The coming and going of a marl lake: multi-indicator palaeolimnology reveals abrupt ecological change and alternative views of reference conditions

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Abstract

Eutrophication is the most pressing threat to highly calcareous (marl) lakes in Europe. Despite their unique chemistry and biology, comprehensive studies into their unimpacted conditions and eutrophication responses are underrepresented in conservation literature. A multi-indicator palaeolimnological study was undertaken at Cunswick Tarn (UK), a small, presently eutrophic marl lake, in order to capture centennial timescales of impact. Specific aims were to 1) establish temporal patterns of change (gradual/abrupt) across biological groups, thereby testing theories of resistance of marl lake benthic communities to enrichment, and 2) compare the core record of reference condition with prevailing descriptions of high ecological status. Analysis of sediment calcium (Ca), phosphorus (P), pigments, diatoms, testate amoebae, cladocerans, and macrofossils, revealed three abrupt changes in ecosystem structure. The first (1900s), with biomass increases in charophytes and other benthic nutrient-poor indicators, supported ideas of resistance to eutrophication in *Chara* lakes. The second transition (1930s), from charophyte to angiosperm dominance, occurred alongside reductions in macrophyte cover, increases in eutrophic indicators, and a breakdown in marling, in support of ideas of threshold responses to enrichment. Core P increased consistently into the 1990s when rapid transitions into pelagic shallow lake ecology occurred and Cunswick Tarn became biologically unidentifiable as a marl lake. The moderate total P at which these changes occurred suggests high sensitivity of marl lakes to eutrophication. Further, the early record challenges ideas of correlation between ecological condition, charophyte biomass and sediment Ca. Instead, low benthic production, macrophyte cover, and Ca sedimentation, was inferred. Management measures must focus on reducing external nutrient and sediment loads at early stages of impact in order to preserve marl lakes.

1 Introduction

Globally, freshwater habitats are among the most anthropogenically impacted (Geist 2011). Increasing population density along with technological advances in food production have increased hydrological modification, landscape homogenisation, as well as nutrient loading and sediment losses from terrestrial to aquatic habitats especially over the 20th century (Stoate *et al.* 2001; Geist 2011). The effects on freshwater ecosystems include eutrophication (Hasler 1947; Ulén *et al.* 2007), reductions in biodiversity (Baastrup-Spohr *et al.* 2013), and diminished recreational value (Pretty *et al.* 2003; Priskin 2008). The widespread alteration of fresh waters especially in lowland areas where population densities are highest, has likely changed how freshwater habitats are perceived following increasingly few incidences of human encounters with truly natural habitat. Therefore cultural perceptions of what constitutes natural, undisturbed conditions, may have become biased (i.e. shifting baseline syndrome) (Papworth *et al.* 2009). In turn, where records of pre-disturbance conditions is lacking, restoration can often be misguided when based on increasingly old and scattered anecdotal evidence (Tibby *et al.* 2008).

In terms of freshwater biology, it is desirable to characterise lake ecosystems prior to significant human impact, a prerequisite for drafting international legislation and guidelines on environmental protection and restoration (European Commission 2000; Lake 2001). Science and legislation, in turn, need to shape the decisions and actions of monitoring agencies, site managers, and owners of private land, in order to have a tangible positive impact on the environment. It is difficult to ascertain pre-impact conditions without historical information, yet in Europe especially, human impact extends beyond the beginning of the Industrial Revolution to Mediaeval, Roman and prehistoric times, for which ecological literature is scarce. Consequently, knowledge of the natural state of the environment requires additional methods such as palaeolimnology (Brenner *et al.* 1993; Bennion *et al.* 2011). Palaeolimnological methods for tracking changes in ecological structure and function in response to multiple drivers such as eutrophication (Sayer *et al.* 2010; Davidson and Jeppesen 2013; Bennion *et al.*, 2015), climate (Last and Smol 2001; Leng *et al.* 2006), hydrology, and chemistry (Smol *et al.* 2001) have developed substantially over the previous decades, allowing for increasingly confident ecosystem reconstructions.

In the UK, most of the highly calcareous (marl) lakes lie in heavily agricultural areas where human

impact has a long history (Pentecost 2009). Marl lakes in their natural state are highly alkaline, carbonate-rich lakes that precipitate calcite and contain distinct macrophyte communities dominated by Characeae and Potamogetonaceae (Pentecost 2009; Wiik *et al.* 2013). Further, owing to their geochemistry, the water is naturally of a translucent blue-green colour (Spence 1982). However, marl lakes may be sensitive to even minor increases in nutrient unputs, with substantial changes in macrophyte communities (Krause & King 1994; Free *et al.* 2007) and extirpations of key biodiversity species at a European scale (Stewart 2001; Blaženčić *et al.* 2006). In lakes, moderately clear water combined with dense aquatic flora is frequently considered near-pristine conditions, yet may not reflect truly unimpacted ecology.

Cunswick Tarn in northern England, despite being listed as a marl lake (Pentecost 2009), currently contains no marl lake indicator species, does not undergo visible marl precipitation in the summer months, and has brown and turbid rather than clear blue-green, water colour. It would not, therefore, be biologically categorised as a marl lake (Wiik *et al.* 2014) and has been classed as a (naturally) eutrophic water body in legal documentation for Sites of Special Scientific Interest (SSSI) (SD 49/2). Sufficient historical records do not exist to characterise unimpacted "reference status" ecology (European Commission 2000) of the site, and therefore a multi-indicator palaeolimnological approach was undertaken to answer the following questions regarding marl lake ecology and Cunswick Tarn specifically: 1) Can reference status and anthropogenic influence be identified from the palaeolimnological record? 2) To what degree have calcium (i.e. marl, carbonate) and phosphorus (eutrophication) defined the biological communities of Cunswick Tarn? 3) Was ecological change limited to a few biological groups or apparent at an ecosystem-level? 4) Was ecological change abrupt or gradual? 5) What are the most realistic and desirable ecological targets for Cunswick Tarn should management measures be implemented?

Given the steep shelving of the margins of Cunswick Tarn, and the sensitivity of charophytes to light penetration through the water column (Middelboe and Markager 1997), eutrophication effects were expected to be reflected by noticeable and relatively rapid changes in the charophyte community (as shown by abundance of charophyte oospores (Zhao *et al.* 2006). These changes were expected to be associated with upcore increases in remains of tall-growing or floating-leaved angiosperms (Blindow *et al.* 1992; Ayres *et al.* 2008; Sayer *et al.* 2010) as well as of groups of algae and cladocerans that reflect increased nutrient availability and an increasingly pelagic shallow lake community (Vadeboncoeur *et al.* 2003; Davidson and Jeppesen 2013). Finally, assuming that marl lakes have distinct biological communities compared with other lake types, and are sensitive to eutrophication, both Ca and P were expected to be significant correlates of biological community composition.

2 Methods

2.1 Study site

Cunswick Tarn (SD489937) is a small (0.8 ha), fishless, relatively shallow (Z_{max} 6.4 m; Z_{mean} 3.7 m) kettlehole lake in Cumbria, UK (Fig. 1). The limestone catchment comprises improved pasture to the north and west, and woodland along a sheltering hillside to the east. A low-gradient, likely artificial, outflow lies in the southwest corner (Fig. 1). The main inflow lies at the southeast corner, in addition to which small, low-nutrient and carbonate-rich streams issue from springs in the east (Fig. 1). Water high in phosphorus (P) seeps from woodland and pastures to the north, and a drain pipe from the north pasture feeds directly into the lake. Further, grain for duck rearing has been deposited at the northern lake margins where soil erosion also occurs. The Tarn is currently eutrophic with mean annual total phosphorus (TP) of 56 µg L^{-1}. Phytoplankton blooms occur in summer months and anoxia develops below 2.5-3 m. Macrophytes are abundant to approximately 4 m depth and dominated by two species (*Nuphar lutea*, *Elodea canadensis*) (Wiik *et al.* 2014).

2.2 Core collection

Two littoral sediment cores were taken from Cunswick Tarn (Fig. 1). CUNS1 (74 cm) was taken in January 2008 at a depth of 2.4 m from the southwestern margins using a "fat" Livingstone piston corer (internal diameter 71 mm). CUNS2 (94 cm) was taken in October 2009 from the northern margins at a water depth of 4 m using a "Big Ben" piston corer (internal diameter 140 mm) (Patmore *et al.* 2014). Most palaeolimnological analyses were undertaken on CUNS2, but analysis of macrofossils and loss-on-

ignition in CUNS1 confirmed a lakewide signal. The cores were extruded at 1cm intervals, and sediment samples for pigment analysis (CUNS2) were placed in separate bags and frozen.

2.3 Core chronology and lithostratigraphy

Core CUNS2 was dated by a combination of ^{210}Pb and ^{14}C accelerator mass spectrometry (AMS) method. Freeze-dried sediment samples were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay in the Bloomsbury Environmental Isotope Facility (BEIF) at University College London (UK) (Appleby *et al.* 1986). The chronology of CUNS2 followed the CRS model (Appleby 2001), adjusted to a well-resolved ^{137}Cs peak marking 1963. AMS on terrestrial macrofossils was undertaken at the Natural Environment Research Council Radiocarbon Facility (East Kilbride, UK) and the Keck C cycle AMS Lab (University of California, Irvine). For samples under 100 µg C, a correction based on small NIST Oxalic acid II was used to account for the effect of old carbon. Further, data were corrected for modern carbon contamination following Santos et al. (2007). The full chronology of CUNS2 was modelled with the Bayesian-based Bacon package (Blaauw and Christen 2013) of R version 3.1.2 (R Development Core Team 2010) using 17 ^{210}Pb, and 3 ^{14}C samples (Table 1).

Carbonate and organic carbon content of the cores were quantified by loss on ignition (LOI) following Dean (1974). P and Ca in CUNS2 were measured by X-ray fluorescence (XRF) (Boyle 2002) at 1 cm intervals for the uppermost 10 cm, and 2 cm thereafter. In order to track hydrological changes in the Tarn, core CUNS2 carbonate δ^{18}O was measured at 5 cm intervals at the NERC Isotope Geosciences Laboratory (Keyworth, UK). Samples were disaggregated in 5% sodium hypochlorite solution (10% chlorox) for 24 hours followed by washing and sieving at 85 µm. The residue was filtered, washed, dried (40 °C) and ground in agate. The isolated material was reacted with anhydrous phosphoric acid in vacuo overnight at a constant 25 °C to liberate CO_2 for measurement. δ^{18}O are reported as per mil (‰) deviations of the isotopic ratios (^{18}O/^{16}O) calculated to the Vienna Pee Dee Belemnite (VPDB) scale using a within-run laboratory standard calibrated against National Bureau of Standards (NBS) standards.

2.4 Biological groups

Analysis of pigments and macrofossils followed Moorhouse *et al*. (2014) and Sayer *et al.* (2010), respectively. Chlorophyll and carotenoid pigments were analysed at all levels of CUNS2, and macrofossils for every 6 cm of CUNS2, and for 16 levels of CUNS1. Diatom analysis of CUNS2 followed Battarbee et al. (2001) and was undertaken at 2 cm intervals to a depth of 45 cm, beyond which preservation was poor. Where a strong preference for epiphytic or benthic substrates was absent, percentage abundance by habitat was calculated with an equal weighting for both habitats.

