chon
Eunotia incisa
Tabellaria flocculosa
Peronia fibula
Navicula leptostriata
Brachysira vitrea
Achnanthes minutissima
Cyclotella kuetzingiana
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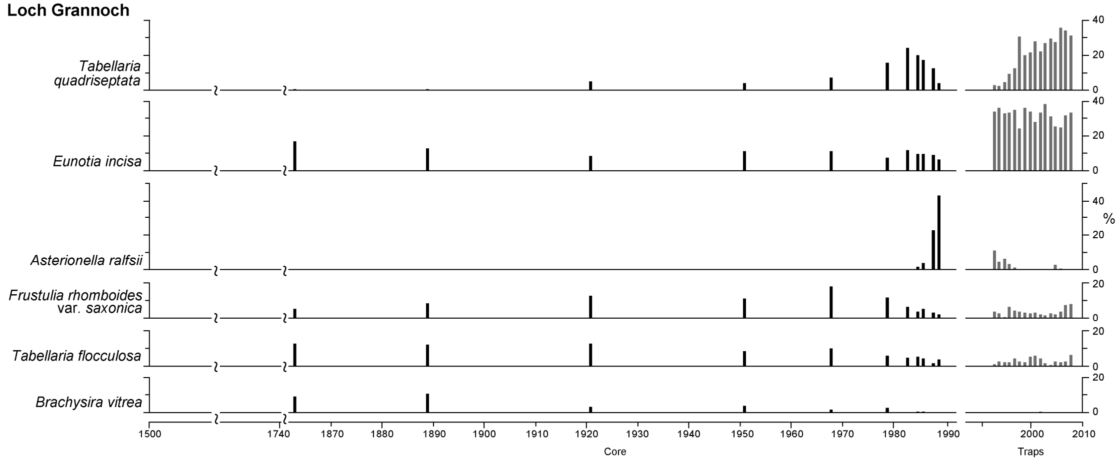
Core
Traps
h)
Loch Tinker
Brachysira vitrea
Tabellaria flocculosa
Frustulia rhomboides var. saxonica
Fragilaria virescens var. exigua
Achnanthes minutissima
Cyclotella kuetzingiana
i)
Burnmoor Tarn
Fragilaria virescens var. exigua
Achnanthes minutissima
Frustulia rhomboides var. saxonica
Brachysira vitrea
Cyclotella kuetzingiana var. minor
60
Years (AD)

j)
Loch Grannoch



k)
Llyn Cwm Mynach

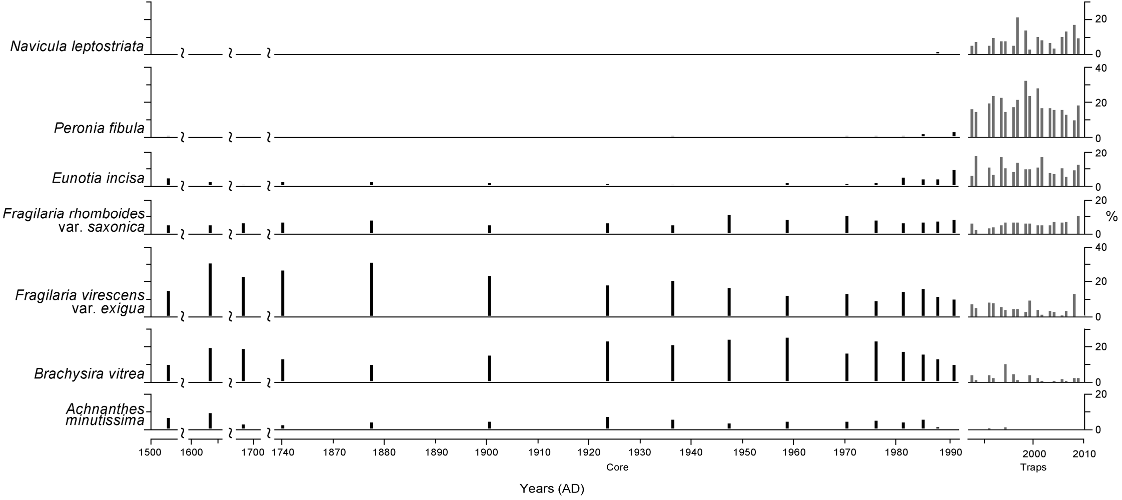
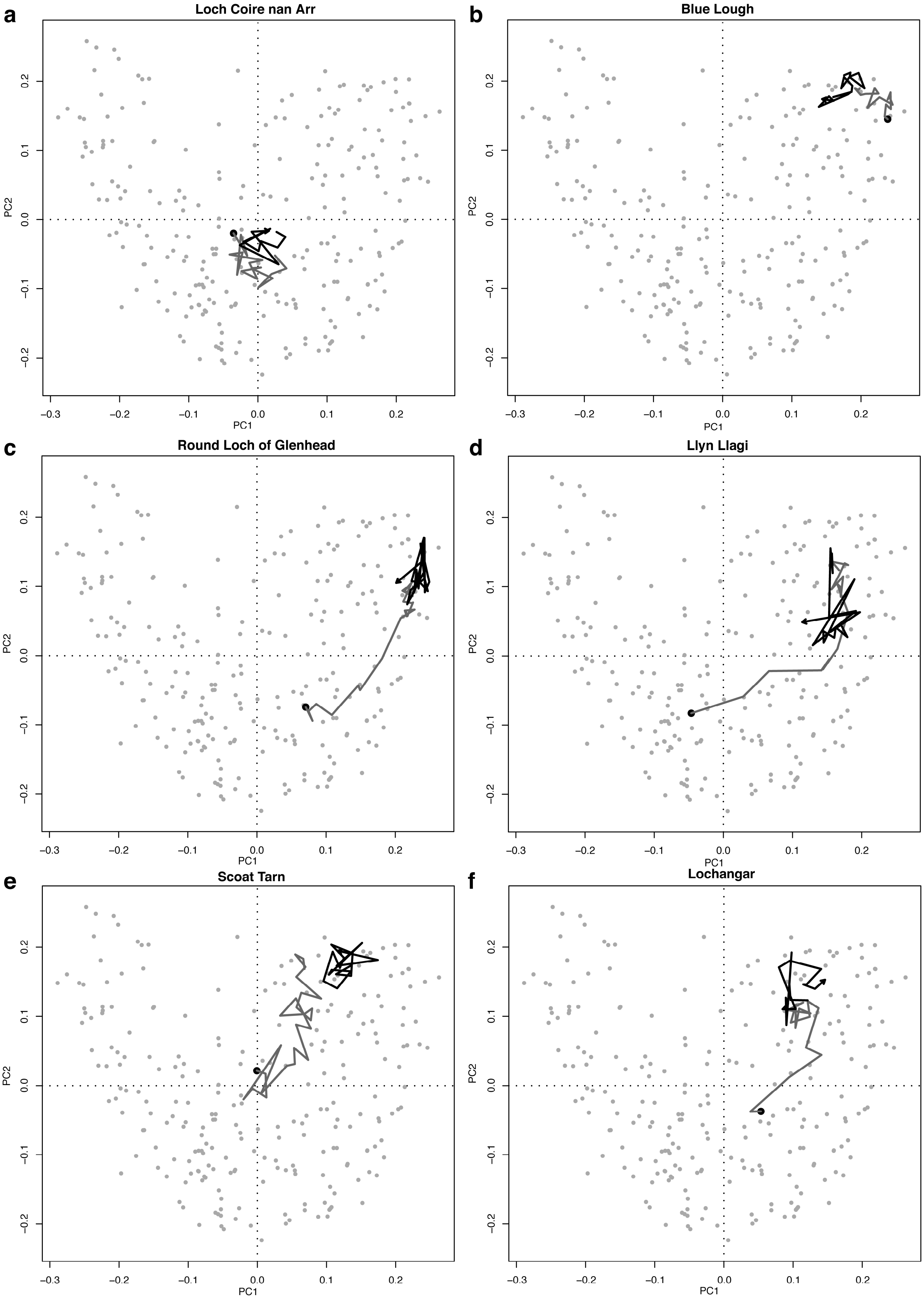


Figure 3 a-k


a
Loch Coire nan Arr
b
Blue Lough
c
Round Loch of Glenhead
d
Llyn Llagi
e
Scoat Tarn
f
Lochangar
PC1
PC2
−0.3
−0.2
−0.1
0.0
0.1
0.2

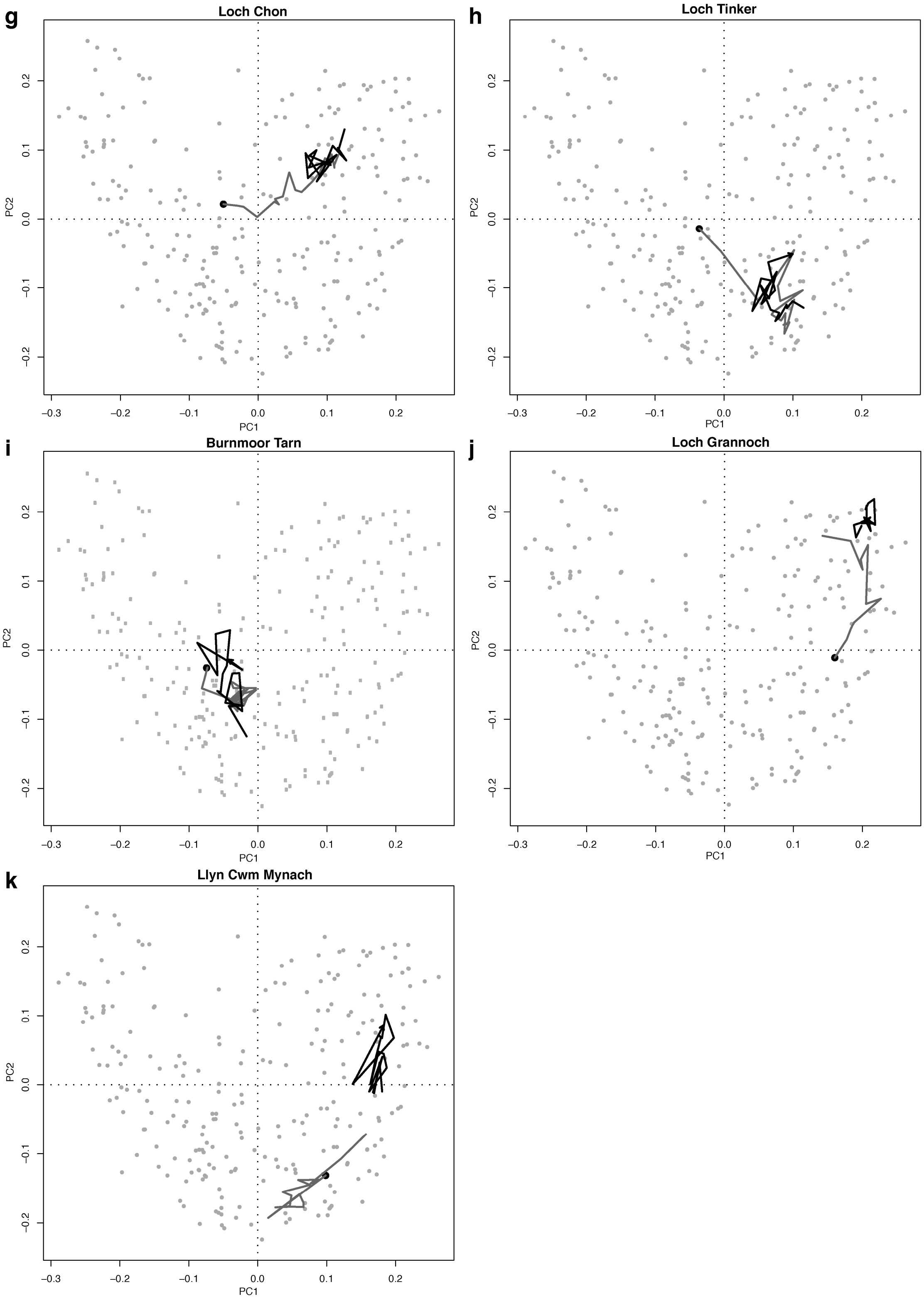

g
Loch Chon
h
Loch Tinker
i
Burnmoor Tarn
j
Loch Grannoch
k
Llyn Cwm Mynach
PC1
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Figure 4 a-k

Paper 6

Changes in diatom biodiversity based on data-sets from both low-alkalinity and nutrient - rich surface waters

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Environmental Change Research Centre, University College London, Gower St.,London, WC1E 6BT

Diatoms are not only excellent indicators of surface water quality used extensively in monitoring programmes but are preserved in lake sediments, thereby enabling the long-term history of lake ecosystems to be reconstructed. However, there have been none or few studies that have been concerned with diatom biodiversity patterns in space and time in response to pollution pressures or that have examined their value as indicators of biodiversity, rather than water quality change.

Here we have assessed the impact of acidification and eutrophication on diatom biodiversity using a range of existing or newly collated data-sets. These include:

- Surface sediment data-sets from the European Diatom Database (EDDI) that includes sites covering pH, total phosphorus and salinity gradients (web);
- Sediment core data from an 121 site database of UK low-alkalinity lakes (cf. Battarbee et al. 2011);
- Epilithic data from the Acid Waters Monitoring Network (cf. Shilland et al. 2012) that includes 22 lake and stream sites in the UK;
- A sediment core data-set from Loch of the Lowes, Scotland that includes diatom palaeoecological evidence for eutrophication;

In our analyses we have also investigated the value of different biodiversity metrics and explore the use of new methods.

1. Diatom diversity change across a European pH gradient (Figure 1)

To assess the response of diatom biodiversity to pH we used a large data-set of diatom assemblage data from the EDDI database, spanning a gradient from pH 4 to approximately pH 9. The results (Figure 1) showed increasing turnover in species composition along the gradient towards higher pH, accompanied by decreasing richness and evenness at pH values above 7.5. As pH is a very important driving variable the species turnover findings are not unexpected. The reasons for the changes in richness and evenness, however, are not certain and await future inspection of the primary data, but one possibility is that the assemblages at higher pH are composed of fewer, but more abundant planktonic taxa.

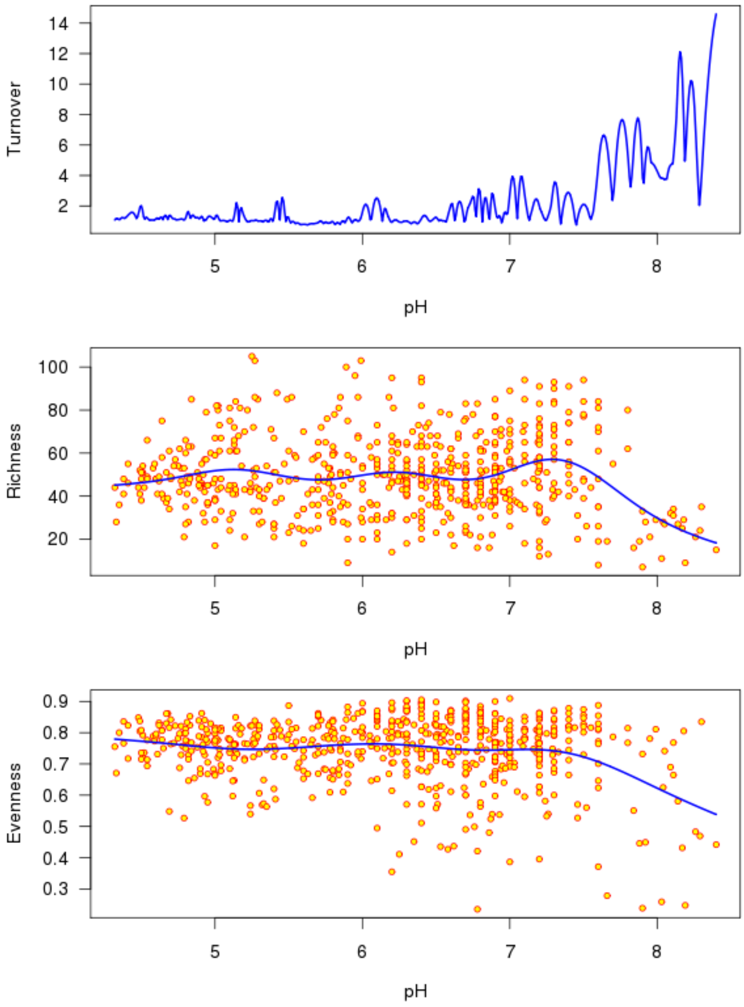

Figure 1. Diatom turnover, richness and evenness patterns along a pH gradient

2. Diatom diversity along a European total phosphorus (TP) gradient (Figure 2)

As for pH, to assess the changes in the biodiversity distribution of diatoms across a TP gradient we used the EDDI database that includes surface sediment diatom assemblages spanning a gradient of TP from approximately 10 to 1,000 µg/l. The data show a constant background turnover in species composition which is not unexpected given the importance of TP as a primary controlling nutrient on diatom community composition. There is no general pattern in richness across the gradient but there is a statistically significant increase in evenness from low to high TP. This is an unexpected finding as highly enriched lakes are usually dominated by small numbers of predominantly planktonic taxa and contain reduced numbers of benthic taxa restricted by light. Inspection of the primary data is needed. A further feature of the data is the considerable scatter in evenness values across the gradient, possibly reflecting lakes with alternative states at a given TP. Clear water sites are likely to have more diverse communities and an equitable (close to 1) species composition whereas turbid ones at the same TP are likely to be dominated by a small number of species and have an uneven composition (close to 0).

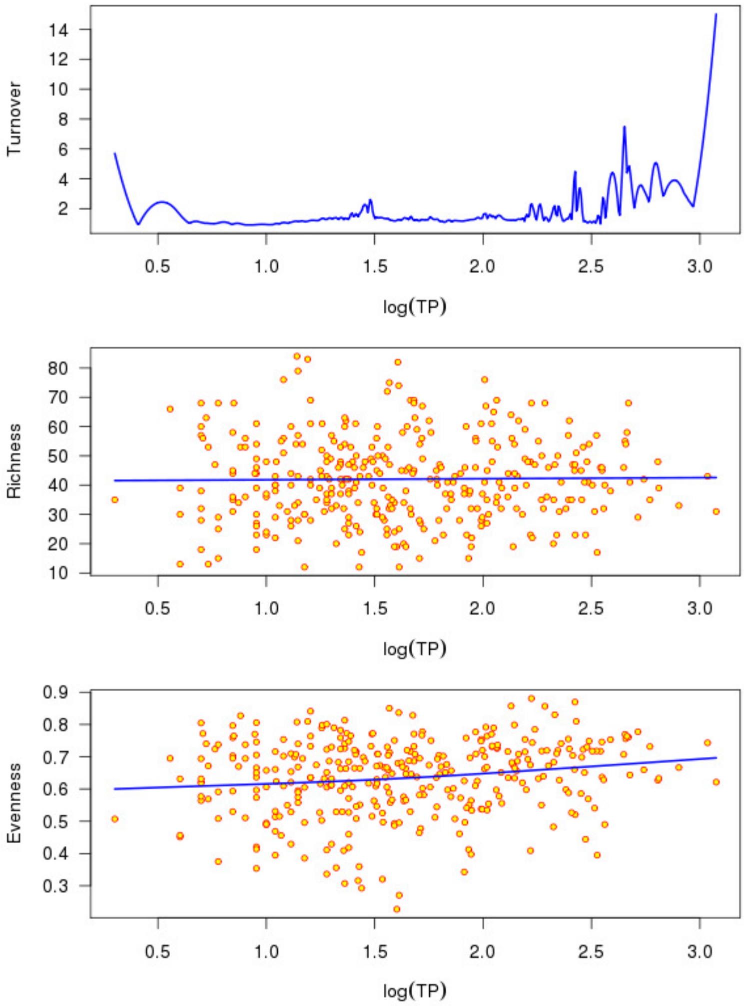

Figure 2. Diatom turnover, richness and evenness patterns across a total phosphorus gradient. Data from EDDI (http://craticula.ncl.ac.uk/Eddi/jsp/).

3. Response of diatom diversity to changes in pH through time

We have analysed epilithic diatom data from samples collected annually from 22 lakes and streams in the UK Acid Waters Monitoring Network (AWMN) since 1988. Hydrochemical data collected from the sites over the same time period show that pH has been increasing at most of the sites as they have been recovering from the effects of acid deposition and small but significant linear trends in diatom species composition have been identified at many of these sites (Kernan et al. 2010). We have compared data for 1991, 2000 and 2007, separately for lakes and streams. The results (Figure 3) show that there is no evidence for increasing richness in response to recovery from acidification between the three time periods and that richness can be considerably variable from year to year. In addition the results show that lake epilithon is considerably more species rich than epilithon from streams. We attribute this to the greater stability of the substrate in lakes compared with streams. Upland streams in the UK are especially prone to high velocity flow conditions that can destabilise stream beds and scour biofilms.

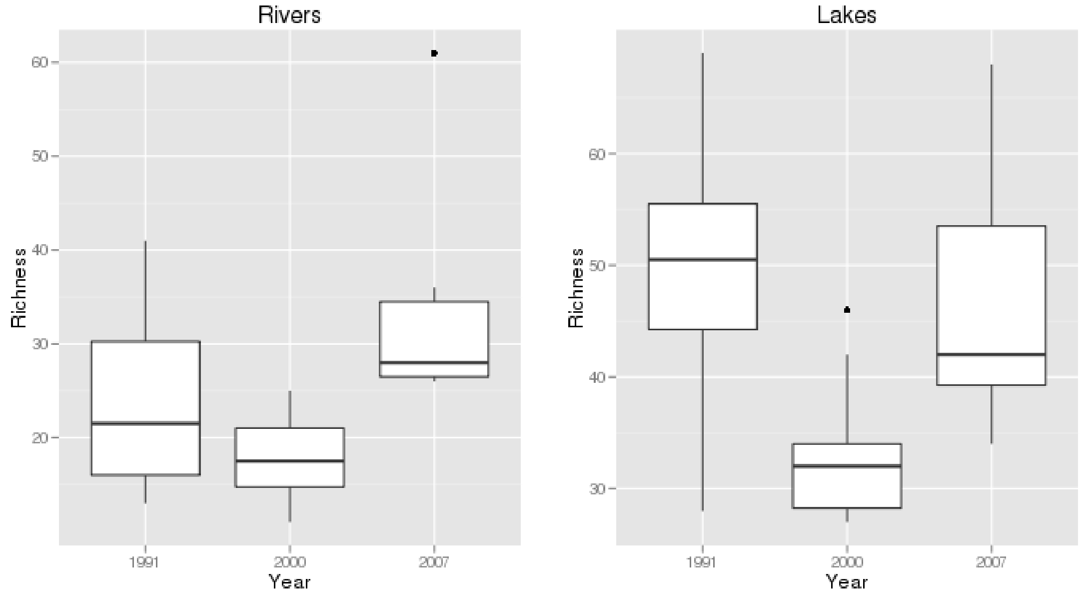

Figure 3. Comparison of diatom epilithon richness between lakes and streams for the years 1991, 2000 and 2007. Data from the UK Acid Waters Monitoring Network (http://awmn.defra.gov.uk/).

To explore these results in more detail we have carried out analyses on all 22 sites individually. Figures 4-6 show the results for richness, Shannon diversity and evenness. At most sites there is no significant linear trend in any of the biodiversity metrics through time although there are fluctuations over the course of the record and the results show there is an apparent reduction in diversity at some sites as pH increases. The patterns of diversity change are complex at these sites and require further investigation.

The lack of a clear trend at any individual site may reflect: (i) that, despite the shifts in diatom composition that have taken place at many sites as a result of recovery from acidification, the change has so far been insufficient to affect biodiversity as judged by these metrics; or (ii) that, despite the species turnover, diatom diversity remains stable along this part of the pH gradient (i.e. from pH 7 to 5) and that no real change in diversity is likely to occur (excepting at the most acidic sites) even if further increases in pH take place. This latter conjecture is supported by a comparison between sites that shows only the extremely acidic sites (pH <4.5), such as Afon Gwy and Afon Hafren (Figure 4) have low richness scores. Diatom assemblages at such low pH sites tend to be dominated by only a small number of acid and labile aluminium tolerant species (such as *Eunotia exigua*) as is reflected by the low evenness scores for these two sites (cf. Figure 6). To explore this hypothesis we need to examine more sites with water chemistries spanning the extreme acidic end of the pH gradient (i.e. between pH 5 and 4) where a threshold for diatom diversity seems to occur.

Figure 4. Trends in epilithon taxon richness for all AWMN sites.

Figure 5. Trends in epilithon Shannon Diversity for all AWMN sites.

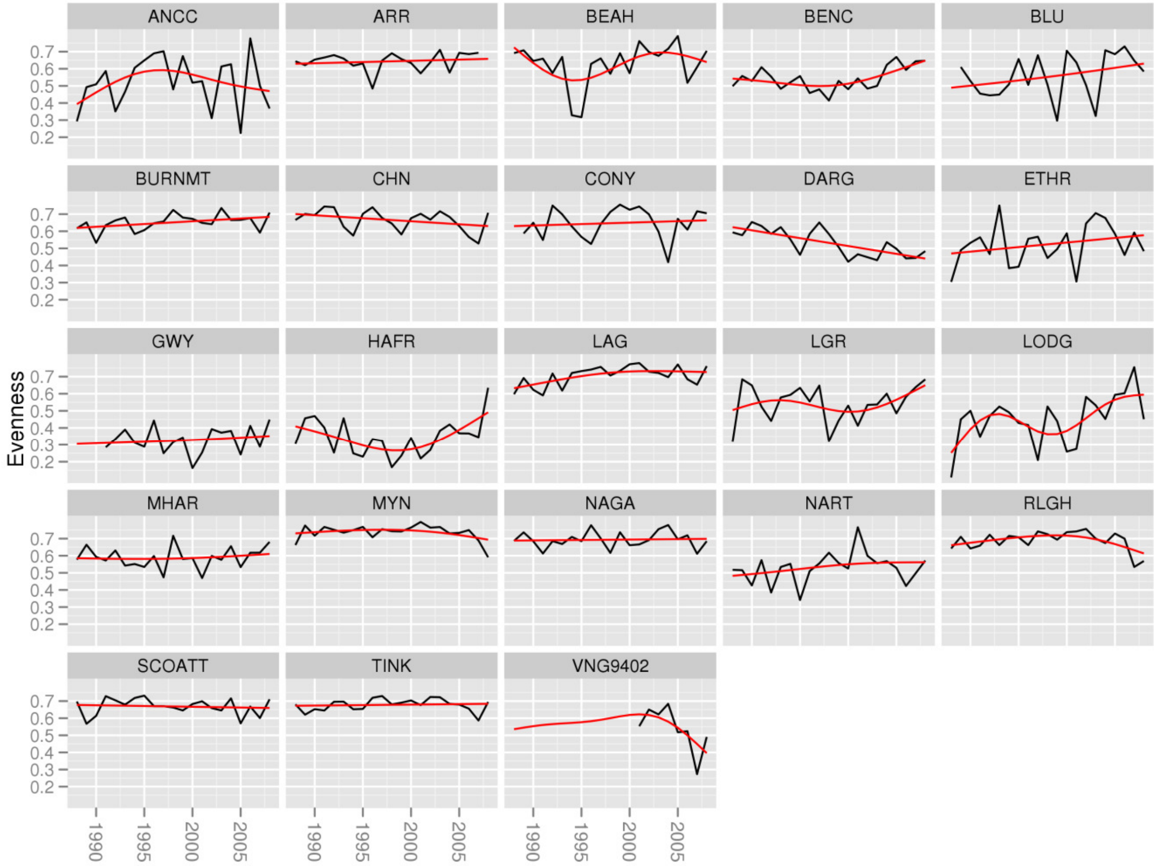

Figure 6. Trends in epilithon taxon evenness at all AWMN sites

4. The impact of acidification on diatom biodiversity based on a comparison of reference and modern samples from low-alkalinity UK lakes

We have attempted to assess the impact of acidification on the diatom biodiversity of low-alkalinity lakes in the UK by comparing modern (top) sediment samples (ca. 1980-1990AD) with pre-acidification or reference (bottom) samples (from ca. 1800-1850 AD) of sediment cores from 121 sites. The data-set has been described previously and used to define reference diatom assemblages for acidified UK lakes (Battarbee et al. 2011).

To compare the diversity of the bottom and top samples we used the multivariate dispersion method of Anderson (2006), with permutation testing, to show differences in the degree of dispersion of the two groups of samples in multivariate space.

The results showed that the top samples were more dispersed (therefore more diverse) than the bottom (reference) ones (Figure 7, left) with a shift in the mean of the distribution (red dot in Figure 7 right) toward more acid taxa (toward the top right). While the shift towards more acid taxa would be expected, by definition, the increase in diversity is not expected. Consequently, we repeated the exercise using three previously defined sample clusters (Battarbee et al. 2011) rather than the whole data-set.

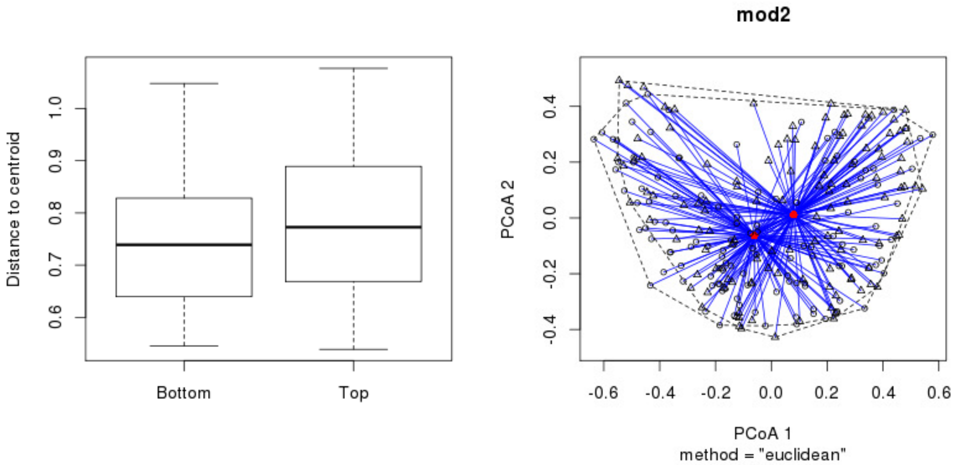

Figure 7. Diatom diversity difference between top (modern) and bottom (reference) samples in cores from a 121 UK low alkalinity lake data-set (see text for explanation).