Testate amoebae, specifically arcellaceans, were analysed roughly at 2 to 3 cm intervals throughout the core. Subsamples of 2 cm^3 were wet sieved through a 250 µm mesh to remove course organics and a 35 µm mesh to remove clay and fine silt. The resulting residues were split into eight aliquots using a wet-splitter (Scott and Hermelin 1993) and quantified to > 150 specimens per sample where abundance was permitting (Patterson and Fishbein 1989). Species and strains were identified according to lacustrine arcellacean keys (Medioli and Scott 1983; Kumar and Dalby 1998) and published scanning electron micrographs (Roe *et al.* 2010; Patterson *et al.* 2012).

Subfossil cladocerans were analysed at 3 cm intervals for CUNS2 following Korhola and Rautio (2000). Due to high sediment carbonate concentrations, samples were treated with 10% HCl prior to 10% KOH. All samples were sieved into 150 and 45 µm size fractions and counted following Davidson *et al.* (2007) to a minimum count of 300 individuals of the most abundant species, or the entire large size fraction where counts were low. Post-abdominal claws other than those o*f Daphnia pule*x were aggregated to *Ceriodaphnia* and *Daphnia* spp. Morphological plasticity o*f Chydorus* remains was interpreted as variability within *Chydorus sphaericus sensu lato. Bosmina longirostr*is was the only species o*f Bosmina* confirmed in the core, however the abundance of fragmented and non-diagnostic remains led to aggregation to *Bosmina* sp(p). Identification was undertaken using Frey (1965), Flößner (2000) and Szeroczyńska and Sarmaja-Korjonen (2007).

Historical presence of fish in Cunswick Tarn was determined by identification of chaoborid larval

mandibles using the cladoceran method. *Chaoborus obscuripes* and *Chaoborus crystallinus* are non-migratory species associated with fishless lakes (Luoto and Nevalainen 2009; Palm *et al.* 2012; Tolonen *et al.* 2012) and therefore their consistent presence in the core record was interpreted as a proxy for fishlessness. Mandibles were identified using Aitken (1954), Uutala (1990), Živić and Marković (2006), and Palm et al. (2011). *Chaoborus obscuripes* and *Chaoborus crystallinus* were not separated and are referred to as *C. obsuripes/crystallinus*.

2.5 Historical evidence

Diagrammatic reconstructions of the macrophyte communities and colonisation depths in Cunswick Tarn for the present, the mid-1900s, and the late 1800s/early 1900s were constructed based on 1) the CUNS1 and CUNS2 macrofossil records; 2) Historical macrophyte presence and spatial distribution data collated from records held by UCL and Natural England, and other field naturalists; 3) macrophyte community composition and zonation in other marl lakes (Jupp *et al.* 1974; Spence *et al.* 1984; Pentecost 2009; Hilt *et al.* 2010) or lakes with similar species composition (Spence 1967, 1982).

2.6 Statistical analysis

All data analysis was performed with R versions 3.1.2 (R Development Core Team, 2010) using packages analogue (Simpson 2007; Simpson and Oksanen 2011), vegan (Oksanen *et al.* 2011), and mvpart (De'ath 2002). Statistical analysis was only undertaken on CUNS2 data owing to the low resolution of the chronology for CUNS1.

Diatom and arcellacean data were transformed into percentage abundances and taxa with < 5% abundance and less than 5 occurrences in the core profile were omitted. They were also square-root transformed. Pigment and macrofossil data were ($\log_{10} + 1$), and XRF data ($\log_{ln}$)-transformed and normalised with respect to organic matter, respectively. Cladoceran data were transformed into percentage data for principal curves and multivariate regression trees, and square-root transformed for all analyses. Finally, pigment data were further standardised to abundances between 0 and 1 to control for preservation differences across pigments.

2.6.1 Principal curves

Principal curves (PC) are a multivariate ordination-based method particularly suitable for data sets with a single dominant gradient (Hastie and Stuetzle 1989; De'ath 1999) which applied to Cunswick Tarn. For CUNS2 data, PCA axis 1 scores were used for all data sets as a starting point for PCs. The complexity of the smoothing splines fitted to each species was allowed to vary, and the spline degrees of freedom were chosen using the GCV criterion following Simpson and Birks (2012).

2.6.2 Multivariate regression trees

Multivariate regression trees (MRT; De'ath 2002) are a form of constrained cluster method that allow for multiple constraining variables on a response data set (). The response data set can be a species abundance table or a dissimilarity matrix, clustered by age to add chronological constraint on temporal series (Simpson and Birks 2012). MRT was applied to geochemical (P, Ca) and biological data (pigments, diatoms, arcellaceans, cladocerans, macrofossils) for all analysed levels using age (in yrs AD) as a constraining parameter in order to determine the timing of major shifts in geochemistry and ecological responses (see Simpson and Birks, 2012; p. 261). Analysing each response separately allowed for a high number of data points and therefore confidence in grouping. The number of data points was n = 94 (pigments), n = 54 (P, Ca), n = 39 (arcellaceans), n = 32 (cladocerans), n = 24 (diatoms) and n = 16 (macrofossils).

A previously developed cladoceran-based model capable of semi-quantitative inference of macrophyte and fish abundance, employing MRT (Davidson *et al.* 2010a) was also applied to the cladoceran data set (n = 32) in order to estimate past plant abundance (late summer plant volume infestation (PVI) (Davidson *et al.* 2010b). The number of *Daphnia* spp. ephippia (counted only at macrofossil resolution) for missing levels was modeled based on the relationship between ephippia (macrofossils) and post-abdominal claws (cladocerans).

2.6.3 Redundancy analysis

Relationships between P, Ca, and biological data sets were tested using redundancy analysis (RDA). Owing to the varying resolution of the data, RDAs were fitted to matching observations, giving subsets of n = 54 (pigments), n = 18 (testate amoeba, cladocerans), and n = 15 (macrofossils). Analysis of the diatom data set was omitted due to the low number of matching observations. To allow for temporal ordering of the data, significance of variance explained was tested using anova with cyclic permutations. The lowest attainable p value of such permutations depends on the number of observations tested (1/n) and therefore significance was unattainable for most data sets at a .05 level (e.g. 1/18 = .056). Therefore, although too liberal, permutation tests were also performed without restrictions.

3. Results

3.1 Core chronology and lithostratigraphy

Core CUNS2 spanned a period of approximately 1250 to 2009 AD (date of core collection) with highest age uncertainties in the middle section of the core (Fig. 2). The gap in measured ages was unavoidable given the constraints of the time spans of ^{210}Pb (to ca 150 yrs from present) and radiocarbon dating (minimum age several hundreds of years). Sedimentation rates (SRs), core carbonate, and Ca followed a similar pattern, the latter two of which were considered equivalent owing to deposition as calcite/marl ($CaCO_3$) and their high correlation (Spearman's rho = .97, p < .001).

Four carbonate Zones were apparent in CUNS2. Zone 1 encompassed the base of the core (1250s) to the early 1400s, characterised by relatively low carbonate content (< 10%) and variability, and low SR (ca .12 cm yr^{-1}). Carbonate and SR were at their lowest values in Zone 2 (ca 5% and .07 cm yr^{-1}, respectively), which encompassed the 1400s to the 1890s. Thereafter, substantial increases in carbonate (to 36%) and SR (to ca 1 cm yr^{-1}), with a second carbonate peak of 40% in the 1920s followed by a rapid decline (ca 10 yrs). Zone 3 encompassed these fluctuations in marl deposition, while slightly lower carbonate (ca 20 - 30%) and SRs (ca 0.2 - 0.5 cm yr^{-1}) occurred in Zone 4 from the 1930s to 2009.

CUNS1 followed a similar LOI pattern to CUNS2, allowing cross-correlation to estimate the chronology of CUNS1 (Fig. 3). A CUNS1 parallel for CUNS2 Zone 1 was not appropriate owing to the brevity of the CUNS1 sequence and differences in carbonate concentration in this core section. The zone limits for CUNS1, therefore, are Zone 2: core base to 42.5 cm (base to ca 1890s), Zone 3: 42.5 to 26.5 cm (1890s to 1930s), and Zone 4: 26.5 cm to top (1930s to 2008) (Fig. 3). Higher carbonate concentrations than in CUNS2 were found in Zone 2 (ca 20% vs ca 5%), and similar carbonate peaks (> 40%) occurred in Zone 3.

CUNS2 carbonate δ^{18}O could not be measured for most of Zone 2 owing to insufficient carbonate (data not shown). Therefore only 14 samples were analysed, five of which were in Zones 1 and 2 and had highly variable δ^{18}O out of equilibrium with rainfall (-3 - -6‰), indicating a hydrologically closed system (Leng and Marshall 2004; Leng *et al.* 2006). The uppermost 9 samples ranged between -6 and -7‰ and were in equilibrium with rainfall, suggesting that Cunswick Tarn became a hydrologically open system between the 1800s and 1900. It is unlikely that the disequilibrium values reflect fractionation during *Chara* stem and oospore calcification (Andrews *et al.* 2004) considering that the highest and lowest abundances of these remains were recorded in the sections of equilibrium values.

CUNS2 P concentrations were expressed relative to core organic matter to correct for dilution by calcite, and are therefore only interpretable as relative values within the core sequence. Ranged between 0 and 1 for simplicity, the lowest concentrations occurred before the 1530s (.5 - .6) and between the 1530s and the 1890s (.4 -.45). Rapid increases occurred in the early 1900s coincident with increases in Ca, with concentrations between .55 and .8. From the 1930s to 2009, concentrations increased consistently from .7 to 1.

3.2 Zone 1: ca 1250 - 1400 (CUNS2 only; no diatom data)

Pigments of algae, higher plants and cyanobacteria were low in Zone 1 (Supp. 2). Compared with Zone 2, slightly higher concentrations of diatom (diatoxanthin), cyanobacteria (zeaxanthin) and cryptophyte (alloxanthin) pigments occurred throughout. The notable difference between the Zones was the

concentration of a purple sulphur bacterial pigment (okenone) which was highest at the base of the core and declined to levels below detection at the upper limit of Zone 1.

The arcellacean community (data not shown) in this Zone included moderate abundances of *Difflugia oblonga* "oblonga" (ca 15-30%) and *Centropyxis aculeata* "aculeata" (ca 10-25%) with lesser amounts (ca <10%) of *Arcella vulgaris* and other centropyxid taxa (*Centropyxis aculeata* "discoides", *Centropyxis constricta* "aerophila" and *Centropyxis constricta* "constricta") and the oligotrophic indicator *Cyclopyxis kahli* (Ellison 1995). The eutrophic indicator species *Cucurbitella tricuspis* (Medioli and Scott 1983) is present in small amounts (<5%) as are *Difflugia glans* "glans" and *Lagenodifflugia* vas.

Remains of pelagic cladocerans at the base of the core were relatively abundant, and declined slightly towards the upper end of the zone (e.g. *Bosmina longirostris*/spp. 42% to < 10%) (Supp. 3). Other filter-feeding and/or pelagic species included *Daphnia pulex*, *Daphnia hyalina* agg. and *Simocephalus* spp. Plant- and mud-associated species included *Alonella exigua*, *Alonella nana*, *Eurycercus lamellatus*, *Graptoleberis testudinaria*, *Alona affinis* and *Leydigia leydigi*. Species exclusive to Zone 1 included *Pleuroxus truncatus*, *Chydorus piger* and *Alona rustica*.

Plant macrofossils included terrestrial *Juncus* spp. seeds, fragments of *Nymphaea alba* seeds, and uncalcified oospores of *Chara hispida* agg., *Chara contraria* agg. and *Nitella* cf. *flexilis* (Supp. 4). Oblong *Plumatella* sp. statoblasts were particularly abundant in Zone 1 compared to the rest of the core (Supp. 5). Mollusca were largely absent with the exception of Sphaeriidae.

3.3 Zone 2: ca 1400 - 1890

Okenone remained below detection limits throughout Zone 2 and overall pigment concentrations were lower compared to other zones (Supp. 2). Benthic species (e.g. *Pseudostaurosira brevistriata* ca 50 - 60%) dominated the CUNS2 diatom record at the latter end of the Zone (three samples counted), forming 60 - 80% of the community (Supp. 6). Periphytic taxa formed 10 - 30% of the community and included *Gomphonema angustum* and *Amphora pediculus*, while planktonic species accounted for < 5%. *Cyclotella* and *Fragilaria* compositions indicated pre-eutrophication conditions of high light penetration (Moss 1979; Padisak and Reynolds 1998; Meriläinen *et al.* 2000),

Changes among the dominant arcellacean taxa included gradual increases in *C. tricuspis* (to ca 23%), and decreases in *D. oblonga* "oblonga", towards the end of the 18th century. *C. constricta* "aerophila", *D. glans* "glans" and *A. vulgaris* increased in abundance. *L.* vas was a minor component in the composition excepting a peak in the mid-18th century (ca 17%).

Diversity and total abundance of cladocerans were at their lowest in Zone 2, and pelagic taxa were rare (Supp. 3). The community was dominated by benthic taxa (e.g. Tremel *et al*. 2000; Thienpont *et al*. 2015) including *Chydorus sphaericus*, *Alona guttata/rectangula* and *Alona quadrangularis*. In contrast, in the macrofossil record of CUNS1, planktonic *Ceriodaphnia* spp. ephippia were abundant (n > 1000 100 ml $^{-1}$) at the beginning of Zone 2 (ca 1400-1500s), followed by consistent decreases to the upper end of the zone (n <100 100 ml $^{-1}$).

In CUNS2 Zone 2, there were fewer plant macrofossils of both terrestrial and aquatic origin compared with Zone 1 (Supp. 4). Whilst species composition was similar, Charophyta differed as *Nitella* spp. were absent and *C. hispida* agg. dominated. In CUNS1, there were high abundances of calcified *Chara aspera* oospores in Zone 2, which was not recorded in CUNS2 (Supp. 7). One other submerged macrophyte species, *Potamogeton praelongus* (CUNS1), occurred in this Zone. Floating-leaved macrophyte remains included Nymphaeaceae trichosclereids (leaf cells), occurring in CUNS1 and CUNS2 at slightly higher abundance than in Zone 1, and increasing substantially towards the end of Zone 2 in CUNS1. Only *N. alba* seed remains were recorded, although *Nuphar lutea* occurred in the Tarn in the early 1800s (Baker 1885). *Potamogeton natans* seeds occurred throughout this Zone (CUNS1). Mollusc remains were more diverse and abundant in Zone 2 compared with Zone 1 (Supp. 5). In CUNS2, the Sphaeriidae dominated the record (maximum of n = 50-100 100 ml $^{-1}$) whereas in CUNS1 several different taxa became more abundant toward the latter part of the Zone (*Bithynia leachi/tentaculata*, *Planorbis* cf. *albus*, *Valvata* cf. *macrostoma*) (Supp. 8).

3.4 Zone 3: ca 1890 - 1930

The CUNS2 Zone 3 pigment assemblage remained largely similar to Zone 2 with low biomarker concentrations of cyanobacteria (zeaxanthin, canthaxanthin) and cryptophytes (alloxanthin), and purple sulphur bacteria (okenone) below the limit of detection (Supp. 2). Consistent increases towards the top of the Zone occurred in chlorophyte (lutein, pheophytin *b*) and diatom (diatoxanthin) pigments. Increases in biomarkers of all algae (chl *a*, ß-carotene) occurred abruptly at the end of the sequence around the 1920s. In the CUNS1 and CUNS2 macrofossil record, *Gloeotrichia* cf. *pisum*, a nitrogen-fixing colonial cyanobacterium, increased approximately three-fold in abundance throughout the Zone (Supps 4, 7). The proportion of periphytic diatoms in the CUNS2 record increased from ca 40% to 70%, dominated by *G. angustum* and *A. pediculus*. (Supp. 6). Throughout Zone 3, diatoms were more abundant than in the other zones. Persistence of the nutrient-sensitive *Cymbella microcephala* suggested relatively low nutrient concentrations (Schneider *et al.* 2000) (Supp. 6).

The most substantial and rapid changes in the arcellacean community occurred in this Zone with peaks of *A. vulgaris* and *C. aculeata* "aculeata" (ca 50%). The proportions of *D. oblonga* "oblonga" and *C. tricuspis* (to ca <5%), and *C. kahli*, *C. constricta* "aerophila" and *D. glans* "glans" decreased further in this zone. Species diversity was at a minimum in this zone.

Cladoceran abundances were highest in Zone 3 (Fig. 5). Benthic taxa remained dominant, however community composition changed towards a dominance of strictly plant-associated species: *Pleuroxus laevis* and *A. harpae* became more abundant than *A. quadrangularis* and *Alonella excisa*, and *Alonella exigua* became absent. Ephippia of pelagic cladoceran taxa were largely absent or rare in CUNS1 and CUNS2.

Two macrophyte phases within Zone 3 were identified in the cores (Supps 4, 7). Oospores attained maximum abundances in the first phase (CUNS1 n = 2698 ml^{-1} and CUNS2 n = 8707 100 ml^{-1}) which corresponded to high abundances of encrusted stem remains. Six different oospore morphotypes were identified to *C. aspera*, *C. hispida* agg. *Chara* cf. *vulgaris* and *Chara* cf. *globularis*. Historical records further identified *Chara curta* in the Tarn at the end of the 1890s (Stewart 2001), and *Chara aculeolata*, *Chara desmacantha* [syn *C. curta*] (1890s), and *Chara fragilis* [syn. *Chara globularis*] (1902) (Wilson 1938). Nymphaeaceae were less abundant compared with Zone 2. In the latter phase (from ca 1910s) oospores remained numerous, but declined with respect to the earlier phase (CUNS1 < 400 ml^{-1}, CUNS2 ca 200 - 1600 ml^{-1}). Remains of floating-leaved species (*P. natans*, Nymphaeaceae incl. *N. lutea*) increased and narrow-leaved *Potamogeton* species (*Potamogeton pusillus*/*berchtoldii*, *Potamogeton obtusifolius*) appeared in the record for the first time. Maximum abundances of molluscs occurred in the early part of Zone 3 (Supps 5, 8; Fig. 5).

3.5 Zone 4: ca 1930 - 2000s

Diatom, cyanobacteria, and cryptophyte pigment concentrations in CUNS2 increased substantially from the 1930s to maximum abundances in the 2000s (Supp. 2) indicative of increasing eutrophication (Supp. 2) (Leavitt 1993; McGowan *et al.* 2005). In contrast, biomarkers of all algae (chl *a*, ß-carotene) peaked around the 1930s followed by declines to concentrations similar to the early 1900s. In the diatom record, nutrient-sensitive species were succeeded by the more ubiquitous *Amphora pediculus* (Kwandrans *et al.* 1998; Garcia-Rodriguez *et al.* 2007; Stenger-Kovács *et al.* 2007). Okenone reappeared in the pigment record and increased from the 1980s, coinciding with a decrease in *G.* cf. *pisum* (Supps 4, 7) and an increase in the proportion of planktonic diatoms such as *Aulacoseira* spp. and *Stephanodiscus hantzchii* indicative of eutrophication (Reynolds *et al.* 2002; Negro and de Hoyos 2005) from ca 5% to ca 30% (Supp. 6; Fig. 5).

Remains of pelagic cladocerans, *Daphnia* spp. in particular, increased consistently from the 1930s to the 2000s in the macrofossil (CUNS1, CUNS2) and cladoceran record (CUNS2) (Supps 3, 5, 8). *Bosmina* spp., which had been absent from the record after the 1400s, were found in the most recent sediment. Five plant-associated cladoceran species characteristic of Zone 3 declined in abundance in contrast to increases in uibquitous species (*Alonella nana*), filter feeders (*Sida crystallina*) and sediment-associated species (*Leydigia leydigi*).

A substantial increase occurred in relative abundances of *D. oblonga* "oblonga", *L.* vas, and *Difflugia protaeiformis* strains in the 1930s. In contrast, relative abundances of *A. vulgaris* and all centropyxid taxa, in particular *C. aculeata* "aculeata", decreased. Some recovery in the uppermost part of the core was evident for *A. vulgaris* and *C. aculeata* "aculeata" with modest increases also in *C. kahli* and *C. tricuspis* (to ca 9%). Species diversity and arcellacean concentrations returned to levels similar to those in Zones 1 and 2.

In the 1930s, *P. natans* seeds disappeared from the core record, and charophyte remains declined substantially (Supps 4, 7). In CUNS1, oospore numbers fell two-three orders of magnitude from maximal abundances in Zones 2 and 3, while CUNS2 numbers fell to levels comparable with Zone 1. Nymphaeaceae trichoscleroids increased to > 3 times their previous abundance (CUNS1, CUNS2). Linear-leaved *Potamogeton* remains persisted in the core record (CUNS2). Of the Nymphaeaceae, only seeds of *N. lutea* were found. The Tarn was at the time (1936) described as "very rich in aquatic plants" (Wilson 1938). The first core record of *Myriophyllum spicatum* (CUNS1) in the 1950s coincided with descriptions of Cunswick Tarn as an "excellent calcareous tarn with *Cladium mariscus*" (NC SSSI citation), however, concerns were raised regarding the spreading of *Phragmites* [*australis*] which dominated the east side (Lewis 1954).

The abundance of mollusc remains decreased markedly following the 1940s and *Bithynia* spp. became the dominant taxon until the 1980s after which numbers declined to Zone 2 levels (Supps 5, 8).

3.6 Constrained analyses

Ca and P were correlated with between 10 and 37% of the CUNS2 biological data (Table 2). Relationships were strongest for P, and for pigments and cladocerans for which the cyclic permutation test was either significant (pigments) or took the smallest p value possible given the number of samples (cladocerans). Owing to the possibility of Type II errors with relatively low numbers of data points, the significance of all relationships (pigments, arcellaceans, cladocerans, macrofossils) under unconstrained permutation tests suggests that P and Ca were strongly associated with biological change. Macrofossils were the only biological group explained more by Ca (26%) than P (20%) (Table 2), however, it is likely that bimodality, which could not be removed, negatively influenced the strength of the test with Ca.