The results (Figure 8) were similar to those for the whole data-set. All three clusters showed that the top samples were more dispersed than the bottom samples and all three showed shifts in distribution towards more acidic taxa. These results are counter to initial expectation whereby diversity was expected to decrease or be unchanged as a result of acidification. To explain this, we believe that the top samples of the entire data-set and of each cluster contain a mixture of acidified and non-acidified sites and are therefore more diverse than the bottom samples that only contain non-acidified sites. This hypothesis needs testing by repeating the analysis after a detailed inspection of the individual sites and a stratification of the data set into acidified and non-acidified sites.

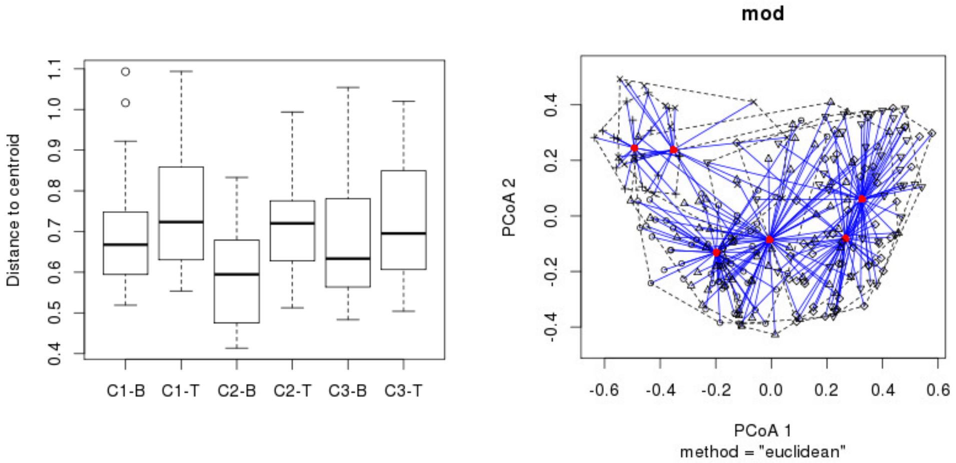

Figure 8. Diatom diversity difference between top (modern) and bottom (reference) samples in cores from a 121 UK low alkalinity lakes divided into three clusters (C1, C2 and C3).

5. Diatom diversity change in Loch of the Lowes, Scotland, as a result of eutrophication change using Rank Abundance Diagrams (RAD)

We explored the use of Rank Abundance Diagrams as a means of representing changes in diatom biodiversity in a sediment core using data from Loch of the Lowes, Scotland. In Figure 9 each panel represents the abundance of taxa in a sediment sample ranked by abundance. The diagram thereby combines both richness and evenness metrics and indicates clearly in this case study the decrease in diversity and evenness expected as a lake becomes more eutrophic and dominated by a few planktonic taxa. Different RAD models are available to describe the relationship and the ones best fitted to the individual samples are shown in the diagram.

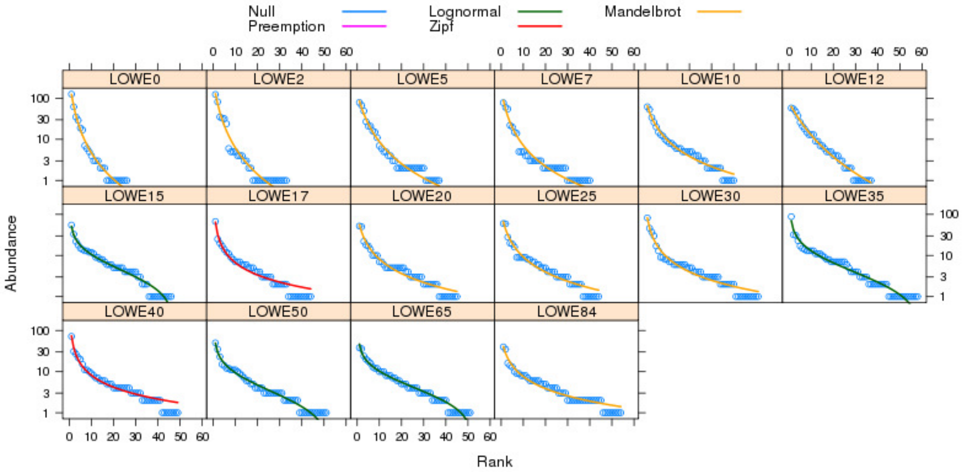

Figure 8. Rank abundance diagram for diatom assemblages from a sediment core from Loch of the Lowes, Scotland. Best fit RAD models are shown by different colours as indicated.

An alternative method of presenting rank abundance curves is to use log a log scale for abundance as described by Tokeshi (1993). In this case (Figure 9) the curves become straight lines and the steepness of the fitted regression line is a measure of community evenness. Changes that occur as a result of disturbance can be tracked by the shifts in the lines and colour coded. Here reds and greys indicate pre-disturbance periods whilst dark blues indicate communities strongly affected by eutrophication.

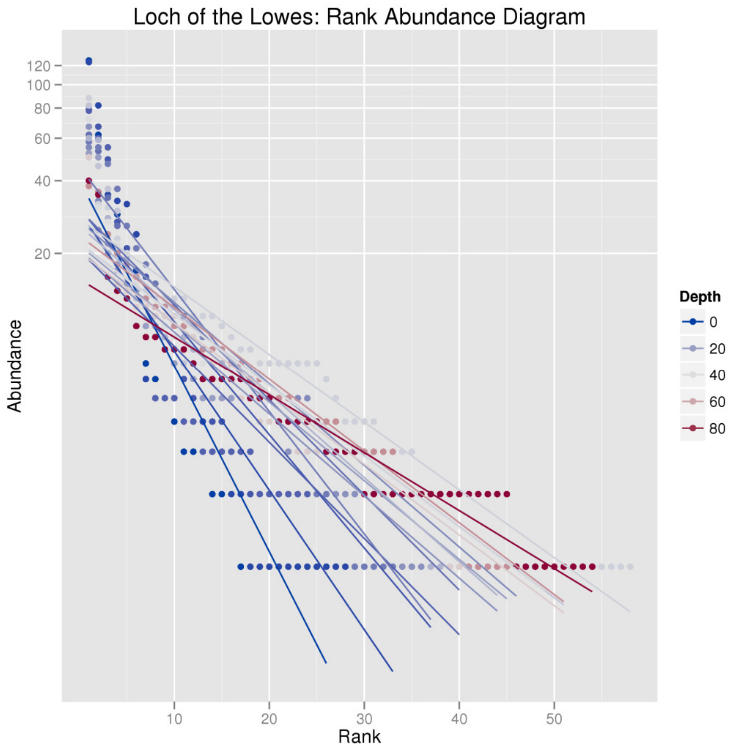

Figure 9. Diatom rank abundance diagram for Loch of the Lowes using the approach of Tokeshi (1993)

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Paper 7

Effects of disturbance on the biodiversity of shallow lakes

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Abstract

This study investigates the relative importance of eutrophication and connectivity (dispersal) in structuring macrophyte and invertebrate lake assemblages across spatial and temporal scales in the Upper Lough Erne (ULE) system, Northern Ireland.

Riverine systems and their associated flood-plains and lakes comprise dynamic diverse landscapes in which water flow plays a key role in affecting connectivity. However, as for many other freshwater systems, their ecological integrity is threatened by eutrophication and hydrological alteration. Eutrophication results in a shift from primarily benthic to primarily pelagic primary production and reductions in species diversity, while flow regulation often reduces water level fluctuation and hydrological connectivity in linked riverine systems. Low water levels promote isolation between areas and increases the importance of local driving forces (e.g. eutrophication). Conversely, enhanced water flow and flooding events promote connectivity in systems thus potentially increasing local diversity and homogenising habitats through the exchange of species. Therefore, connectivity may help to override the local effects of eutrophication.

Attempts at testing the above ideas are rare and typically involve the examination of current community patterns using space for time substitution. However, biological community responses to eutrophication and changes in hydrological connectivity may involve lags, historical contingency, and may be manifested over intergenerational timescales (10s - 100s of years), rendering modern studies less than satisfactory for building an understanding of processes that drive community structure and effect change. By combining contemporary and palaeolimnological data this study demonstrates that the ULE system is far from its pre-disturbance state as an oligotrophic-mesotrophic system. Furthermore, contemporary and palaeo-data suggest there has been a strong interaction between eutrophication and hydrological change, which influences the distributions and abundances of representative taxa in the ULE system. Thus, while eutrophication has promoted a decrease in compositional heterogeneity of organisms and has exerted a homogenising effect over time, connectivity has buffered the effects of eutrophication helping to maintain local diversity via re-introductions.

Background

The factors controlling the distribution and abundance of organisms in communities have long been of interest (see Stokstad 2009 for review) and historically these forces have been widely investigated at two levels (Pianka 1966, MacArthur and Levins 1967, MacArthur and Wilson 1967, Loreau and Mouquet 1999). First, variation in the distribution and abundance of species has been examined at a local scale, where fluctuations have been attributed to local biotic processes like competition, predation and environmental heterogeneity (MacArthur and Wilson 1967). Second, species diversities and distributions have been investigated at the regional scale by focusing on processes of emigration and immigration and population extinction (MacArthur and Wilson 1967, Hanski 1999, Hubbell 2001).

Due to the island-like nature of lakes, which are distinctly bounded habitats most studies of community structure have addressed the local within-lake scale. Particular focus has been on eutrophication, which is widely recognized as a key driver of ecological change in these ecosystems (Moss et al. 1996; Jeppesen et al. 2000). Over the last decade, however, it has been recognised that limnetic ecosystems (e.g. lake districts, riverine landscapes and wetlands consisting of many shallow lakes and ponds) can be understood using the framework of "metacommunities", in which species distributions and abundances reflect both regional processes (e.g. dispersal) and local processes (e.g. Cottenie et al. 2003; Beisner et al. 2006; Capers et al. 2010).

The term ‘metacommunity’ refers to a set of local communities that are connected by dispersal of multiple, potentially interacting species (Gilpin and Hanski 1991, Wilson 1992) (Fig. 1). Metacommunity theory constitutes a theoretical framework to explain the interdependence of local processes (e.g. between species and the environment) and regional processes (e.g. dispersal) in explaining local and regional diversity (Leibold et al 2004; Holyoak et al. 2005; Logue et al. 2011).

Figure 1. *Visual example of pond metacommunities. The metacommunities consists of multiple local communities (ponds) connected by dispersal of individuals among ponds. Aerial of tundra ponds Arctic Coast near Colville River Alaska (http://www.nationalgeographicstock.com)*

Dispersal plays a key role in influencing local communities in two ways: (1) by providing a source of colonists; and (2) by altering local population dynamics via emigration and immigration (Leibold and Nornberg 2004). Dispersal rates depend on the degree of connectedness between sites in a metacommunity and environmental heterogeneity (Leibold and Nornberg 2004). If dispersal rates are low relative to environmental change (e.g.

disturbances, altered abiotic conditions), the latter will be the main factor regulating species assembly at local sites (Kneitel et al. 2001, Leibold and Nornberg 2004, Leibold et al. 2004). Nonetheless, dispersal events will still influence the species present at local sites in a metacommunity especially after a “favourable” environmental change. In contrast, when dispersal is high, local population abundances will be affected by both the emigration and immigration of individuals from other sites via "source-sink" relations between sites (Shmida and Wilson 1996). Under these conditions, dispersal will influence community assembly by supplementing local populations that, in an unfavourable environment, will not be self-sustaining (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). As a consequence, at a regional scale, dispersal may enhance the degree to which communities respond to favourable environmental change or may override local effects of environmental change by maintaining local populations through source-sink dynamics.

Riverine systems

Riverine systems (henceforth referred to as riverscapes following Amoros and Bornette 2002) include all floodplain water bodies (side arms, backwaters, cut-off braided channels, oxbow lakes, floodplain shallow lakes, ponds and marshes) that are more or less connected through surface or subsurface waterways to a main river. They are active ecosystems characterised by variable environmental and fluvial dynamics that create complex habitats and connectivity gradients (Ward 1999). Hydrological connectivity, the transfer of water and matter between water bodies, acts as a homogenising force at the landscape level. At intermediate levels, connectivity will enhance diversity within water bodies (α-diversity) (Amoros and Bornette 2002). In contrast, environmental heterogeneity will determine local conditions and create differences in diversity (β-diversity) between habitats and water bodies. The interrelationship between connectivity and environmental heterogeneity jointly contribute to the level of biodiversity in riverscapes (Junk et al., 1989; Ward 1998).

Riverscapes may harbour high levels of biodiversity, including numerous rare and highly specialized species, and may therefore be of high conservation value. They also provide important ecological services such as flood mitigation and nutrient retention (Tockner and Standford, 2002, Van Diggelen et al., 2006, Brauman et al., 2007, Tockner et al., 2008 Klaus et al. 2011). Nevertheless, as with many other freshwater systems, the ecological integrity of European riverscapes has been heavily diminished (Paillex et al. 2009). Increasing demands for water regulation and drainage schemes, and increased nutrient-loading (eutrophication), emerge as the most pervasive causes of degradation in riverscapes (Pringle 2001, Paillex et al 2009, Klaus et al. 2011).

Eutrophication

Eutrophication stimulates primary productivity causing a shift in community assemblages from the low levels of diversity which characterise nutrient-poor habitats, to more diverse communities of submerged macrophytes and associated fauna, which characterise intermediate levels of eutrophication. This is followed by a strong reduction in diversity at high levels of eutrophication (Jeppesen et al. 2000, Sayer et al. 2010a) (Fig. 2). In addition to these direct shifts in community composition, eutrophication indirectly affects the biota by influencing other environmental processes (Donohue et al. 2009; Chase 2007). Increased levels of nutrients can reduce availability of light, oxygen and carbon dioxide, and modify habitat structure (changes in macrophyte assemblages), food webs (greater reliance on open-water planktonic productivity) and predation pressure (reduction in macrophyte cover) (e.g. Cadotte et al. 2006, Brauns et al. 2007, Declerck et al. 2007).

Hydrological alteration

Hydrological alteration can be defined as any natural or anthropogenic disruption in the magnitude or timing of natural water flows (Rosenberg et al. 1997, Pringle 2001). Impacts of hydrological alteration include habitat fragmentation and isolation (Rosenberg et al. 1997) and upstream or downstream habitat modifications, including loss of floodplains, riparian zones and adjacent wetlands, and modification and/or loss of river deltas and estuaries (Rosenberg et al. 1997). All these alterations substantially impact aquatic biodiversity by affecting the movement of organisms (Rosenberg et al. 1997, Pringle 2001, Paillex et al. 2009). Conversely, hydrological alteration in the form of flood events enhances connectivity, resulting in a homogenisation of biological communities across the habitats that comprise a riverscape (Thomaz et al. 1999).