3.7 Principal curves and Multivariate Regression Trees

Chronological MRT splits are indicated as the midpoint between samples either side of a split and therefore are not, for data with differing resolutions, an exact reflection of the temporal relationship across groups. While P and Ca data occurred at identical depths, the splits for pigments (median age gap 6 yrs) will necessarily be more precise than those for macrofossils (median age gap 40 yrs). In order to remain unambiguous about split locations given the exact dates put into the model, dating errors were not incorporated into split estimates.

Four significant MRT zones were identified for P (Fig. 4). For Ca, three or four significant zones were identified by MRT depending on the data transformation used (bimodality in the density distribution of Ca values interfered with the method). In order to cohere with P and biological data groupings, and to delineate the decline in Ca content in the uppermost section of the core (Fig. 3), four zones were selected. Relatively small changes occurred in P and Ca concentrations between 1200s and the late 1800s within which one split was found at ca 1400 (Ca) (Zone 1/2) and 1530 (P). Changes were more synchronous in the latter end of the sequence where splits were identified at 1896 (Ca),1902 (P), 1930 (Ca), and 1935 (P). The first split marks an increase in the concentration of both elements, and the second a decrease in Ca and continued increase in P.

Principal curves identified modest changes in biological communities between the 1200s and the late 1800s. MRTs located shifts of cladocerans and pigments around 1427, and 1370 and 1458, respectively, followed by macrofossils around 1500, and arcellaceans around 1516 (Fig. 4).

Substantial community change occurred between the 1890s and the 2000s during which splits in biological groups showed clear synchronicity. Split 2 as per P (1902) and Ca (1896) (Zone 2/3), where

both elements increased, coincided with splits in pigments (1903), diatoms (1900), cladocerans (1898) and macrofossils (1901). Split 3, where Ca declined (1930) (Zone 3/4) and P continued to increase (1935) coincided with splits in pigments (1936), diatoms (1933), arcellaceans (1933) and macrofossils (1936), with a slight lag in cladocerans (1940).

The highest number of significant splits occurred in primary producers (pigments n = 8, diatoms n = 5), which also changed significantly in the most recent years (pigments: 2000, diatoms: 1995), coincident with the most recent split in cladocerans (1990) (Fig. 4). The highest frequency of splits occurred between the 1900s and 1930s. The most important pigment splits are indicated by solid lines (Fig. 4).

3.8 Fish abundance and the Cladocera-macrophyte-fish model

Absence of fish throughout the core record was indicated by the presence of *C. obscuripes/crystallinus*, and the absence of fish scales and fish leech cocoons (*Piscicola geometra*) (Odgaard and Rasmussen 2001). Zooplanktivorous fish densities indicated by the cladoceran-based MRT model (Davidson *et al.* 2010a) were low (< .001 ZF density m^{-2}) for most data points with the highest density (ca 0.5) indicated for the lowermost sample in the cladoceran record with high numbers of *Bosmina* spp (Fig. 6). These values are low compared with the range of zooplanktivorous fish used to construct the model (0 - 3.26) (Davidson *et al.* 2010a) and support the idea that fish were absent from the lake particularly through Zones 2 - 4. Primary producer and cladoceran community changes were therefore assumed to be independent of top-down effects from fish.

Reconstructed August PVI was low (< 10%) prior to the 1400s (Zone 1) and following the 1950s (Zone 4). Very low PVI (< 3%) was indicated for the uppermost two levels (> 2000 AD). The MRT model is semi-quantitative and strictly speaking it is only the changing of the MRT end group that strongly supports the idea of changes in macrophyte abundance (Davidson *et al.* 2010b). However, the direction of movement in the two-dimensional space of the biplot can also be used to infer past dynamics in macrophyte abundance. This suggests an increase in macrophyte abundance after 1890 which peaked between 1900 and 1915 followed by a consistent decline of plant abundance to the present day where plant abundance is rather low (Fig. 6).

4 Discussion

Cunswick Tarn proved particularly suited for detailing bottom-up effects of eutrophication owing to the absence of fish throughout the core record, and therefore the elimination of higher trophic cascades. With reference to the original research questions, the high correlation of both core P (15 - 37%) and Ca (13 – 27%) with all biological data sets (Table 2) supported expectations of eutrophication (P) and marling (Ca) as correlates of biological community structure at the whole ecosystem level (Fig. 4). The two main patterns of change were the abrupt shift between two different benthic phases (low *Chara* + organic sediment to high *Chara* + marl sediment), and the erosion of benthic primary production pathways as the Tarn became increasingly eutrophic. While the latter followed initial hypotheses and is widely documented (Bumby 1977; Carbiener *et al.* 1990; Vadeboncoeur *et al.*, 2003), the former is a previously undocumented eutrophication-driven switch in marl deposition with important consequences to lake management targets and marl lake reference conditions.

4.1 Drivers of ecosystem change

4.1.0 Hydrology

The first substantial changes in Ca, P, and ecosystem structure occured following lake drainage in the 1890s, corresponding to a period of intensifying land management in the area following land enclosures and attempts at drainage of local lakes (Otley 1830; Walker 1955; Cousins 2013). Both lake shallowing and eutrophication can have similar ecological effects and their synchrony in the core record render strict eutrophication responses difficult to identify. For example, increases in calcified *Chara* oospore and stem abundance (Supp. 4, 7), as well as of epiphytic diatoms and macrophyte-associated molluscs (Fig. 5) may reflect improved light conditions. Higher light availability expands benthic photosynthetic habitat (Leavitt 1993), and also modulates the optimal depth of calcite deposition (Pukacz *et al.* 2014), which may confound simplistic responses to nutrients.

Shallowing is supported in the oospore record of CUNS2 by a shift from a dominance of the *Chara hispida* group to the more littoral lower-growing *Chara aspera*. However, evidence for a predominant effect of eutrophication following an initial pulse of lake shallowing is supported by a few factors. Firstly, the Ca and oospore increase also occurred in CUNS1, the location of which was 1.5 m shallower than that of CUNS2 (Fig. 1). Secondly, CUNS1 reflected littoral conditions (high carbonate content and *Chara aspera* oospores) throughout the record and therefore did not undergo charophyte community shifts, suggesting that increased nutrient availability was in part responsible for the change. Thirdly, the change in Ca and charophytes was a continuous rather than a stepwise transition, suggesting underlying eutrophication responses independent of a simple water level change. Indeed, the positive relationship between Ca and P in the early 1900s strongly suggest a eutrophication effect on *Chara* biomass and marl deposition.

4.1.1 Internal drivers: Marl lake ecology and Ca-P cycling

The reasons behind notions of self-sustaining, eutrophication-buffering properties of charophytes include the maintenance of clear water via nutrient uptake from the water column, coprecipitation of Ca with P, and sediment stabilisation owing to dense growth (Otsuki and Wetzel 1972; Kufel & Kufel 2002; Robertson *et al.* 2007). This so-called inertia to external pressure, and therefore internal driving mechanisms underlie ideas of occasional abrupt and rapid ecological changes following extended periods of eutrophication (Scheffer *et al* 1993; Scheffer and van Nes 2007). While punctuated change has been largely absent in other palaeolimnological studies of (formerly) *Chara*-dominated lakes (Davidson *et al.* 2005; Ayres *et al.* 2008; Sayer *et al.* 2010), elements of rapid change driven by internal mechanisms could be inferred in the Cunswick Tarn record. These events corresponded to key changes in community composition within a marl lake framework, namely changes in *Chara* abundance, transitions from *Chara* to angiosperm dominance, and finally transitions from benthic to pelagic ecosystem structure (Fig. 7).

The first shift occurred in the 1890s with sub-decadal changes across all biological groups. The positive relationship between Ca, P and *Chara* biomass in Cunswick Tarn, mirrored by increased cladoceran-inferred PVI (Fig. 6), support ideas of self-stabilising mechanisms especially in the early stages of eutrophication via increased nutrient uptake in the benthos and prevention of phytoplankton increases. Importantly, the structuring role of charophytes was also apparent in the close association of charophyte biomass with abundance responses in other benthic primary producers and consumers (Fig. 5). Also importantly, these numerical changes were synchronous with strictly qualitative ecosystem change as seen in the multivariate analyses of cladocerans, diatoms, and arcellaceans (Fig. 4), all of which were transformed to remove effects of total abundance.

The importance of plant biomass responses as buffers to eutrophication were further supported by the lack of association between P and Ca in CUNS2, which argues against significant chemical defenses against eutrophication via coprecipitation (see also Hobbs *et al.* 2005; Hutorowicz and Dziedzic 2008). Further, the second abrupt change in the core record corresponded to the breaking down of marling, substantial declines in macrophyte biomass (Fig. 6), particularly that of charophytes (Fig. 7), and increases in eutrophic indicator taxa, suggesting that high charophyte densities were the main factor in maintaining clear water and ecology reflective of nutrient-poor conditions.

The third point change in pigments, diatoms, arcellaceans and cladocera occurred in the 1990s (Figs 4, 7) Increases in planktonic taxa such as eutrophic indicator diatoms (Supp. 6), cryptophytes (Supp. 2) and *Daphnia* spp. (Fig. 5) occurred together with increases in Nymphaeaceae and declines in concentrations of ubiquitous pigments, supporting the idea of a larger change in ecosystem structure towards pelagic shallow lake ecology (McGowan *et al.* 2005). Reciprocally, major declines in cladoceran-inferred PVI (Fig. 6) and reductions in macrophyte species diversity from 9 to 4 between the 1980s and the early 2000s (Wiik *et al.* 2014) indicated a substantial decline in benthic production.

Given the modest concentrations of TP in the lake currently (56 µg L^{-1}), and increasing P concentrations towards the upper core, the decoupling between marling and P loading following the 1930s likely occurred at very low TP concentrations and opened up a slippery slope towards the loss of marl lake characteristics in Cunswick Tarn. The buffering capacity of charophytes may function over lower ranges of impact than previously thought. Indeed, sensitivity of charophytes to eutrophication is supported by

studies of other marl lakes through time (Krolikowska 1997; Hargeby *et al.* 2007; Krause and King 1994), and also via space-for-time substitution (Kornijów *et al.* 2002; Free *et al.* 2007).

Interestingly, there are several marl lakes which have sustained high abundances of precipitating *Chara* meadows, also to considerable water depth (ca 4 m), despite high nutrient loading and limnetic TP concentrations. These include several lakes in Poland with TP between 40 – 220 µg L-1 (Pełechaty *et al.* 2004; Pełechaty *et al.* 2013). There are also charophyte-dominated clear marl lakes with intermediate and variable TP, including Lakes Jasne (TP 30 - 50) and Słone (TP 10 - 74) (Pukacz *et al.* 2014; Peczuła *et al.* 2014). More detailed studies would be required to establish whether the variability is random, or driven by some other factor such as water hardness, sediment structure, or other spectral characteristics of the water. For example, a TP-independent negative relationship has been found between charophyte abundance and DOC (Kłosowski *et al.* 2006). The relationship does not, however, preclude the existence of marl lakes (such as Cunswick Tarn) in peaty, wetland catchments (Pentecost 2000; Jones *et al.* 2011; Peczuła *et al.* 2014).