Riverscapes and metacommunities

Currently the independent effects of eutrophication and connectivity are relatively well-known. However, due to inherent difficulties in measuring the effects of eutrophication and connectivity, the joint interaction of these two processes, and how this influences riverscape biodiversity, has rarely been addressed. Recent studies, however, have emphasised the striking metacommunity structure of limnetic systems in which species respond to both regional processes and local environmental changes (e.g. Cottenie et al. 2003; Leibold and Norberg 2004, Beisner et al. 2006). For instance, Cottenie et al. (2003) showed that zooplankton communities in a system of highly interconnected Belgium ponds were structured by both eutrophication and site connectivity and provided evidence for the importance of emigration-immigration events in maintaining zooplankton diversity. Nevertheless, this study revealed that even under high connectedness, local nutrient-enrichment was strong enough to act as the main driver structuring the zooplankton assemblages. In contrast, in a study of 18 Canadian lakes (Beisner et al. 2006), the distributions and abundances of poor-dispersing species (e.g. zooplankton and fish) were better predicted by spatial relationships (dispersal and connectivity) than by local environmental factors. Brown and Swan (2011) found macroinvertebrate communities varied according to river configuration in North America. Here the balance of both environmental variation and spatial factors changed according to location within the network and environmental components dictated community structure in headwaters, while dispersal dominated the structuring of main-stem communities.

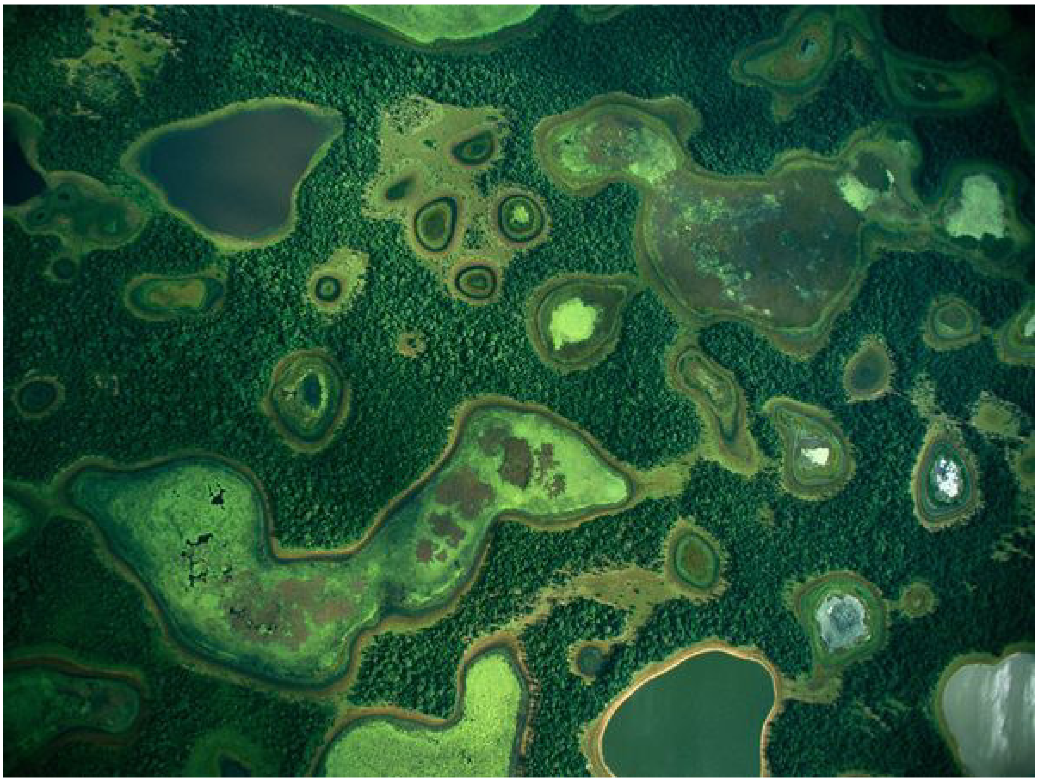

Figure 2. *Visual example of a well-connected system (metacommunity) affected by eutrophication. Pantanal*

lagoons, Brazil. **(**http://travel.nationalgeographic.com**)**

To date, inherent difficulties in measuring the combined effects of eutrophication and dispersal over time have limited studies of their influence on structuring freshwater communities to a snapshot in time (Allen et al. 2011). Consequently, a space for time assumption has been implicit in understanding metacommunity dynamics (e.g. Cottenie et al. 2003; Cottenie 2005, Brown and Swan 2011). However, riverscapes are ecosystems that change constantly over time (Amoros and Bornette 2002). Likewise, eutrophication is a gradual process that progresses over time (Schindler 1974, Davidson et al. 2005, Conley et al. 2009, Sayer et al. 2010a). Thus, to fully understand the interaction of connectivity and eutrophication, it is vital to focus research at both spatial and temporal scales, the latter ranging from decades to centuries.

Long-term records and metacommunity

A problem for many long-term metacommunity studies is the frequent lack of long-term monitoring data (Allen et al. 2011). Shallow lakes, however, offer a unique opportunity for such investigations since their sediment records allow the detection of changes in the distribution and abundance of taxa over long periods of time (Brodersen et al. 2001, Odgaard and Rasmussen, 2001, Rasmussen and Anderson, 2005, Ayres et al., 2008, Salgado et al. 2010, Allen et al. 2011). The presence of plant leaf and animal body remains and resistant stages, such as seeds, spores and eggs in lake sediments, thus provides unique insights into temporal changes in communities (Jeppesen et al. 2001, Birks 2001). Such palaeolimnological data can provide evidence of local community changes, historical dynamics of communities, population turnover via extinction and re-colonization, and biotic responses to anthropogenic impacts (Jeppesen et al. 2001, Hill et al. 2007, Birks 2001).

Aquatic plant macrofossils have long been analysed alone or together with other proxies, to reconstruct long-term changes in catchment vegetation (Birks 1973, Birks et al. 2000) and to infer water level change in lakes (Hannon and Gaillard 1997, Dieffenbacher-Krall and Halteman 2000). More recently, plant remains have been used to infer historical dynamics of submerged macrophyte communities (Rasmussen and Anderson, 2005, Davidson et al. 2005; Salgado et al. 2010), to reconstruct primary producer responses to eutrophication (Davis 1985, Sayer et al. 2010b), and to reconstruct associations between macrophyte community changes and freshwater invertebrate community structure (Davis 1985, Brodersen et al. 2001, Davidson et al. 2010, Davidson et al. 2011).

Overall aim and specific research questions

The primary aim of this project is to investigate the relative importance of eutrophication and connectivity (dispersal) in structuring freshwater communities in the Upper Lough Erne (ULE) system, a riverscape of well-connected satellite lakes in Northern Ireland, at both spatial and temporal scales. To this end, the following specific research questions are addressed:

- Do eutrophication and dispersal processes structure contemporary community assemblages? If so, does the effect of these structuring processes vary across different taxonomic groups?
- Do eutrophication and dispersal influence different aspects of species diversity (α-diversity, β-diversity and γ-diversity)? If so how are they related? Are there other attributes of the riverscape (e.g. lake size and lake maximum water depth) that contribute?
- Can palaeolimnological techniques be used to track metacommunity dynamics over time?

Study site

The Upper Lough Erne (ULE) system is situated in Co. Fermanagh, Northern Ireland (Fig. 3). It is a complex and dynamic riverscape that offers a unique opportunity to assess the effects of eutrophication and connectivity in structuring riverscape biotic assemblages. The system is formed as the channel of the River Erne splits and widens across a landscape of drumlins creating the main Upper Lough Erne (ULE), a large (34.5 km^2) mainly shallow (mean depth 2.3 m) and eutrophic (TP 70 µg/L) lake (Table 1). Associated with this large water body is a complex of interconnected smaller (range of 1-50 ha), shallow (mean depth < 2 m) satellite lakes that vary in degree of nutrient-enrichment and hydrological connectivity (mediated by rivers, streams and agricultural channels).

The shores of ULE and the associated satellite lakes are mostly thickly wooded, and the contiguous drumlins are divided by a dense patchwork of fields and hedges. Small settlements are scattered throughout the area, which is otherwise characterized by arable farmland, improved and unimproved grassland, meadows, swamps and deciduous forest. The ULE system has an extraordinary biodiversity. It is designated as a Special Area of Conservation (SAC) under the EC Habitats Directive (www.ni-environment.gov.uk) and is divided into four major Sites of Special Scientific Interest (SSSI) (Belleisle in the North, Trannish in the middle part of the ULE, and Crom and Galloon in the southern part), each supporting many plant and animal species of restricted distribution in the British Isles. These include whiskered bat (*Myotis mystacinus*), shoveler (*Anas clypeata* L.), pochard (*Aythya* spp.), brook lamprey (*Lampetra planeri*), white-clawed crayfish (*Austropotamobius pallipes*), lunar hornet moth (*Sesia apiformis*), the pondskater (*Limnoporus rufoscutellatus*) and the water beetles, *Donacia aquatica, Donacia bicolora, Gyrinus distinctus, Gyrinus natator* and *Hydroporus glabriusculus.* Uncommon or locally rare plant species include arrowhead (*Sagittaria sagittifolia),* narrow-leaved water plantain (*Alisma lanceolatum)*, needle-spike rush *(Eleocharis acicularis)* and the nationally (N. Ireland) rare frogbit (*Hydrocharis morsus-ranae)*. Populations of European otter (*Lutra lutra*) and wintering whooper swan (*Cygnus cygnus*) further enhance the conservation value of the system.

Figure 3. *Aerial photo of the Lough Erne system, County Fermanagh, Northern Ireland. (http://www.nationalgeographicstock.com)*

A history of eutrophication and connectivity

Previous research and historical records demonstrate that over the last 150 years, the ULE system has been subject to processes of hydrological change and eutrophication that may have influenced its ecology (Price 1890, Battarbee 1986, Gibson et al. 1995, Smith et al. 2005). Frequent flood events in the ULE catchment caused by high rainfall (annual average of 6.3 mm day^{-1}) (Price 1890) and an inability of the River Erne to discharge the incoming water back to the sea (Cunningham 1992) led to a major drainage scheme between 1880-1890 (Fig. 4). The main ULE and associated channels were excavated to increase water depth and, as consequence, water levels dropped from around 48 to 46 m above sea level (Price 1890). Recurrent flood events prompted a second attempt at water level regulation under the Erne Drainage and Development Act (Northern Ireland) in the early 1950s. At this time 30 km of channel were dredged between the ULE system and the Lower Lough Erne system. Since this time water levels in the ULE system have been maintained between around 43-45 m above sea level (Mathers et al. 2002, Smith et al. 2005). Despite these efforts, the ULE system is still prone to flood events (Cunningham 1992).

Diatom-based palaeolimnological studies in the main ULE indicate a gradual increase in nutrient-enrichment since the 1900s and a further acceleration of this process after 1950 (Battarbee 1986, Gibson et al. 1995, Smith et al. 2005) (Fig. 1-5). Early eutrophication probably arose from domestic effluents from storm drains that were introduced in the local towns (Battarbee 1986). The acceleration of eutrophication in the 1950s likely resulted from the interaction of various factors including post-war agricultural intensification, increased sewage and synthetic detergent inputs, development of rural septic-tank sanitation, and increased organic pollution from industry (Battarbee 1986).

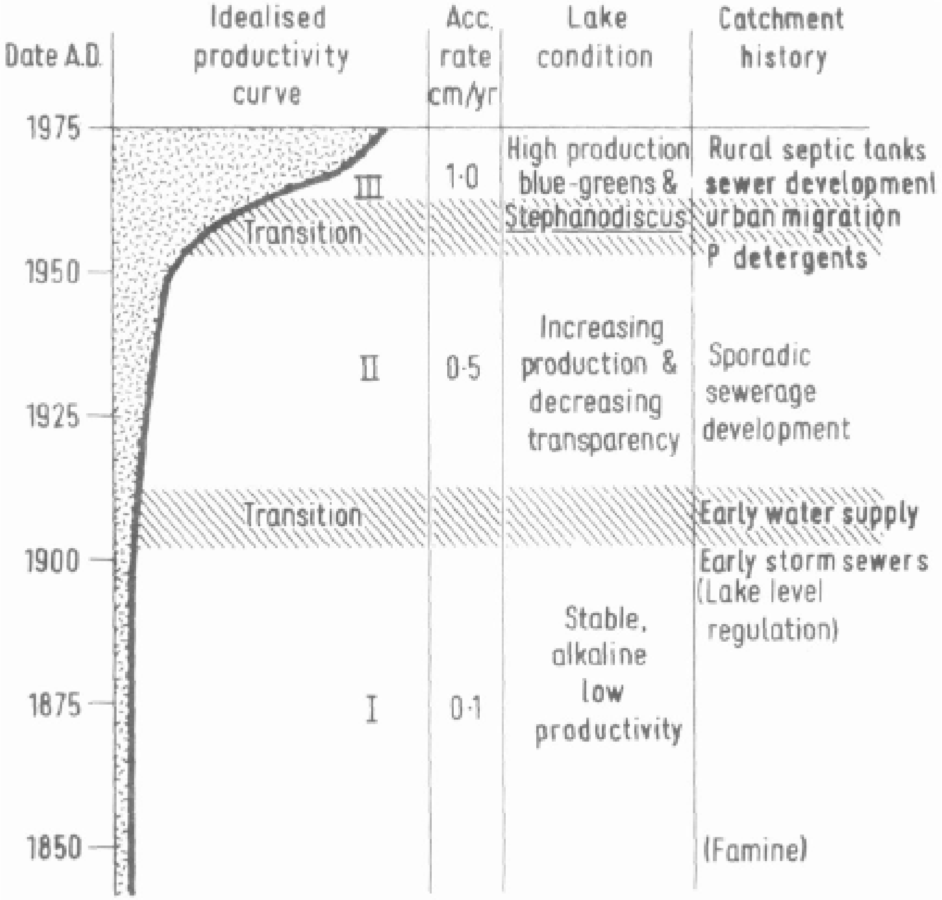

Figure 4. *Summary diagram showing a three-stage eutrophication of Lough Erne, with periods of initial change between 1900 and 1910 and rapid change between 1950 and 1960. (Figure obtained from Battarbee 1986).*

Methods

This project presents results and analyses in four sections that describe studies on both temporal and spatial dynamics in the ULE system and its associated water bodies as follows:

Spatial contemporary dynamics

Section 1 – The factors determining the composition of contemporary assemblages of overland and watercourse dispersing organisms (chironomids, macrophytes and filter-feeding invertebrates) from a set of 20 satellite shallow lakes are analysed. Multivariate Redundancy Analyses (RDA) and partial RDA are employed to identify the relative contributions of eutrophication and dispersal in structuring the species assemblages. Mantel tests are employed to examine whether community similarity is correlated with environmental and geographical gradients.

Section 2 – The effects of eutrophication and connectivity on macrophyte species diversity within and between the Upper Lough Erne (ULE) and a set of 20 well-connected shallow satellite lakes are examined. A combination of permutational analyses of multivariate dispersions and permutational multivariate analyses of variance are employed to quantify within- and between-lake compositional heterogeneity. To test predictable patterns of within- and between-lake macrophyte compositional heterogeneity along environmental and spatial gradients, least squares regression analyses between the distance to centroid for each lake and a set of different local and regional variables are conducted.

Temporal dynamics

Section 3 –The long-term effects of nutrient-enrichment on species turnover, community compositional heterogeneity and the potential mechanisms of coexistence of submerged macrophytes and invertebrates from three areas of Castle Lough are investigated. More specifically, this study tests whether nutrient-enrichment promoted local dominance by some species and reduced compositional heterogeneity between sub-localities over time. A combination of permutational analyses of multivariate dispersions, permutational multivariate analyses of variance and non-metric multivariate analyses are employed to quantify species turnover and changes in dominance over time.

Section 4 – By using a multi-proxy, multi-lake palaeoecological approach, this final chapter addresses how species turnover and compositional heterogeneity developed through time in five lakes in response to eutrophication and hydrological alterations. Non-metric multivariate analyses and principal curve analyses are used to visualise trajectories of community change and to identify major phases of compositional change. A combination of permutational analyses of multivariate dispersions and permutational multivariate analyses of variance is employed to quantify variability in compositional heterogeneity over time.

Summary of results

Spatial contemporary dynamics

The first part of this project focused on whether contemporary biological communities are influenced by both eutrophication and connectivity processes and if there are any geographically predictable patterns between community similarity and environmental or spatial gradients.

Section 1 –This study assessed the relative importance of eutrophication and connectedness (dispersal) in structuring mainly overland dispersing (chironomids) and overland and/or watercourse dispersing (macrophytes and invertebrates) organisms in a set of 20 satellite shallow lakes. Using macrophyte, and invertebrate relative abundances, lake environmental variables (water chemistry and physical parameters) and dispersal predictors (overland and watercourse distances between lakes), the study suggests that eutrophication, lake surface area and lake maximum water depth play a significant role in structuring contemporary communities and that the relative importance of spatial predictors (overland and watercourse distances) varied according to dispersal mode of the organism. Submerged macrophyte distributions were explained by both overland and watercourse distances, while watercourse distances best predicted invertebrate distributions and overland distances best predicted chironomid distributions. There was no spatial autocorrelation between community similarity and environmental or spatial gradients, implying that the main Upper Lough Erne mediates extensive dispersal.

Section 2 – This study further explored the effects of eutrophication and connectivity in structuring contemporary macrophyte species diversity and compositional heterogeneity within and between the Upper Lough Erne (ULE) and a set of 20 well-connected shallow satellite lakes. The results indicated that despite high nutrient levels most study sites are characterized by high macrophyte α-diversity, a trend attributed to the hydrological connectedness of the system. Local (within-lake) variation in macrophyte assemblages was reflected by differences in relative abundances and composition. Total nitrogen, total phosphorous, chlorophyll-a, surface area and water depth emerged as the most significant variables explaining within-lake macrophyte compositional heterogeneity at the regional scale. Within-lake heterogeneity was related inversely to nutrient enrichment (as indicated by measurements of total phosphorus, total nitrogen and chlorophyll-a). Nutrient-rich lakes had more homogenous macrophyte assemblages than lakes with lower nutrient levels. Larger lakes were characterized by more heterogeneous and diverse macrophyte assemblages. Homogenous lakes were mostly associated with higher levels of chlorophyll-a, low α-diversity and were relatively small and shallow. Low chlorophyll-a, high α-diversity, large surface area and deeper waters generally characterized highly heterogeneous lakes.

Temporal dynamics

The second part of this study was to understand how patterns of species turnover, diversity and compositional heterogeneity developed within and between lakes over time.

Section 3 – This study focused on the long-term effects of nutrient enrichment on species turnover and community compositional heterogeneity, and the potential mechanisms allowing coexistence of submerged macrophytes, invertebrates and chironomids from three areas of Castle Lough. Temporal assembly dynamics showed that communities in each lake area changed from c. pre-1900 being heterogeneous to being more homogenous (dominated by a few species) in the present day (Fig. 5). This change was accompanied by an increase in temporal β-diversity and little extinction over time. These trends are consistent with transitions that would be expected as a result of dispersal and advancing eutrophication. Spatial assembly dynamics revealed that c. pre- 1900 differences between areas (spatial β-diversity) were low and increased over time being highest from c. 1950 to present. Changes in dominance occurred more rapidly than changes in species richness and evidence suggest that within-lake source-sink dynamics may have allowed persistence of species that are poorly adapted to enrichment.

Section 4 – By using a multi-proxy, multi-lake palaeoecological approach, this final study addressed how species turnover and compositional heterogeneity developed through time between five lakes in response to advancing eutrophication and hydrological change. This study demonstrated that the Upper Lough Erne system is now far from its preindustrial oligotrophic-mesotrophic ecological condition (Fig. 6) Three relatively distinct phases that corresponded to c. pre-1900 (oligo-mesotrophic assemblages), to c. 1950-1900 (meso-eutrophic assemblages) and to c. present-day-1950 (eutrophic assemblages) were inferred from the long-term dynamics of passively (macrophytes and invertebrates) and actively (chironomids**)** dispersing organisms in the cores. These phases reflected a progressive increase in eutrophication since the early 1900s and to two hydrological dredging schemes that occurred at the end of the 1800s and 1950s. The data also revealed that within-lake compositional heterogeneity declined with eutrophication, while regional β-diversity attributable to within-lake variation in the identity of species increased. These findings accord well with previous studies that have found a decrease in the compositional variability of organisms within and between eutrophic lakes and bring new evidence of the homogenising effects of eutrophication at the local and regional scale. By incorporating metacommunity theory, this study also provides evidence that hydrological connectedness has buffered the effects of eutrophication and maintained local diversity over time via species re-introductions.

Conclusions

By undertaking comparative analyses over spatial and temporal scales for three groups of organisms, which differ in their dispersal modes from a set of shallow lakes in the ULE system, this work demonstrates that eutrophication and connectivity play fundamental and complex roles in determining community structure. The incorporation of a metacommunity theory perspective has been particularly effective in identifying key drivers of the changing ecology of the ULE system. Thus, despite eutrophication, the high connectedness of the system is helping to maintain surprisingly high levels of local diversity. Although, dispersal rates were not quantified per se, the co-occurrence of species less tolerant to high nutrient conditions at most sites and the relatively greater representation of actively dispersing organisms agree with previous theoretical and experimental work that demonstrates the importance of intermediate dispersal rates on species richness and abundance patterns. In addition, variability in compositional heterogeneity of contemporary macrophyte assemblages revealed a significant negative association with nutrient concentrations. This trend was supported by the sedimentary data from multiple lakes, which collectively revealed a homogenisation of within-lake aquatic assemblages as eutrophication advanced through time. Closely associated therewith was an increase in the within-lake variability of species composition between lakes (β-diversity) as eutrophication progressed. Furthermore, the study gained evidence that lake surface area and water depth were positively associated with macrophyte species diversity and assemblage variability. This finding suggests that the main ULE plays a vital role in maintaining species diversity of all groups by acting as both a refuge and source of colonists within the system.

There are two main caveats for using the palaeoecological records to infer changes in species composition in this study. First, some macrophyte species like *U. vulgaris, S. sagittifolia* and *E. canadensis* are poorly preserved in the fossil record. The second is the lack of radiometric dating for the main ULE and Lough Head. Fortunately, the sedimentary records contained many of the modern predominant taxa that are required to quantify major transitions in community structure through time (Heino et al 2010; Allen et al 2011). Furthermore, trends of community change observed in the sedimentary data were consistent among the three biological groups, the five lakes for which palaeo-records were examined and the 20 study lakes for which contemporary assemblages were studied. These features indicate that the conclusions of the study appear to be robust and demonstrate that palaeoecological studies can provide a unique opportunity to track the development and responses of communities over multiple decades. This time frame is commonly neglected in metacommunity studies but can be essential to improve understanding the mechanisms that drive community assembly.

Management implications

As a result of an increase in nutrient loading over the last century there has been a dramatic decline in the ecological integrity of most temperate shallow lakes (Roelofs 2002). As this process continues, plantless lakes or lakes with mono-specific macrophyte stands are becoming more and more common and macrophyte-diverse lakes are a rare exception. This study illustrates that the ULE system is one of those rare remaining hydrological systems with wonderfully diverse macrophyte assemblages in most of its associated lakes.

Nonetheless, reductions in the number of species, the homogenisation of communities through time, the variability in the identities of species between lakes and the significant negative trend observed between within-lake compositional heterogeneity and nutrient concentration all provide evidence that the system may be on the verge of major change. This is strongly supported by the palaeolimnological data, which revealed that in spite of being characterised by currently diverse communities, the ULE system is long way from its earlier pre-industrial ecological condition.

It is common practice to focus management actions on the effects of environmental change (e.g. eutrophication) and loss or gain of species richness (Hillebrand et al. 2008). However, concentrating exclusively on species richness and the effects of eutrophication may limit a full understanding of the structure and function of well-connected freshwater landscapes. Evidence from this study stressed the need to integrate other aspects such as connectivity, surface area and other attributes of diversity like species evenness. Hydrological connectedness is a key geomorphological feature in the ULE system. Despite nutrient-enrichment connectedness has helped to maintain high levels of diversity in most lakes as a result of dispersal. In addition, sedimentary data have demonstrated that changes in species evenness or dominance are likely to occur more rapidly than changes in species richness. Consequently, is imperative for the conservation and management of the system to acknowledge that species richness and evenness can respond in different ways to human impacts. The results also indicate that the main ULE maintains diversity by acting as a species refuge and source of colonists within the system. Hence, management and restoration strategies must pay special attention on the main ULE.

Future directions

Using contemporary and palaeolimnological techniques to characterise the abundances of different biological groups represents a novel way to understand the mechanisms of community assembly in well-connected systems (metacommunities) at both the spatial and temporal scales. In particular, the inclusion of a temporal scale (decadal to centennial) provides better inferences than the great majority of metacommunity studies that incorporate only a spatial perspective. Temporal studies also reveal how the relative importance of regional and historical processes can change substantially over time. Below I elaborate on future directions for research that would further improve understanding of the dynamics of the ULE system and how it is assembled.

Although a substantial number of lakes were sampled by both contemporary surveys and palaeolimnological analyses, a larger data set that incorporates a greater gradient in connectivity and environmental heterogeneity would be of great interest with regard to firmly substantiating the inferences I have made on the basis of the studies conducted so far. The current study was supported by a large data set of macrophyte surveys and environmental variables obtained from ENSIS ltda., and Goldsmith et al. (2008). A subset of lakes from these databases was incorporated in order to gain representation of enrichment gradient and different levels of connectivity. However, both datasets set (ENSIS and Goldsmith et al. 2008) comprised eutrophic to hypertrophic lakes and all lakes had some degree of connectivity to the main ULE. Incorporating a set of lakes that are not affected (or are less affected) by eutrophication or completely isolated is desirable to fully contrast the effects of eutrophication and connectivity in the system.

Closely associated with the above would be an expansion of contemporary surveys into new sites along with further palaeolimnological analyses in order to better characterise rates in homogenisation effects of biological assemblages due to eutrophication. This poorly studied area for shallow lakes and riverine systems requires much further attention. Surveying a larger set of lakes would be time-consuming and expensive but a potentially cheaper and quicker approach that emerged from this study would be to focus on samples from the surface and bottom of cores to establish long-term changes from a larger set of lakes (Smol 2000). Given the fact that the sedimentary data revealed that overall, the largest differences in compositional heterogeneity, were observed between pre-1900 and present day (Chapters 4 and 5), using such a top-bottom approach might be a reliable method to establish homogenisation effects and rates.

Finally, it would be highly relevant to characterise actual dispersal rates. In this study, dispersal rate was inferred indirectly by degree of connectivity (using spatial and watercourse distances), spatial variability in species abundance and composition and assignment of taxa to modes of dispersal. Although watercourse distance was used in this study to infer dispersal rates, direction of water flow was not. This key aspect could be incorporated in future to obtain a more accurate picture of dispersal routes. Dispersal rates and directions are inherently difficult to measure in practice but mesocosms experiments between lakes that are directly connected can provide a direct approximation for some taxa (e.g. Cottenie and De Meestre 2004). Other approaches include measures of gene flow and mark-recapture experiments. No single approach is likely to be applicable to all taxa of interest and it would be necessary to identify focal taxa for such investigation since studying everything would be unrealistic. Such key taxa might include the bryozoan *Cristatella mucedo* and cladoceran species within the genus *Daphnia*. These two groups are relatively easy to sample and have been previously analysed for gene flow and mark-recapture experiments for other temperate lake systems (De meester 1996, Freeland et al. 2001, Charalambidou et al. 2003, Cottenie and De Meestre 2004).

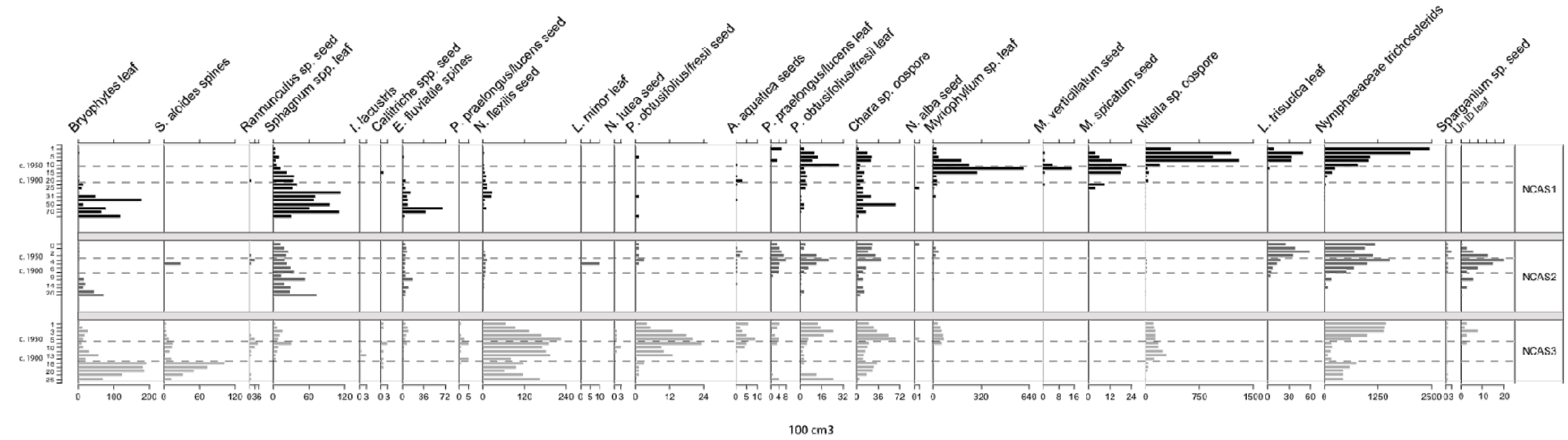

Figure 5. *Plant-macrofossil stratigraphies for cores NCAS1, NCAS2 and NCAS3. Zones correspond to c. present-1950, c. 1950-1900 and c. pre-1900.*