4.1.2 Nitrogen

Proxies for biological nitrogen availability were not measured in the sediment record and therefore the ecological impact of changing major nutrient stoichiometry could not be evaluated. However, atmospheric nitrogen deposition especially in the northwest of England has been high over the 20th century, particularly since the 1950s (Pitcairn and Fowler 1995), which in part reflects increases in nitrogen-rich fertiliser application (Fowler *et al.* 2005). In Cunswick Tarn, increases in fossil nitrogen-fixing *Gloeotrichia* colonies occurred in both cores around the 1900s and peaked in the 1920s-1930s (Supps 4, 7), suggestive of modest eutrophication (Laugaste and Lessok 2004) under conditions of nitrogen limitation (Vis *et al.* 2008; Hudon *et al.* 2009). Concentrations soon after declined to pre-1900 levels while *Cocconeis placentula*, a diatom with potential affinity to nitrogen-rich habitats (Werner 1977; Lebkuecher *et al.* 2014), increased in abundance. The transition corresponded with shifts towards angiosperm dominance and reduced macrophyte biomass in the lake, which may indicate a combined effect of nitrogen and phosphorus in shaping the biological eutrophication responses of Cunswick Tarn.

4.1.3 Climate

The Medieval Climate Anomaly (MCA) was a relatively warm period in the UK, and occurred ca AD 880–1350 (Guiot *et al.* 2010; Dong *et al.* 2012). The MCA was coincident with Zone 1 in the CUNS2 core record (ca 1260 – 1400), during which planktonic-dominated foodwebs in Cunswick Tarn were indicated by low macrophyte PVI (Fig. 6), an abundance of pelagic cladocerans, and relatively high concentrations of cyanobacterial pigments (Supps 2, 3). The presence of considerable concentrations of purple sulphur bacteria pigments further indicated hypolimnetic anoxia at this time. However, high total production was unlikely given low core P and Ca concentrations, the presence of cladoceran clearwater oligotrophic indicators *Alonella exigua* (Whiteside 1970; De Eyto *et al.* 2003) and *Chydorus piger* (Whiteside 1970; Bos and Cumming 2003), and the low concentration of Nymphaeaceae trichosclereids.

While it is plausible that warmer climate could have promoted primary production, effecting carbonate precipitation (Mullins 1998; Mirosław-Grabowska and Niska 2007), high relative abundances of plankton (Jeppesen *et al.* 2012), and high thermal stability in the water column leading to strong stratification and hypolomnetic anoxia (Viner 1985; Foley *et al.* 2012), it is likely that climate was a subsidiary rather than dominant driver of the observed changes. Firstly, interannual temperature variability was considerable through the MCA and the Little Ice Age in the UK (Cage and Austin 2010; Guiot *et al.* 2010), implying a more noisy signal should have been detected in the CUNS2 record if the biology was driven solely by temperature patterns. Secondly, numerical analyses of the biological data sets against variably smoothed April-September temperature reconstructions *(Guio*t et al. 2010) combined with Central England temperature time series (HadCET) revealed no detectable impact of temperature (data not shown). It remains possible that 1) climate effects were non-linear and 2) climatic conditions interacted with more discrete change within the catchment over the period between Zones 1 and 2.

4.1.4 Land clearance and DOC

Cunswick Tarn lies in a shallow depression in the landscape and would naturally have been surrounded by

alder carr habitat with shading willows in the margin. In ponds, strong chemical stratification and reduced biodiversity occur in response to shading, due to suppression of photosynthesis and high biological oxygen demand due to litter decomposition (Sayer *et al.* 2012). While more moderate effects are expected in slightly larger water bodies, it is plausible that dense margins could have had similar effects at Cunswick Tarn. Coppicing or marginal clearing for agriculture would have opened up the lake margins to light and increased benthic primary production and water column oxygenation, as suggested by the increase in inferred macrophyte PVI in Zone 2 (Fig. 6) and the disappearance of okenone (Supp. 2). While human impact in the catchment was likely, given the long history of the Cunswick Hall estate (Nicholson 1861), there are unfortunately no detailed records to support the hypothesis.

Some support for shading and DOC as drivers of ecological change can be found in the more recent history of the lake during which okenone has reappeared in the core record. The period coincides with the expansion of willows (*Salix* spp.) at the lake margins, bank erosion at the north end of the lake which has resulted in high DOC and suspended sediment loads, and strong chemical stratification with hypolimnetic anoxia in summer months.

4.2 Implications for management

Most change in the geochemistry and biology of Cunswick Tarn occurred in the late 1800s when larger-scale land improvement occurred in the catchment, consistent with European agriculture and population trends (Battarbee *et al.* 2011). Indeed, based on these trends, palaeolimnology-based reference status for lakes under the European Union Water Framework Directive (WFD: European Commission 2000) is typically derived from the pre-1850s (Bennion *et al.* 2011). Marl lakes fall under the WFD but are also a designated habitat under the EU Habitats Directive (European Commission 1992), hence required to achieve both Good ecological status and "favourable" conservation status, respectively. Sites with such dual designation are additionally considered 'protected areas' under WFD and are consequently given earlier deadlines for achieving their target objectives.

In order to comply with the targets of the river basin management plans, lake condition assessments, and extensive cross-validation of ecological metrics have been undertaken to ensure that effective measures are taken on correctly and consistently classified sites across Europe (Cardoso *et al.* 2007; Carvalho *et al.* 2009; Hering *et al.* 2013). However, concerns have been raised over the effectiveness of macrophyte and chlorophyll *a* metrics for assessing very shallow (Z_{mean} < 3 m) and shallow (Z_{mean} 3-15 m) marl lakes (Wiik *et al.* 2014), with Cunswick Tarn data in particular indicating shifting perceptions of good ecological status, and therefore assessment bias, for marl lakes. Further, this improved understanding of the pre-impact character of Cunswick Tarn has implications for how it is described, protected and restored under national nature conservation designnartions (SSSI); the Tarn is currently identified as a naturally eutrophic water body.

4.2.1 Implications for marl lake conservation assessment and reference status

The uncertainties regarding drivers of biological communities in the lowermost core record (Zones 1 and 2) hinder firm conclusions as to the reference status of Cunswick Tarn. Zone 1, where high DOC loads and/or warmer climate were potentially inferred, depicts the Tarn as an oligotrophic marl lake, with carbonate-precipitating *Chara aspera* and low densities of Nymphaeaceae (especially *N. alba*) in the shallow waters. Abundant organic matter influx created oxygen gradients in the deeper water, where *Nitella flexilis* agg. grew in low densities. The relatively high volume of open water allowed the development of planktonic foodwebs, with *Daphnia* and chaoborids in the deeper regions and *Bosmina longirostris* in the sublittoral (Fig. 8c). Zone 2, in contrast, portrayed oxygenated sediments, higher macrophyte PVI, and foodwebs based on benthic production with planktonic taxa largely absent.

Given the differences between zones 1 and 2, it is important to focus on their similarities to set guidelines for near-pristine status. For example, core carbonate content in both zones was low (< 10%) in the deeper water, with low inferred abundances of charophytes and other submerged macrophytes. Higher but still moderate levels of charophytes and carbonate (< 20%) occurred in the shallower margins (Fig. 3; Supp. 7) suggestive of charophyte-dominated marl benches (Jones *et al.* 2011). The relatively low levels of calcite deposition likely reflected the localised nature of marling in oligotrophic conditions, with calcite

supersaturation occurring primarily in the epilimnion and the littoral compared with dissolution in the deeper water (Gonsiorczyk *et al.* 1997; Ekdahl *et al.* 2004). Near-pristine conditions in Cunswick Tarn were therefore remarkably "non-marly".

In contrast to prevailing associations of dense charophyte meadows, and high production in the benthos, with high ecological quality, the Cunswick Tarn record has shown these characteristics to be an early response to eutrophication (Fig. 8b). The observation is not completely unexpected, considering that biomass responses to nutrient loading as a self-stabilising method in *Chara* lakes inherently imply that these characteristics are a symptom of eutrophication. Indeed, particularly dense (and in cases tall) growth of charophytes has been observed in lakes subject to considerable nutrient loading (Pełechaty *et al.* 2004; Haycock and Hinton 2010) in comparison with the more scarce and modest growth of charophytes in lakes of lower impact (Fuller 1741; Spence 1982; Praeger 1906), which was also indicated in the early record of Cunswick Tarn.

4.3.2 Management and restoration priorities

Cunswick Tarn is currently a marl lake only by geology, and is therefore considerably impacted. It is highly unlikely that conditions similar to the 13th – 18th centuries can be attained given the high load of P in the sediment, low flushing rates, and therefore high potential for internal loading in the lake. However, reductions of external nutrient loads are potentially the most effective means of restoring shallow lakes (Jeppesen *et al.* 2007), especially lakes such as Cunswick Tarn where fish manipulation is irrelevant, and should therefore be implemented as soon as possible. Unless nutrient availability for phytoplankton is restricted, charophytes will not be able to recolonise the Tarn. The most likely sources of nutrients to the Tarn are in the north where a drain pipe leads directly into the lake, and high nutrient concentrations have been measured in the inflow (December TP 44 µg L-1). Streams in the east woodland are likely to contribute less (December TP 14 – 20 µg L-1) Given the potential for hydrology to be complex in limestone catchments, an inclusive and larger scale approach to determining nutrient sources may be important.

Given the lags in macrophyte re-establishment in deeper water owing to the high light requirements of germlings and species with low growth forms (Wang *et al.* 2014), restoration of lake margins is especially important in sites with considerable water depth gradients (Hilt e*t al.* 2010). In this respect, the erosion occurring at the north end of Cunswick Tarn, exacerbated by the feeding of water fowl, is particularly damaging and should be prevented. High external DOC and suspended sediment loads lead to anoxic sediments unfavourable for charophytes (Smith 2003; Sederias and Colman 2009) and maintain conditions suitable for reeds and Nymphaeaceae which are currently dominant.

Tree clearance would further open up light-flooded marginal habitat for charophyte re-establishment, however, could also be seen as interference with natural succession of trees in the lake surrounds. It is therefore a judgement call of whether moderate interference promoting biodiversity (e.g. Sayer *et al.* 2012, see also Flöder and Sommer 1999) is to be preferred over gradual natural successions following neglect (e.g. Biggs *et al.* 2005). Considering the large-scale, centuries-long human alteration of the natural landscape of the UK including the eradication of top predators, and the high global conservation priority of preventing further biodiversity losses (European Parliament 2012), coppicing around the lake would be strongly advisable.

5 Conclusion

Biological community shifts in Cunswick Tarn demonstrated synchroneity in response to gradual eutrophication pressure. Drainage of the lake and land improvement in the lake surrounds in the 1890s led to sub-decadal responses in multiple biological groups (microalgae, macrophytes, molluscs, arcellaceans, cladocerans) and substantial increases in carbonate precipitation. Further abrupt ecosystem shifts occurred in the 1920s, 1930s, and finally the 1990s when the lake changed into its current condition of low macrophyte diversity, high pelagic production, reduced macrophyte colonisation depth and predominance of nutrient-tolerant micro- and macrophyte taxa. The patterns of rapid ecosystem-wide change, partly decoupled from the change in core P, supported ideas of abrupt responses to eutrophication as well as the importance of internal dynamics such as the self-sustaining capacity of charophyte beds, in shaping

ecological lake structure.

As predicted, variance in marl lake biological communities correlated with both Ca and P as expected for marl lake communities responding to external nutrient load. Somewhat surprisingly, the period of least impact in the Tarn was characterised by very low carbonate precipitation in the deeper water, with marling restricted to the shallower littoral zone where charophyte meadows occurred. It is likely that pristine marl lakes do not achieve sufficient levels of photosynthesis for ubiquitous authigenic carbonate precipitation, and macrophyte cover is quite low.

The detection of two periods of accelerated change over intermediate core P concentrations support hypotheses of high eutrophication sensitivity of benthic communities in marl lakes, especially considering the modest concentration of TP in Cunswick Tarn currently (ca 56 µg L^{-1}). Importantly, interpretations of high benthic biomass and calcite deposition as high ecological condition may be biased, reflecting a shift in perception due to the scarcity of truly high quality examples of marl lakes. The complete loss of marl lake biology in Cunswick Tarn argues strongly for restoration interventions at early stages of eutrophication in order to preserve characteristic marl lake communities. Further, if similar lake type transformations have occurred in other (formerly) marl lakes, perceptions of their geographical distribution and scarcity may be misguided.

6 Acknowledgements

7 References

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Table 1

Radiometric sample information

Depth (cm)		Sample type	Material				Sample ID

RDA-based correlations and p values of Ca and P over biological data

Group	n	%VarExp		cyclic p		free p	
		Ca	P	Ca	P	Ca	P
Pigments	54	23	37	.39	.02*	.001***	NA
Cladocerans	18	27	30	.22	.06+	.002**	.002**
Testate ameobae	18	13	15	.88	.55	.02*	.009**
Macrofossils	15	26	20	.13	.40	.002**	.003**

Table 2

RDA-based correlations and p values of Ca and P over biological data

Group	n	%VarExp		cyclic p		free p	
		Ca	P	Ca	P	Ca	P
Pigments	54	23	37	.39	.02*	.001***	NA
Cladocerans	18	27	30	.22	.06+	.002**	.002**
Testate ameobae	18	13	15	.88	.55	.02*	.009**
Macrofossils	15	26	20	.13	.40	.002**	.003**

Figure captions:

1. Cunswick Tarn location and bathymetry, showing the core collection sites and water depths.

2. CUNS2 core chronology.

3. Carbonate concentrations in cores CUNS1 and CUNS2, shown with calendar years obtained by 210Pb-dating of CUNS2 with errors in parentheses.

4. Ca and P, and PCs of biological groups against time. Horizontal lines indicate MRT-derived splits, those dashed to aid inspection indicate least importance.

5. Summary plot of CUNS2 Ca, P, and key absolute and relative abundance changes of biological groups against time.

6. Cladoceran-inferred August Plant Volume Infestation and zooplanktivorous fish abundance of CUNS2 sample depths (cm).

7. Rate of change in P and ecological distances between consecutive samples of biological groups, ranged between 0 and 1.