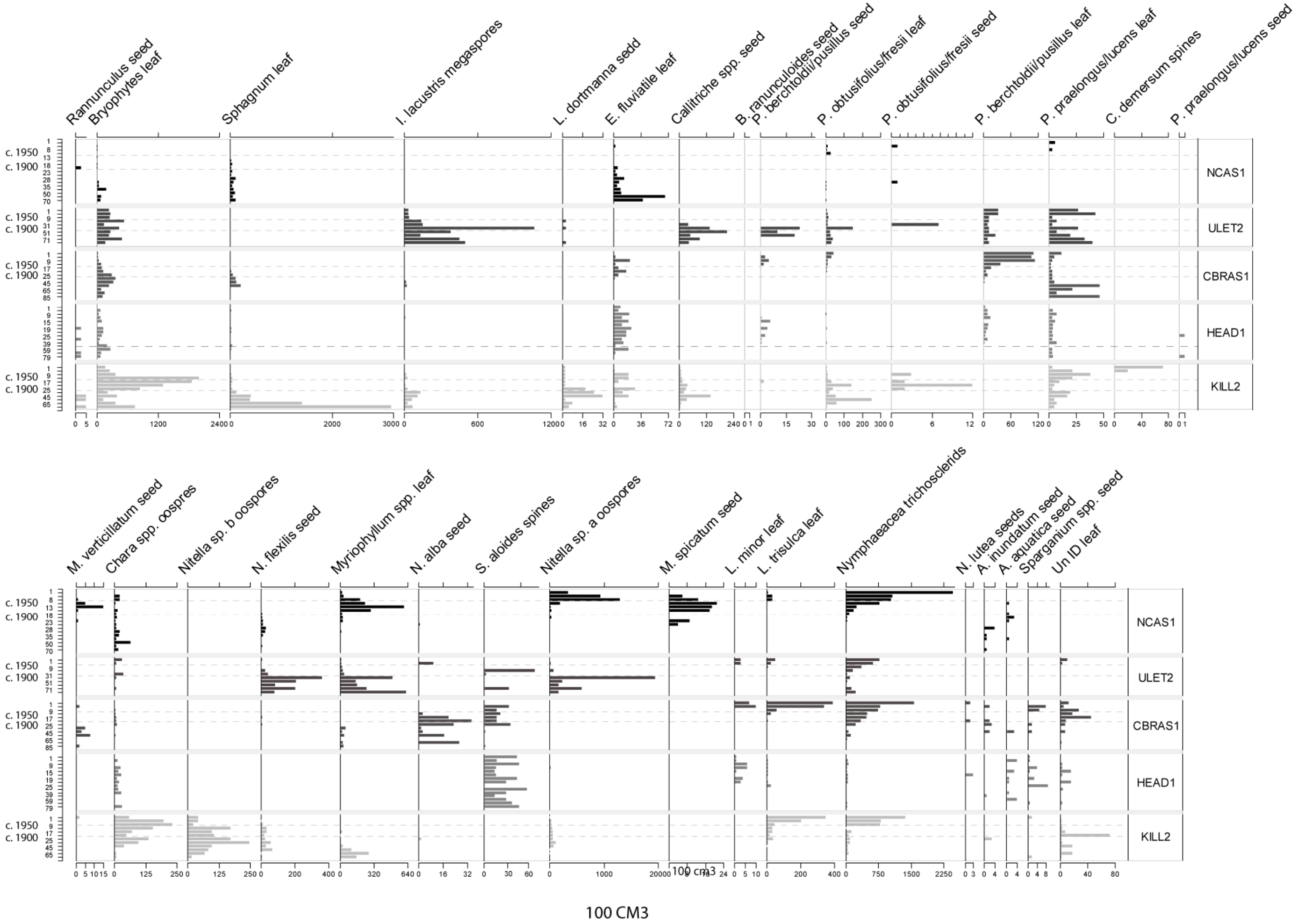

Figure 0-1. Stratigraphic summary of plant-macrofossils of NCAS1, ULET2, CBRAS1, KILL2 and HEAD1 cores. Sediment samples were amalgamated over three periods of approximately 50 years.

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Paper 8

Palaeoecological evidence for biodiversity change as a result of acidification: a case study of the Round Loch of Glenhead, Scotland.

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Introduction

As acidified lakes and streams in Europe begin to recover from the impact of acid deposition there is an increasing interest in the extent and direction of the recovery and whether climate change and other pressures will prevent a full recovery from taking place. Addressing these issues requires a knowledge of the chemical and biological characteristics of acidified surface waters in the absence of acid deposition that can be used both to establish a reference status and, potentially, a target status for restoration. Unfortunately monitoring of acidified waters began only after acidification has been recognised as a water quality and biodiversity problem. Consequently we have no direct observations of the status of acidified waters prior to acidification. To address the question it is therefore necessary to use a combination of approaches, using observational data from non-acidified analogue sites and using palaeoecological data from lake sediment records. Here we assess the value of the palaeoecological approach for a case study site, the Round Loch of Glenhead (RLGH), to address the questions: (i) what evidence does the sediment record contain of the pre-acidification flora and fauna of the lake; and (ii) what have been the changes in biodiversity in the lake as a result of acidification according to the palaeoecological evidence.

The first question is concerned with an examination of the pre-acidification sediments for all types of fossil material but principally for those biological groups that are known to leave a fossil record, diatoms, aquatic plants, Cladocera and chironomids. Presence of any particular taxon in the record is not only related to preservation but also to the size of the sediment sample needed to detect low abundance occurrence and the location of the sediment cores in relation to their proximity to the location of source material. Consequently we used wide diameter corers, combined samples where necessary to increase sediment volume, and cores not only from deep water but also in the margins of the lake, within the littoral habitat.

The second question requires a comparison between the pre-acidification fossil assemblages and the post acidification assemblages of the respective cores. The pre-acidification assemblage can be defined as that immediately before the first evidence for acid deposition. In this case we have used the increase in the stable Pb concentration recorded in the cores that typically occurs in the early 19th century in UK sites reflecting the receipt of the lake basin by air pollution from the combustion of coal at the beginning of the Industrial Revolution. The post-acidification assemblage has been defined here, at least in principle, as that occurring close to the top of the sediment cores when acidification was at its peak (pH at its lowest) dating to the 1980s and identified in sediment cores by a maximum in the abundance of acid-tolerant diatoms. In practice it can be difficult to isolate the assemblage that corresponds to this decade in the sediment where sediment accumulation rate is low and bioturbation can mix material up and down the profile. Comparing the pre- and post acidification assemblage from a biodiversity perspective then requires the assumption that there has been no changes in the quality of preservation between the two time periods. In the case of the biological groups considered here and the specific case of the Round Loch of Glenhead, this seems to be a reasonable assumption as diatoms, aquatic plant macrofossils, chydorid Cladocera and chironomid head capsules are excellently preserved at this site.

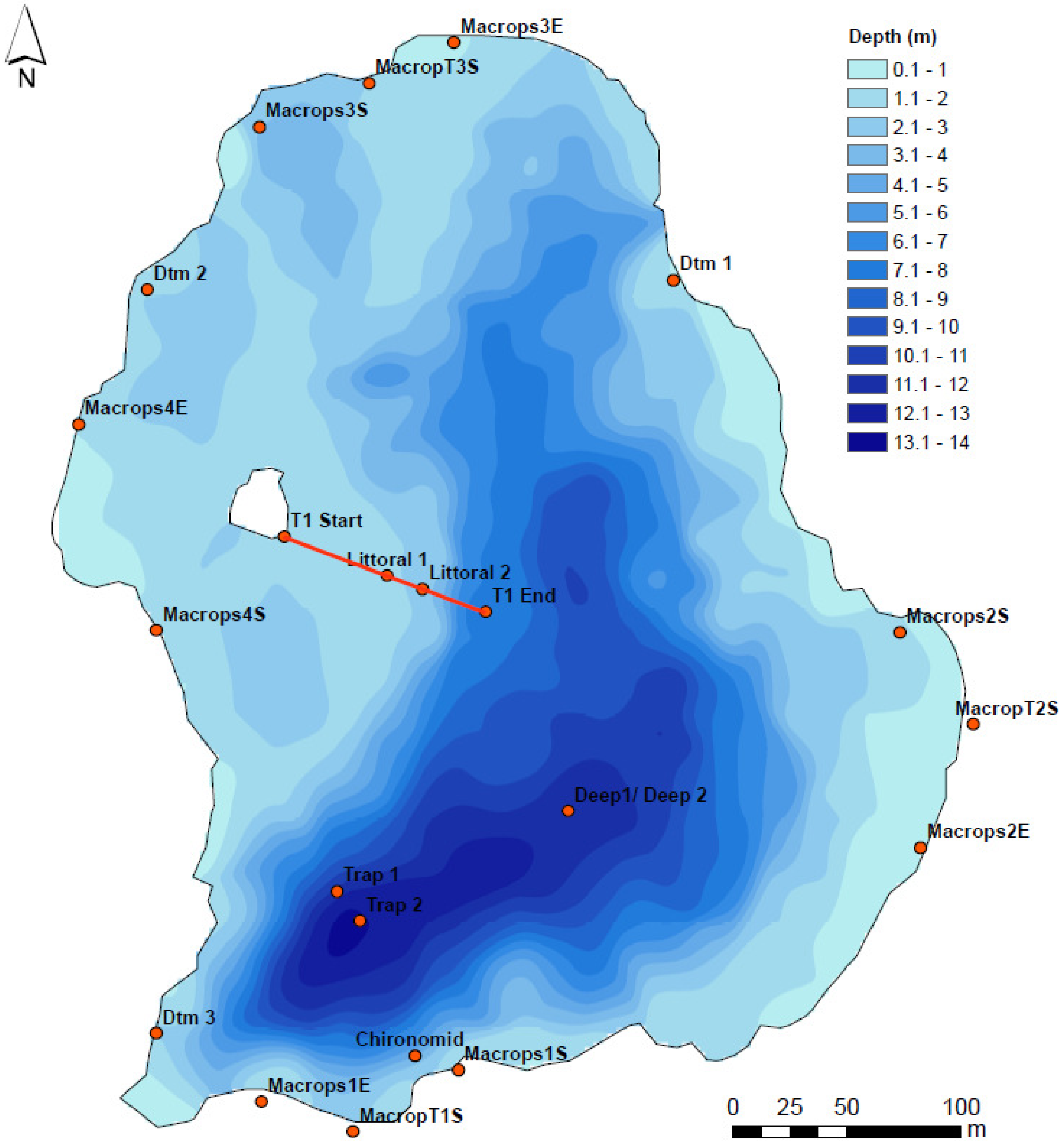

Figure 1. Map of Round Loch of Glenhead showing sample and core locations (courtesy of Simon Turner).

The RLGH (Figure 1) is a small acidified loch in the Galloway district of South-west Scotland. Palaeolimnological studies showed that the loch started to become more acidic in the mid-19th century (Flower & Battarbee 1983) and contemporary monitoring has shown that the site is now beginning to recover. The recovery is best shown by changes in epilithic diatom populations and in diatom assemblages collected in annually exposed sediment traps. Monitoring of the site over the last 24 years has also shown the appearance of aquatic plant and invertebrate species not previously recorded from the site. These include the plant *Myriophyllum alterniflorum*, and the molluscs *Radix baltica* and *Pisidium* spp. However, it is not clear whether these taxa occurred in the loch before it became acidified (and are therefore re-appearing) or whether they are entirely new occurrences. Equally, with the exception of diatoms, we have no direct evidence of which taxa have been lost or become less (or more) abundant as a result of acidification. Judgements of biodiversity change at this and similar sites are based on the probability of occurrence from contemporary species distribution data across a gradient of acidity.

Methods

The diatom data presented here are taken from a core collected in 1989 and from sediment trap data collected annually between 1991 and 2008 (Shilland et al. 2012). All other data are based on four cores collected in July 27th 2010 from deep (Deep1, Deep2, Figure 1) and shallow (Litt1, Litt2, Figure 1) water. Most analyses presented are from the Deep1 core. This core was taken with a Glew corer and was 30 cm long. Deep2 was taken with a tapper corer to obtain a longer core than Deep1 provided by the Glew corer and was 60 cm long. Both these deep water cores were sub-sampled at contiguous 1 cm (10 – 30 cm), 0.5 cm (4-10 cm) and 0.25 cm (0- 4 cm) intervals in the field. Both littoral cores were 60 cm long and were sub-sampled in the field at contiguous 2 cm (20-60 cm) and 1 cm (0-20 cm) intervals. Sub-samples were refrigerated in the laboratory until needed for analysis.

Routine measurements for sediment dry weight and loss on ignition (at 550° C) were made on all cores and XRF analyses were carried out on Deep1 and Litt2 to identify the depth in the sediment immediately prior to the first evidence of contamination of the lake by acid deposition, using Pb as a proxy. Only LOI data for Deep1 and Deep 2 and XRF data for Deep1 are presented here.

The Deep1 core was dated by gamma spectroscopy. Dried sediment samples were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am in the Environmental Radiometric Facility at University College London, using ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. Lead-210 was determined via its gamma emissions at 46.5keV, and ^{226}Ra by the 295keV and 352keV gamma rays emitted by its daughter isotope ^{214}Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. Cesium-137 and ^{241}Am were measured by their emissions at 662kev and 59.5kev (Appleby et al, 1986). The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self absorption of low energy gamma rays within the sample (Appleby et al, 1992).

Diatom analyses followed standard protocols (Battarbee et al. 2001). Microscope slides were prepared using Naphrax as a mounting medium and counts of approximately 300 valves per sample were made using light microscopy at x 1000 magnification. Taxonomy is based on SWAP guidelines and associated AWMN conventions.

Seven sediment samples from the RLGH were subjected to macrofossil analysis. Between 30 and 50cm^3 of fresh sediment was used with the exact volume being determined by water displacement. The samples were gently washed through meshes of 355 and 125 µm. The 355 - µm sample was examined in its entirety using a binocular dissecting microscope at 10-20x magnification and identifiable plant remains were enumerated. A sub sample, approximately a quarter of the total sample, was analysed for the 125- µm sample at a higher magnification of 20-40x. Identifications were made using a reference collection of plant parts held at University College London, as well as seed atlases (Berggren 1964, 1981; Beijerinck 1976). All fossils are presented as number per 100cm^3 of fresh sediment. Although macro- remains in surface sediments are not strictly macrofossils they are referred to as such here to simplify terminology.

Cladocera remains were analysed using an adaptation (Davidson et al. 2007) of standard techniques (Frey 1986; Korhola & Rautio 2000). Approximately 2cc of sediment was washed through a 50 µm sieve and the residue retained on the screen was transferred to a vial and the volume recorded. The remains in each vial were stained with a few drops of safranin solution. Chitinous remains: head shields; carapaces and post abdomens, were enumerated using a Sedgewick-Rafter counting cell on a compound microscope at 40–100 x· magnification. A minimum of 100 of the dominant species were counted from a sub-sample of known volume. Cladocera were identified with reference to Frey (1958; 1959; 1964) Flössner (1972) and Alonso (1996). All individuals were identified to species level where possible. Species-level identification proved difficult for some of the daphnids and the guild of *Daphnia hyalina* agg. was used for species in this group. Counting of individuals followed the minimum number method; where head shields, carapaces and post abdominal claws were tabulated separately and the count for each species was the number of the most numerous remain. The occurrences of the various taxa represented by chitinous remains are expressed as % relative abundances.

Chironomid samples were collected every 0.5 cm from 5-10 cm (10 samples), and in 1 cm slices from 10-31 cm downcore, these last ones analysed each 2cm. The samples were processed following the standard procedure (Hofmann, 1986): 10% KOH digestion at 70º and 300 rpm during 20 minutes followed by sediment sieving (90 µm). *Chironomidae* larvae head capsules were examined under stereo microscope using a Bolgorov tray, picked out manually and dehydrated in 96% ethanol, and finally mounted ventral side upwards in Euparal® as mounting media in permanent slides. Taxonomic identification was carried out using an optical microscope (Olympus CX41) at 40x magnification. The larval head capsules were identified to the lowest taxonomic level as possible using several specialized guides (Brooks et al. 2007; Rieradevall & Brooks 2001; Wiederholm 1983).