8. Cross sections of macrophyte cover, showing the currently dominant community, and historical communities based on available historical data.
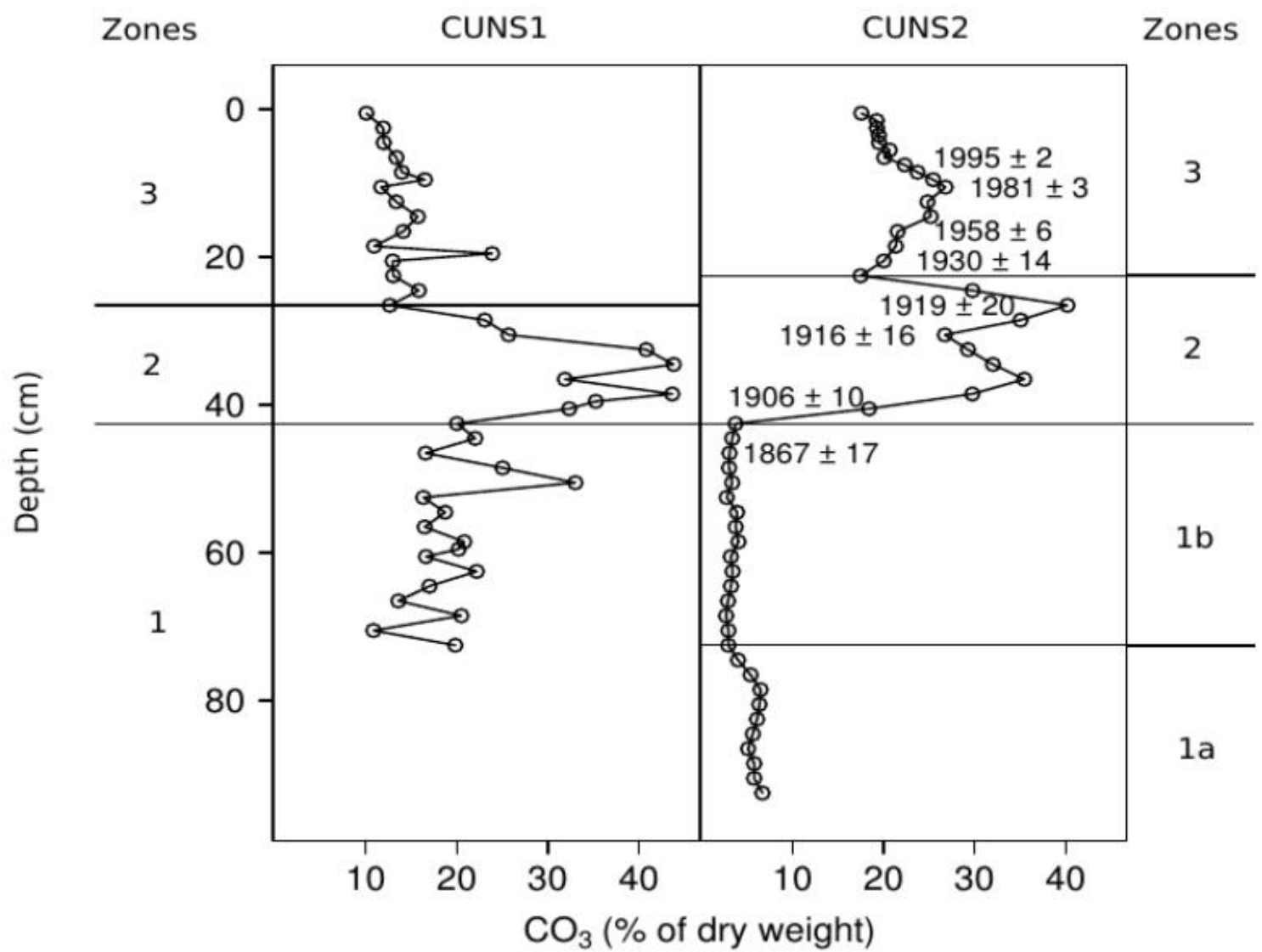
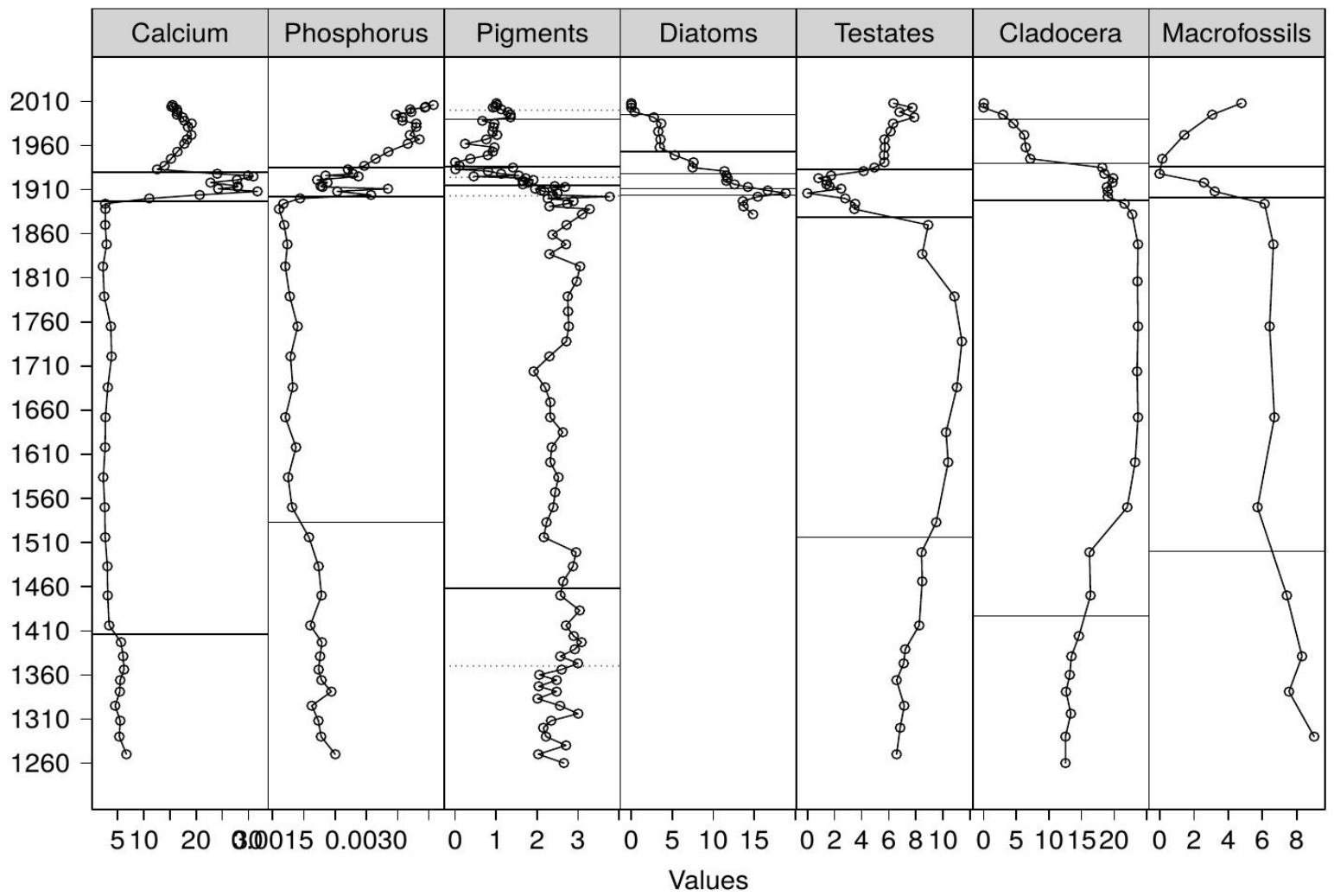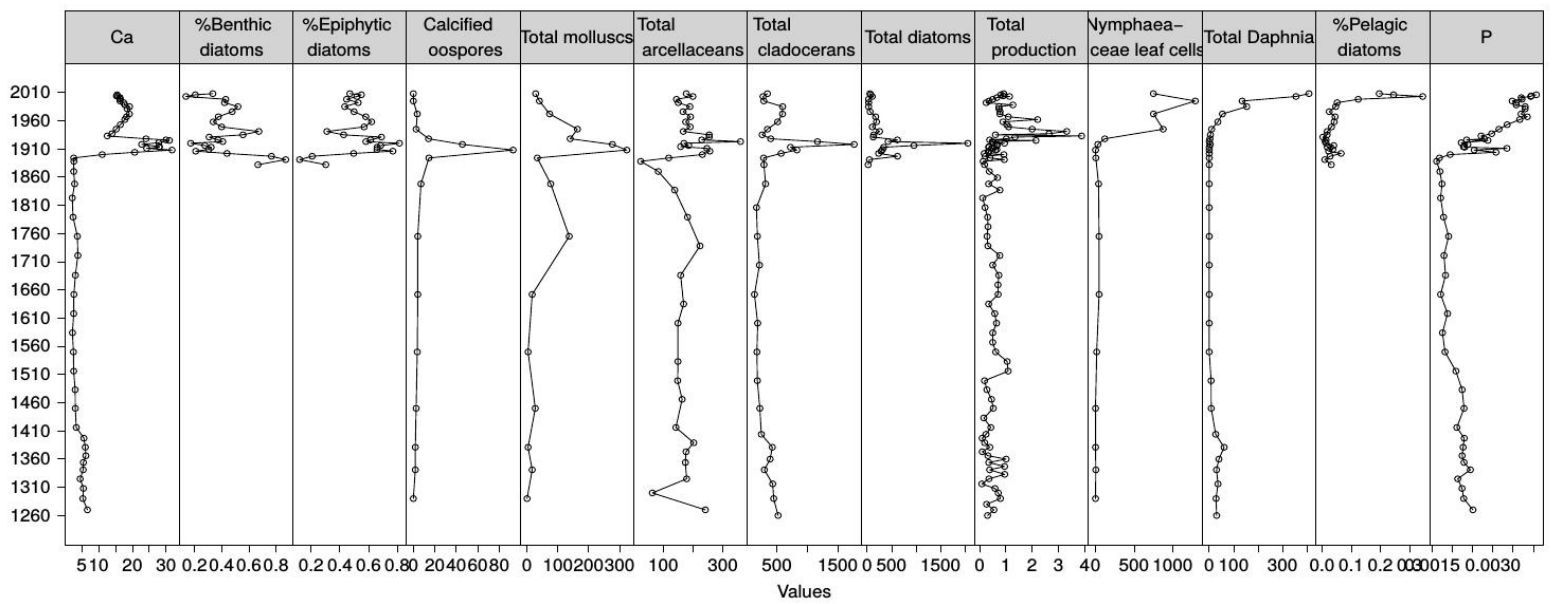Figure 1.JPEG
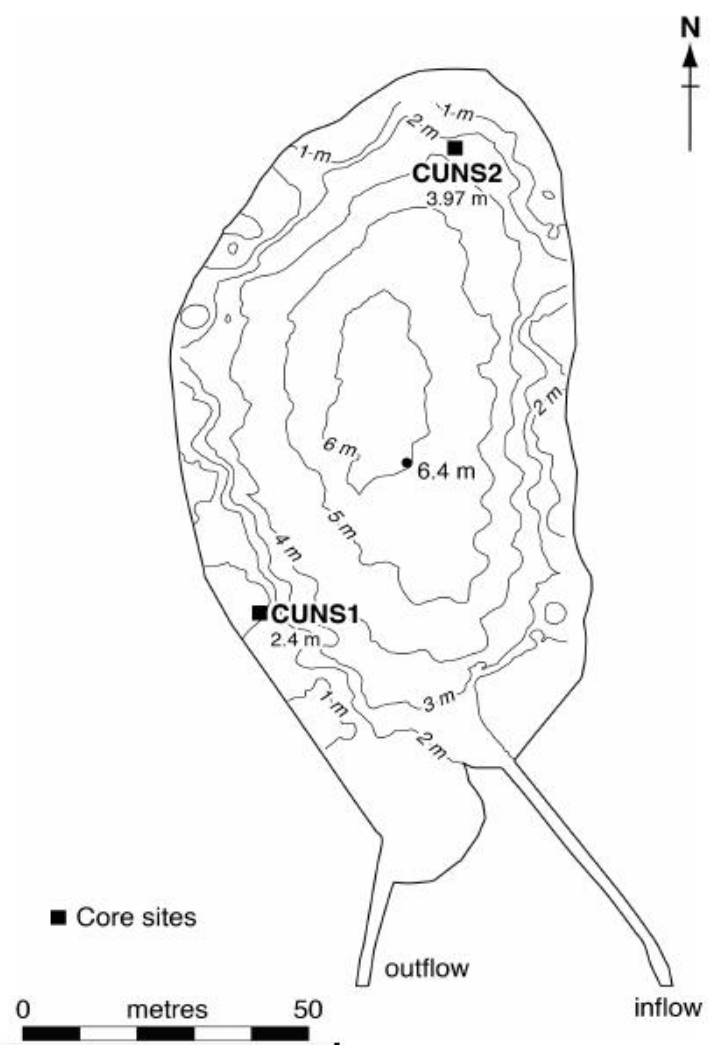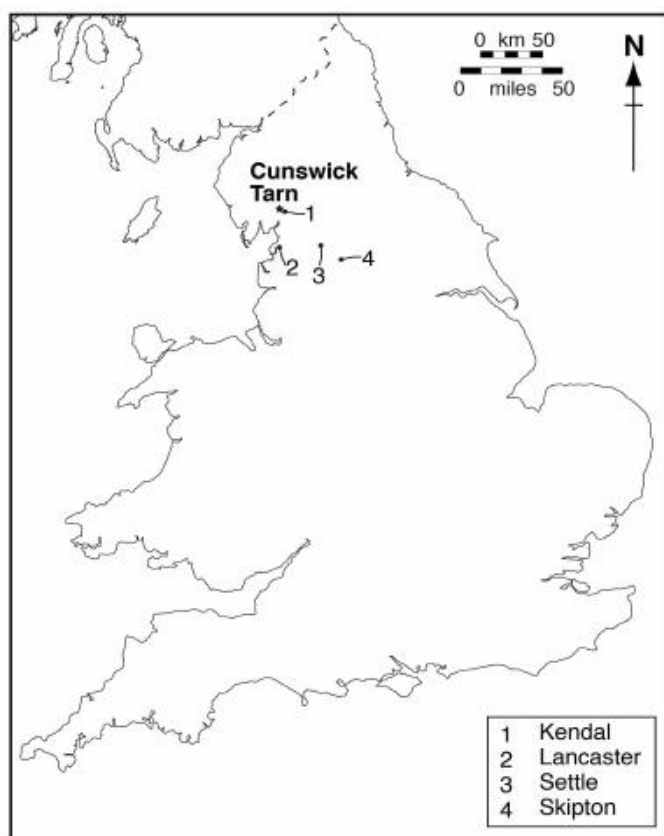
Figure 2.JPEG
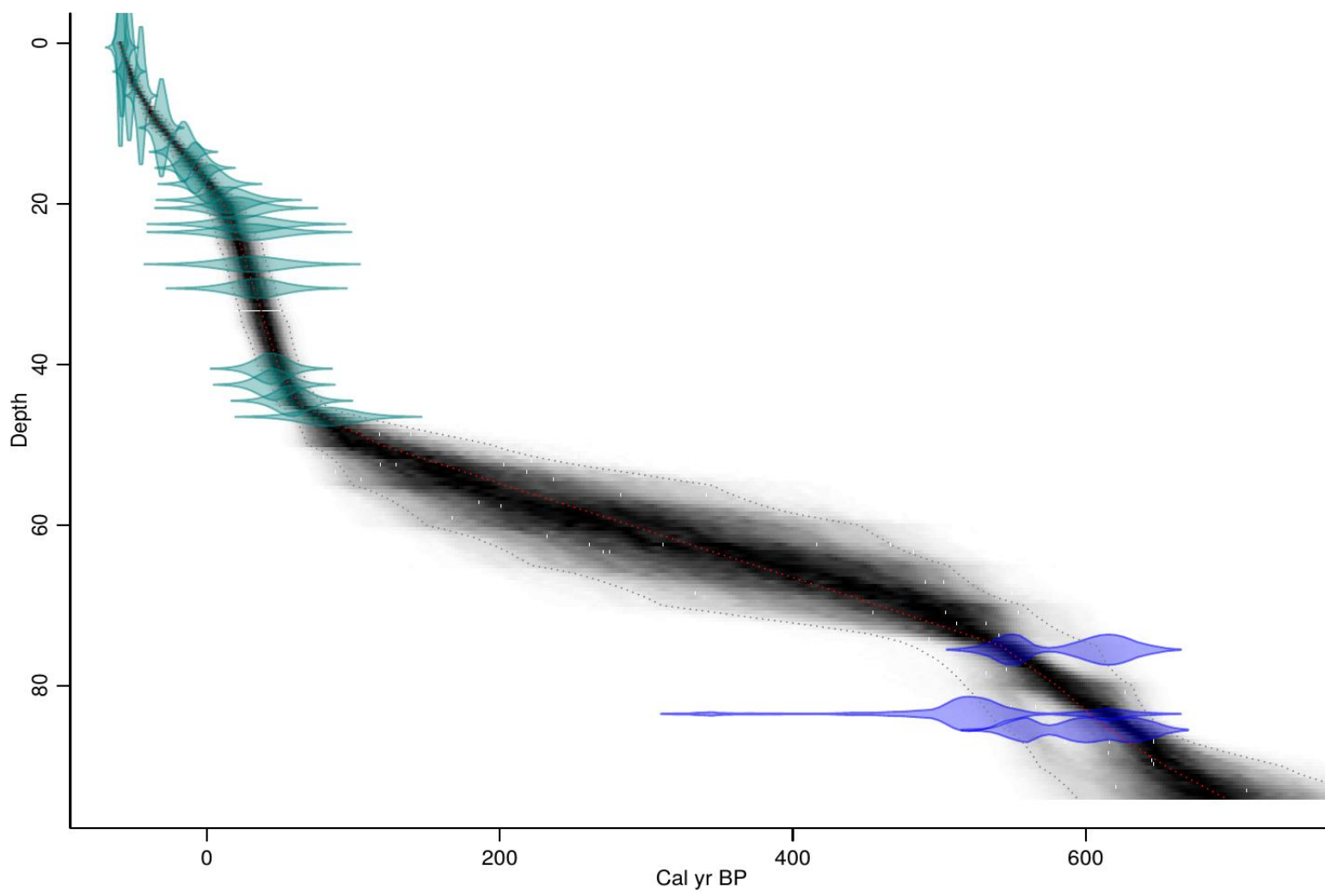
Figure 3.JPEG