Results

Loss on ignition

The loss on ignition data for cores Deep1 and Deep 2 are shown in Figure 2. The data closely match LOI data from previous cores taken from the deep water zone of the lake showing that the upper sediment is very organic with values greater than 40% dry weight. The two cores have similar overall accumulation rates with the increase in organic content occurring at approximately 30 cm in Deep2 matching a level somewhat deeper than 30 cm in Deep 1, below the base of the core. The cause of this increase is uncertain but has been associated with an increase in catchment peat erosion. Deep2 is a longer core, extending down to 60 cm and shows relatively stable LOI values of around 20% below 30 cm. Although Deep2 contains more sediment representing the pre-acidification period in the loch, Deep1 was chosen for initial analysis as the surface sediment was thought to be least disturbed by coring. Future work will include analyses of the Deep2 core.

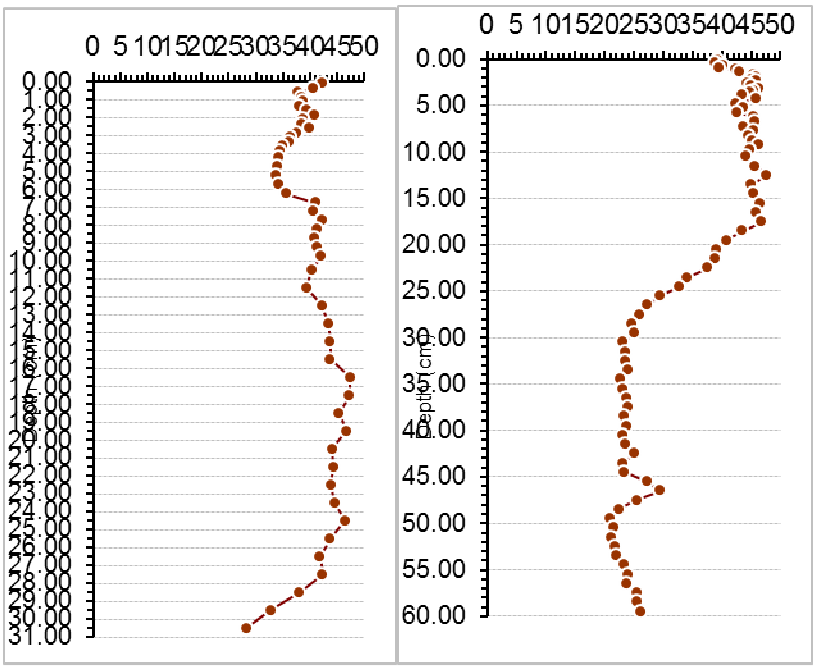

Figure 2. Loss on ignition for Deep1 (left) and Deep2 (cores)

Dating of core Deep1

Lead-210 Activity

Total ^{210}Pb activity reaches equilibrium depth with the supported ^{210}Pb at around 20 cm of the core. Unsupported ^{210}Pb activities, calculated by subtracting supported ^{210}Pb activity from total ^{210}Pb activity, decline irregularly with depth (Figure 3b). The ^{210}Pb profile consists of two sections: there is little net decline in ^{210}Pb activities in top 3 cm, implying a gradual increase in sediment accumulation; ^{210}Pb activities decline more or less exponentially with depth from 3 to 21 cm with some irregular features, suggesting that there are episodic departures from the process of uniform sediment accumulation.

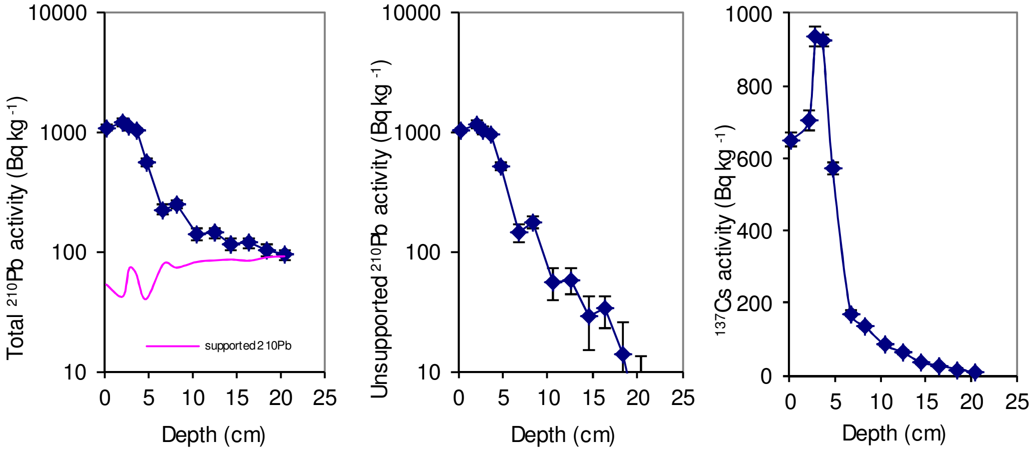

Figure 3. Fallout radionuclide concentrations in core RLGH-D taken from Round Loch of Glenhead in Scotland, showing (a) total ^{210}Pb, (b) unsupported ^{210}Pb, and (c) ^{137}Cs concentrations versus depth.

Artificial Fallout Radionuclides

The ^{137}Cs activity versus depth profile (Figure 3c) has a poorly defined peak between 2.75 and 3.75 cm. Previously dated cores taken from this site show strong diffusion of ^{137}Cs in the sediments, resulting in broad 1986 ^{137}Cs peak with relatively high activities, and indistinct 1963 peak in related ^{137}Cs profiles. It is almost certain that the ^{137}Cs peak between 2.75 and 3.75 cm in this core was derived from the fallout of the 1986 Chernobyl accident.

Core Chronology

^{210}Pb dates were calculated using the CRS model as use of the CIC model was precluded by the non-monotonic features in the unsupported ^{210}Pb profile (Appleby, 2001). The CRS dating model dated 1986 at 3.63 cm, which is in agreement with the ^{137}Cs record. There are some small changes in sediment accumulation rates over the last 140 years or so, with a mean at 0.011 g cm^{-2} yr^{-1} (Table 1).

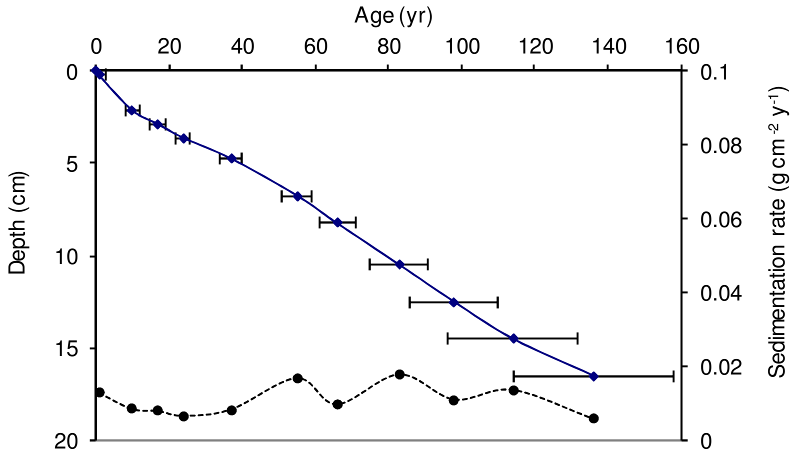

Figure 4. Radiometric chronology of core RLGH-D taken from Round Loch of Glenhead, showing the CRS model ^{210}Pb dates and sedimentation rates. The solid line shows age while the dashed line indicates sediment accumulation rate

Table 1. ^{210}Pb chronology of core RLGH-D taken from the Round Loch of Glenhead, Scotland.

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Depth	Drymass	Chronology			Sediment Accumulation Rate		
		Date	Age				
cm	g cm^{-2}	AD	yr	±	g cm^{-2} yr^{-1}	cm yr^{-1}	± %
0	0	2010	0				
0.25	0.0068	2009	1	2	0.0128	0.25	6.3
2.13	0.1091	2000	10	2	0.0084	0.145	8.1
2.88	0.1596	1993	17	2	0.0079	0.112	8.9
3.63	0.2146	1986	24	2	0.0066	0.084	7.1
4.75	0.3075	1973	37	3	0.0083	0.088	10.9
6.75	0.5083	1955	55	4	0.0168	0.168	19.9
8.25	0.6573	1944	66	5	0.0097	0.1	19.6
10.5	0.8705	1927	83	8	0.0178	0.183	38.3
12.5	1.0703	1912	98	12	0.011	0.111	42.2
14.5	1.2688	1896	114	18	0.0136	0.136	72.3
16.5	1.472	1874	136	22	0.0058	0.056	88.4

Pb concentration of core Deep1

Samples from two cores, Deep1 and Litt2 have been analysed for elemental chemistry using XRF. Figure 5 shows the Pb concentration data for Deep1. It shows a clear increase in concentration from background levels of approximately 50 µg/g dw at ca. 25 cm rising to a maximum of 700 µg/g at a depth of ca. 6 cm and a decline to the surface with a concentration of ca. 200 µg/g. On the basis of this evidence the basal 5 cm of the core represents the time period immediately preceding the onset of acid deposition, dated by extrapolation of the ^{210}Pb data to about 1800 AD. By further extrapolation the basal 5 cm then accumulated between about 1750 and 1800 AD.

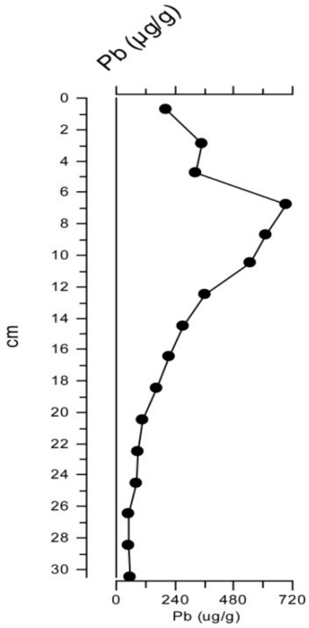

Figure 5. Pb concentration for core Deep1.

Diatoms

The core diatom data presented here (Figure 6) are not taken from Core Deep1 but from a core taken some years previously. The sediment trap diatom data are from the Acid Waters Monitoring Network (http://awmn.defra.gov.uk/).

The core (Figure 6) extends back to the 18th century and thereby includes pre-acidification conditions, as well as subsequent changes as the loch became acidified. In the pre-acidification period the dominant taxa were *Brachysira vitrea*, a very common diatom found in non-acidified low alkalinity lakes, and *Achnanthes minutissima,* a species found in more circumneutral to alkaline water and very sensitive to the effects of acidification. Their decline in the mid-nineteenth century together with the increase in the relative abundance of *Eunotia incisa* provides the first evidence of decreasing pH in the loch. The later expansion of *Tabellaria quadriseptata* and decrease in *Peronia fibula* and *Tabellaria flocculosa* indicates continuing acidification during the 20th century reaching the most acidic state by the 1970s, the time at which the first direct measurements of lake water pH were taken.

The sediment trap data (Figure 6) show little change for the first few years of monitoring (beginning in 1991) but after 1995 there is a gradual reduction in the relative abundance of the acid tolerant taxon *Tabellaria quadriseptata* and an increase in *Navicula leptostriata* reflecting the increase in pH and the slight recovery from acidification that has taken place at this site over the last 15 years. Overall there has been little change in diatom biodiversity, as the acid sensitive taxa dominant in the pre-acidification period have been replaced by acid tolerant taxa with similar habitat preferences. However, so far there is little evidence of the re-appearance of the acid sensitive taxa that would be indicative of a more rapid recovery.

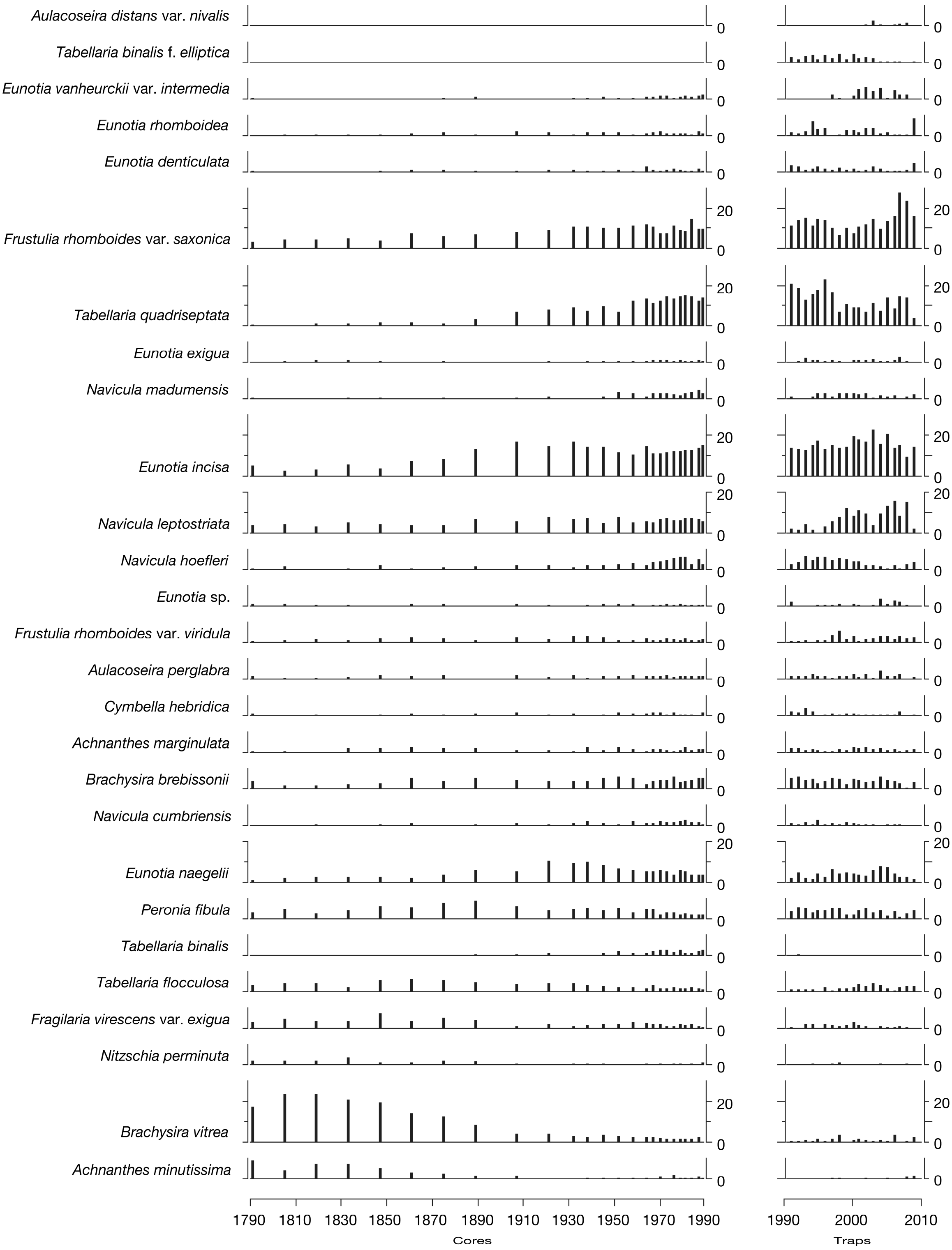

Figure 6. Sediment core and sediment trap diatom record for the Round Loch of Glenhead (courtesy of Roger Flower, Gina Clarke and Hong Yang).

Macrofossil remains

To assess changes in the aquatic plant flora of the lake as a result of acidification the plant macrofossil composition of the basal sample (29 cm) of the Deep1 core was analysed and compared to similar analyses of the surface sample of the core and to the surface sediment samples of cores from the littoral zone (Figure 7). Animal macrofossils were also recovered and compared from these samples (Figure 7).

In figure 7 the bottom and top samples for Deep1 are shaded. *Isoetes lacustris* megaspores and *Lobelia* seeds occur in similar numbers in both samples. In the bottom sample, *Typha latifolia* seeds and *Nymphaea alba* seed fragments were found which are absent from the surface sample. Both represent species that are also absent from the lake today (cf. Battarbee et al. this report). Pollen of *Typha* and *Nymphaea* have been previously found in peat cores from the catchment dating back to the early Holocene (Jones & Stevenson 1993) thereby supporting the probability of their occurrence during the pre-acidification period in the lake. Pollen analysis of the basal sediments from Deep1 could corroborate these findings.

This combined evidence suggests there have been significant changes in the macrophyte flora of the lake as a result of acidification. Evidence for recovery in the aquatic plant community is inconclusive as remains of *Myriophyllum alterniflorum*, a species that appeared in 2003 and is now quite abundant in the lake, have not so far been found in the pre-acidification sediments. As this species is very common in non-acidified low alkalinity lakes it is probable that its appearance is indeed a result of improving water quality. Its absence in the material examined may be due to absence from the lake, poor preservation, patchy distribution within the lake or to below detection limit abundance of remains in the samples

Further paleolimnological work is necessary to evaluate these alternative explanations. In particular examination of the pre-acidification sediments of a littoral core close to the current *Myriophyllum* stands is needed.

Animal macrofossil remains found in the basal sediment but less abundant in the surface sediments include fragments of the stony cases of caddis flies and ephippia of *Daphnia pulex.*

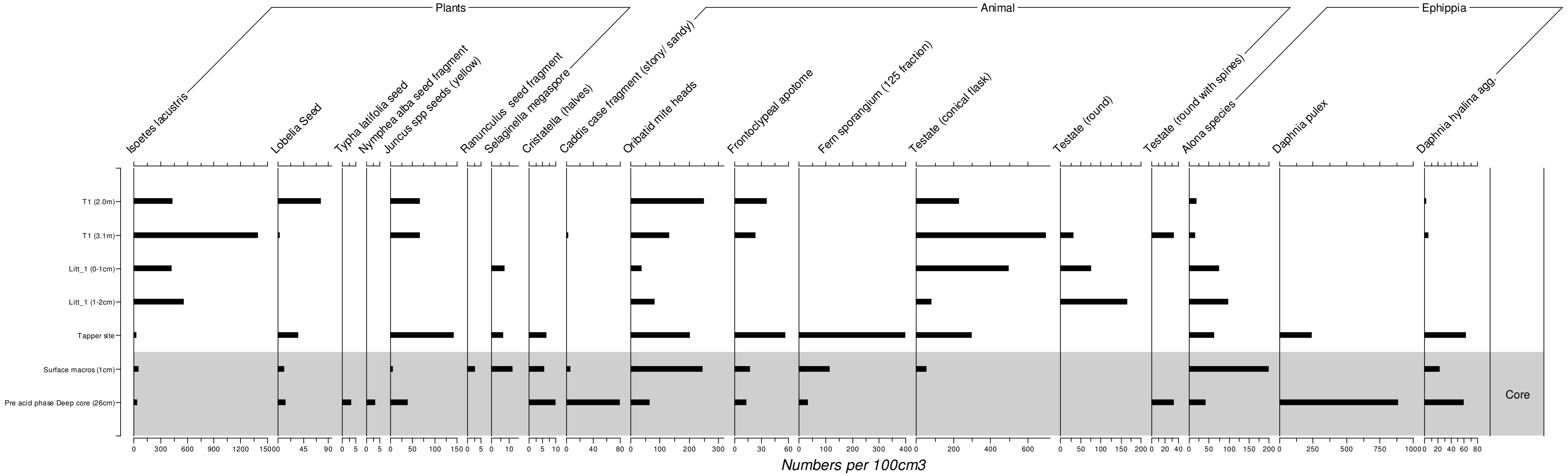

Figure 7: Macrofossil remains expressed as numbers per 100cm^3 from the RLGH surface samples (T1 2m, T1 3.1m, Litt_1 0-1cm, Litt_1 1-2cm and Tapper site) and the top and bottom macrofossil samples (grey shaded).

Cladocera

Three core samples from different depths of the Deep1 core and two surface sediment samples from the littoral cores Litt1 and Litt2 have been analysed (Figure 3). The sample at 29 cm represents the pre-acidification phase, the sample at 5cm represents ca. 1970 AD when the loch was at its most acidic and the 1.75cm sample represents ca. 2006 AD a date by which some measure of recovery might be expected. The surface sediment sample has yet to be analysed. The two surface sediment samples from the littoral cores allows a comparison between the littoral assemblage (Litt 1 0-1 cm and Litt2 0.1 cm) and the deep-water assemblage (Core 1.75 cm).

The most striking shift in the core species assemblage is the presence of *Daphnia longispina* in the bottom pre-acidification sample, which is completely absent from the upper two samples. This decline in *Daphnia* is also supported by the macrofossil evidence (see above and Figure 8) which show a decline in the abundance of the ephippia of *Daphnia pulex.* There is no significant difference, however, in the abundance of *D. hyalina* ephippia between basal and surface sediments. Towards the top of the core the proportion of *Bosmina longispina* and the small *Alona* species increase, suggesting some compositional change due to the acidification of the loch. It is intended that a high resolution study of the core be undertaken to investigate these shifts further and to pin point the exact timing and rate of cladocera community change.

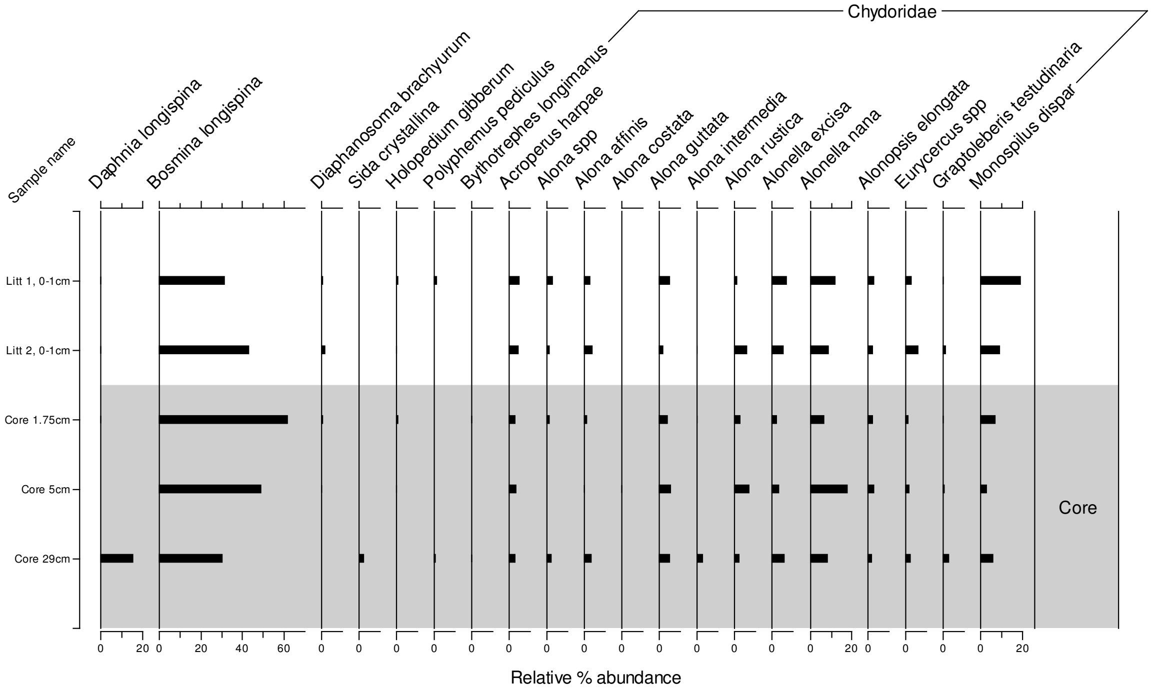

Figure 8: Cladocera species expressed as % relative abundance from two littoral surface samples (Litt1 0-1cm and Litt 2, 0-1cm) and from a deep water sediment core (shaded area, sample depths listed as sample names).

Chironomids

Core Deep1 was analysed for chironomid head capsules not only to identify taxa occurring in the lake in the pre-acidification phase but also to track changes in the chironomid assemblage during the acidification period (Figure 9). All samples have been prepared, but ten (from the 10-31 cm section which have been analysed alternatively) wait for identification. Slice 8.5-9 cm was missing and the uppermost 5 cm remain to be prepared.

The material contained abundant Chironomidae remains with 54 and 148 in the smallest samples (where all available material was treated) and more than 150 head capsules in the rest of the samples. Up to now 3084 individuals have been identified (and around 2000 wait for identification).

The total Chironomidae fossil assemblage of Deep1 contains 58 taxa, of which 35 have not been found in the living samples collected from the shallow to deep water depth transect (Figure 1) or in the AWMN invertebrate samples collected over the last 23 years (Rieradevall unpublished). Nearly all of these taxa are relatively rare (<5%). They comprise species known to live in littoral habitats, including seepage zones and inlets.

The dominant taxa in the core samples are the same as at present. Nevertheless some differences in occurrences can be seen (Table 2). In most cases, species not found in the AWMN samples (that are based on shoreline kick sampling) but found in the core samples are those with profundal muddy habitat preferences. The taxa increasing in relative abundance in recent years correspond to littoral species. However, these results should be interpreted cautiously as, although we are comparing percentage abundances in each case, the core samples refer to the head capsule remains of a pooled assemblage from all habitats within the lake while the AWMN series refer to living assemblage at the sampling site in the littoral zone.

Table 2. Comparison of the relative abundance of the common (>5%) Chironomidae taxa between the palaeorecord (core Deep1) and the contemporary assemblage through the last 23 years, with indication of habitat preferences of the taxa. (<, > indicates more or less abundant in palaeo samples respectively).

Common taxa (>5%)- RLGH	**Littoral 23-yr vs. paleo**	**Habitat**
Ablabesmyia ?phatta	<	Littoral
Arctopelopia griseipennis	>	Littoral
Procladius signatus	<	Profundal/muddy
Heterotanytarsus	<	Littoral
Heterotrissocladius grimshawi	<	Profundal/muddy
Psectrocladius (Monops.)	>	Littoral
Psectrocladius oligosetus	>	Littoral
Dicrotendipes modestus	<	Macrophyte association/muddy
Sergentia	<	Profundal
Stictochironomus rosenschoeldi-type	<	Profundal
Micropsectra	<	Profundal
Paratanytarsus	<	Profundal
Tanytarsus	<	Profundal

The palaeorecord does not show a significant variation in the remain concentration, even though between 1940-1970 the taxa richness is lower (20-24 taxa) than in previous times (24-33 taxa).

Although, as stated, there are no apparent changes in the Chironomidae assemblage dominant taxa, the downcore analysis (Figure 9) reveals abundance changes in some sensitive taxa. Around 1874 (16.5 cm downcore) we can distinguish several shifts in the relative abundances. Among the Tanypods (predators), *Paramerina* disappear after the acidification begins and is still absent today. *Procladius signatus* suffered an important reduction. The same tendency to decrease in a more clear way around the 1970s (5-6 cm) is followed by the shore and upper littoral inhabitants *Limnophyes* and *Synorthocladius semivirens*; and the sediment dwellers *Micropsectra, Paratanytarsus* and more markedly *Tanytarsus*.

Several taxa increased their abundances following the acidification effects on water chemistry, the most significant changes were in *Psectrocladius oligosetus*-type and in *Sergentia* relative abundances. But others show the same tendency (*Heterotrissocladius, Microtendipes,* or *Phaenopsectra*), with higher increases around the ‘70s.

It is interesting to note that some of the species increasing with the acidification process are well known acidophilic taxa, such as *Arctopelopia* or *Heterotanytarsus*. Their constant presence all through the core indicates that Round Loch of Glenhead has been naturally acidic. In this case no changes in the Chironomid assemblage species composition are expected in the recovery process but in the abundances.

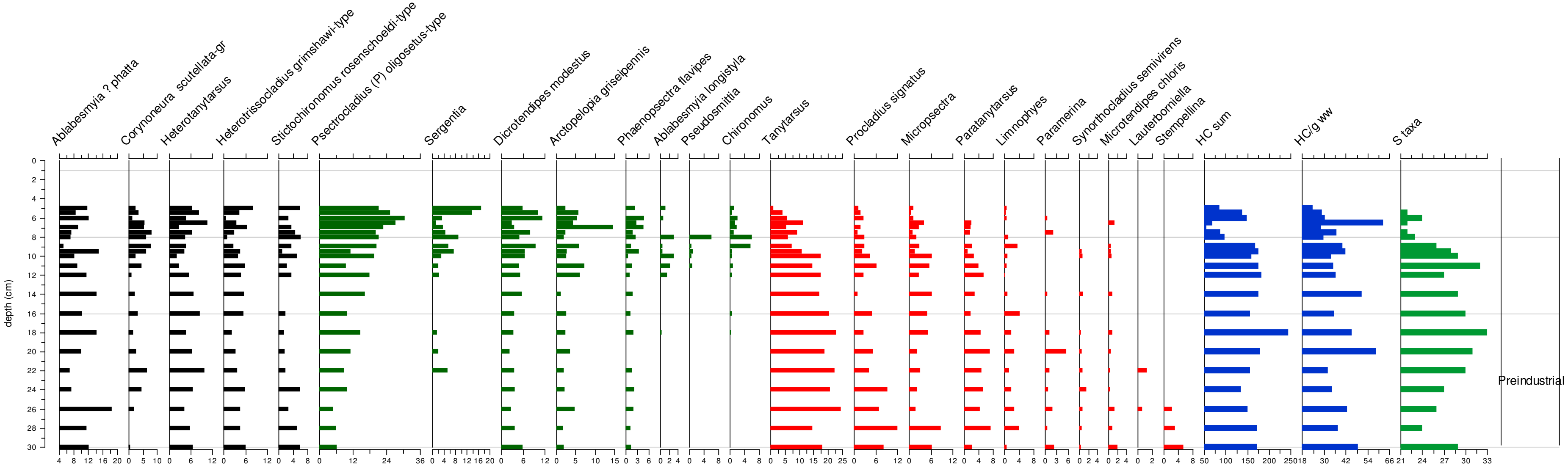

Figure 4: Selected Chironomidae species arranged according to their response to acidification in core Deep1 of Round Loch Glenhead (Scotland). In black, taxa present abundantly but not showing any pattern related with acidification. In green, taxa presenting increases after acidification. In red, taxa presenting a decrease pattern following acidification. Total counts (expressed as % relative abundances), remains concentration (HC/g ww = Head Capsules per gram of wet weight), and Taxa Richness (S taxa) are also presented. (Analyst: M. Rieradevall).

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