Figure 4.JPEG

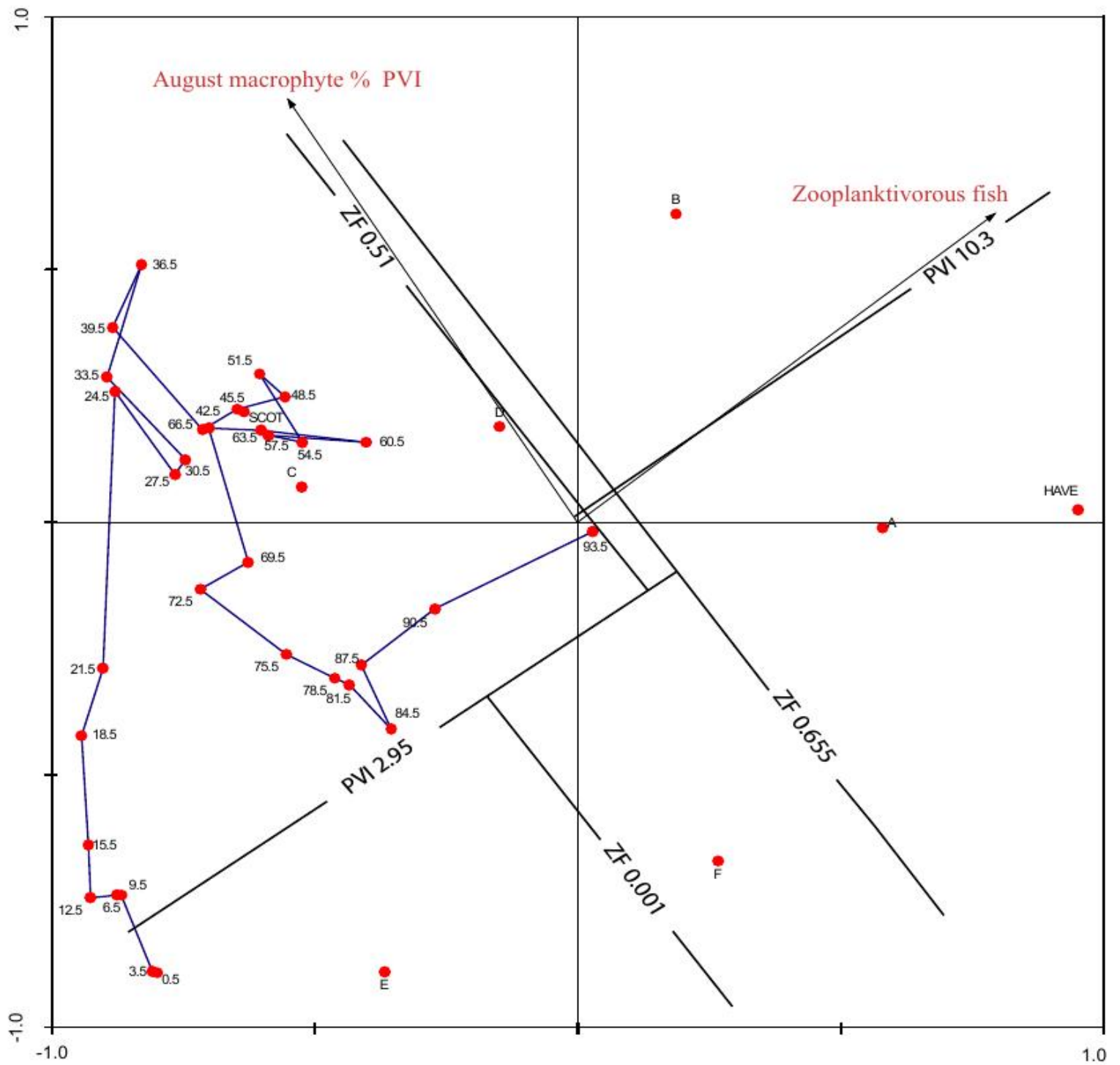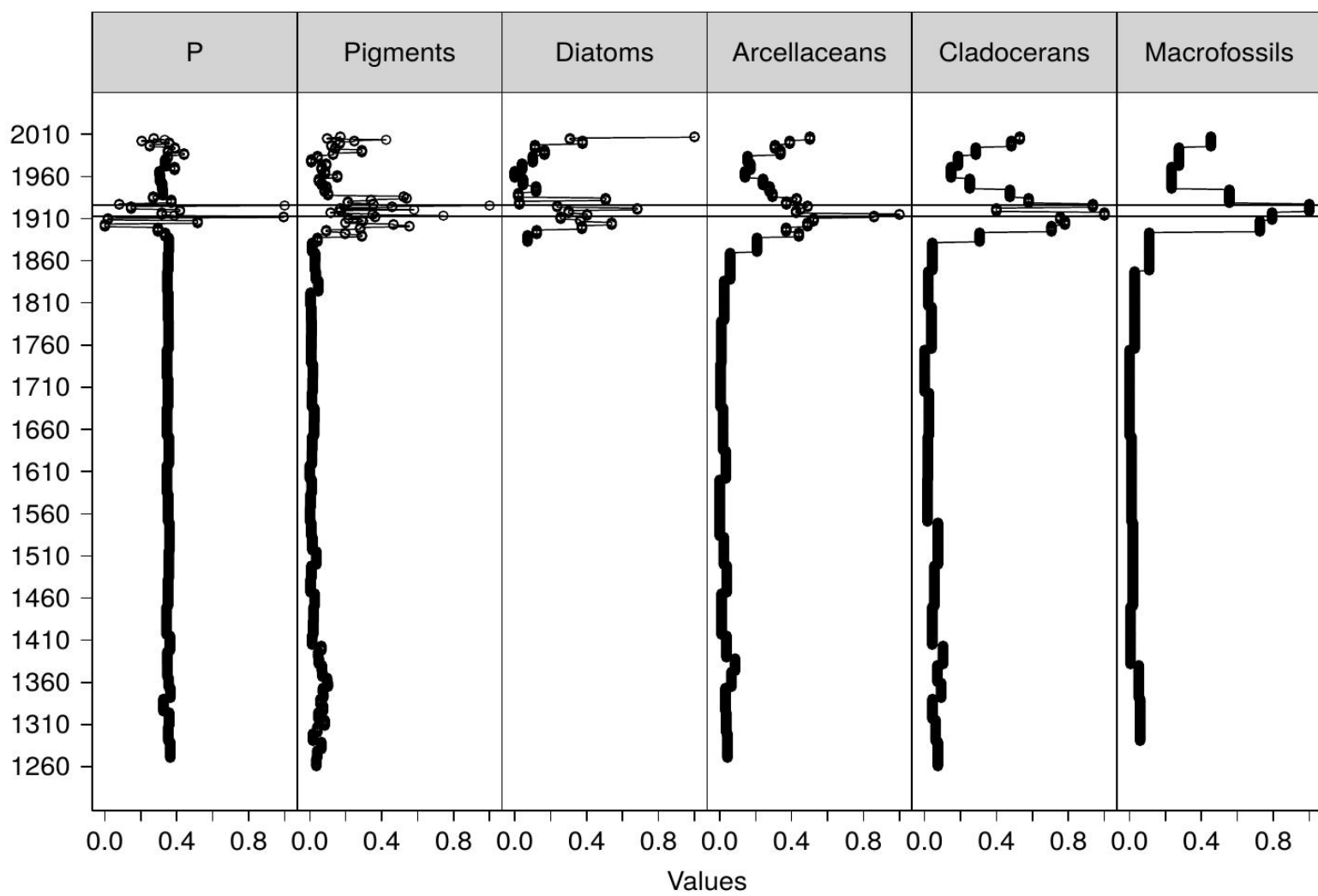Figure 5.JPEG

Figure 6.JPEG

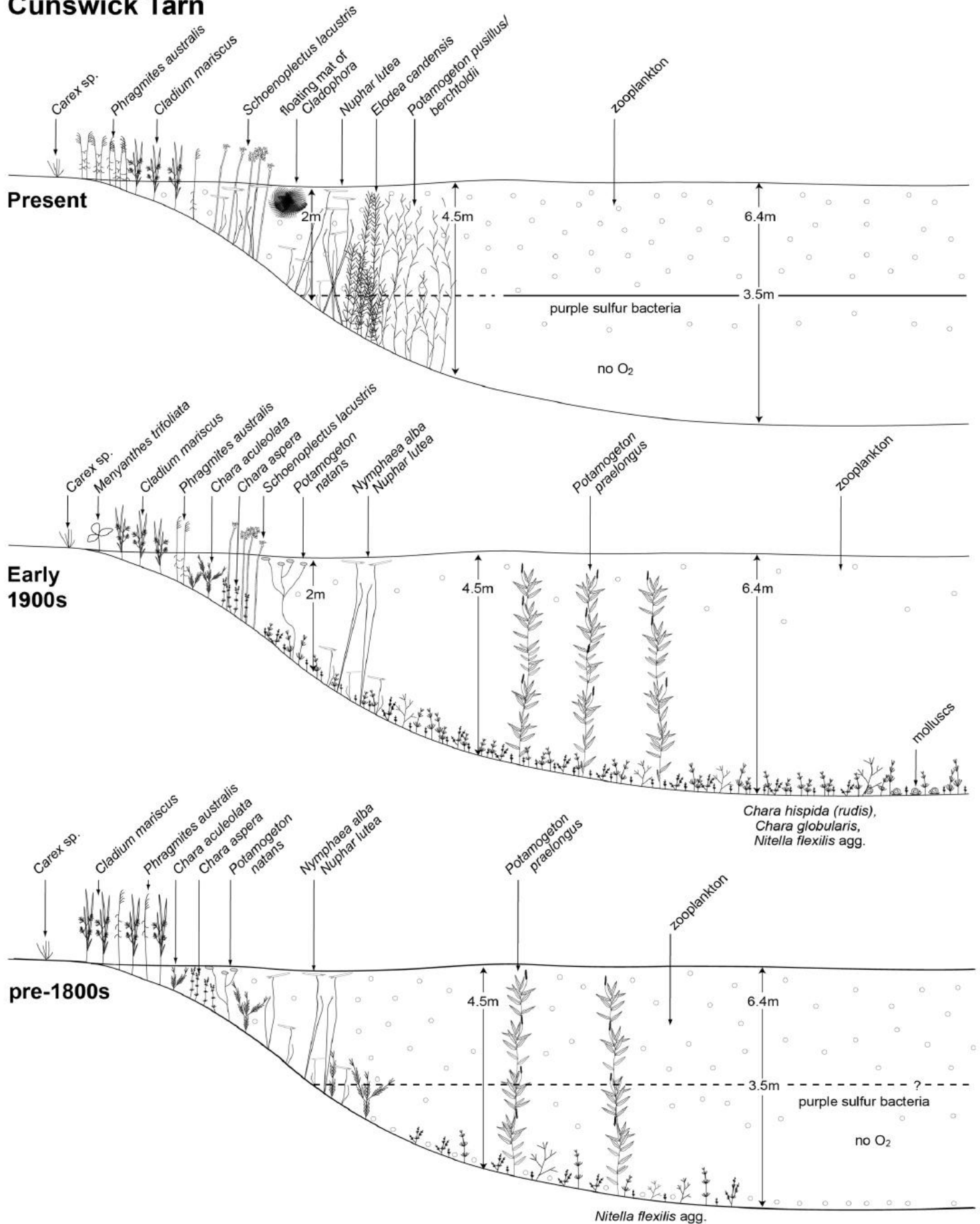Figure 7.JPEG

Figure 8.JPEG

Cunswick Tarn

Figure 4.23: Cross sections of macrophyte cover, showing the currently dominant community, and historical communities based on available historical data.