

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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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 spanning ca. 1260–2009 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. Analyses 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.

Keywords: marl lake, chara, palaeolimnology, eutrophication, lake management, ecological quality, cladocera, macrofossils

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 homogenization, as well as nutrient loading and sediment losses from terrestrial to aquatic habitats especially over the twentieth 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 habitats. 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 are 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 characterize 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 Medieval, 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 color of high transparency (Spence, 1982). Owing to the immobilization of phosphorus (P) via coprecipitation with calcite, which occurs with the highest intensity during summer months,

marl lakes have widely been held resistant to eutrophication (Wiik et al., 2013). However, the immobilization of P may be restricted temporally (e.g., dissociation in winter) and spatially (e.g., dissociation in hypolimnion/sediment) (Wiik et al., 2013), and P may be recycled in the sediment via uptake by macrophytes. Therefore, substantial changes in the benthos may occur despite low limnetic P. Indeed, even minor increases in limnetic nutrient availability have been linked to substantial changes in macrophyte communities (Krause and King, 1994; Free et al., 2007) and extirpations of key biodiversity species at a European scale (Stewart, 2001; Blaženič 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. This may be especially true for marl lakes should further empirical support for sensitivity of their benthic communities arise.

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 color. It would not, therefore, be biologically categorized 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 currently exist to characterize the unimpacted “reference status” ecology (European Commission, 2000) of the site. In order to elaborate on concepts of marl lake ecology and -reference status, a multi-indicator palaeolimnological approach was undertaken with specific aims to (1) establish the centennial-scale temporal patterns of change (gradual/abrupt) across biological groups, thereby testing theories of resistance of marl lake benthic communities to enrichment, (2) test whether ecological change was limited to one or two biological groups or whether it was apparent at an ecosystem level (physical–chemical function; multiple biological groups at all observed trophic levels; synchronicity across responses), and (3) compare the core record evidence of reference condition with prevailing descriptions of high ecological status for marl lakes.

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 abundance of fossil 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, 1992; Ayres et al., 2008; Sayer et al., 2010) as well as of groups of algae and cladocerans that reflect increased nutrient availability and functional change toward increasingly pelagic shallow lake ecology (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 calcium (Ca) and P were expected to be significant correlates of biological community composition.

Methods

Study Site

Cunswick Tarn (SD489937) is a small (0.8 ha), fishless, relatively shallow ($Z_{\max} = 6.4$ m; $Z_{\text{mean}} = 3.7$ m) kettlehole lake in Cumbria, UK (Figure 1). The limestone catchment comprises improved pasture to the north and west, and woodland along a sheltering hillside to the east. A low-gradient outflow lies in the southwest corner (Figure 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 (Figure 1). Water high in 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 lake. The Tarn is currently eutrophic with mean annual total phosphorus (TP) of $56 \mu\text{g L}^{-1}$. 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).

Core Collection

Two littoral sediment cores were taken from Cunswick Tarn (Figure 1). CUNSI (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 (LOI) in CUNSI confirmed a lakewide signal. The cores were extruded at 1 cm intervals, and sediment samples for pigment analysis (CUNS2) were placed in separate bags and frozen.

Core Chronology and Lithostratigraphy

Core CUNS2 was dated by a combination of ^{210}Pb and ^{14}C accelerator mass spectrometry (AMS) methods. Freeze-dried sediment samples were analyzed for ^{210}Pb , ^{226}Ra , ^{137}Cs , and ^{241}Am by direct gamma assay in the Bloomsbury Environmental Isotope Facility 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) (Table 1). For samples under $100 \mu\text{g C}$, 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 modeled 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 LOI following Dean (1974). P and Ca in CUNS2

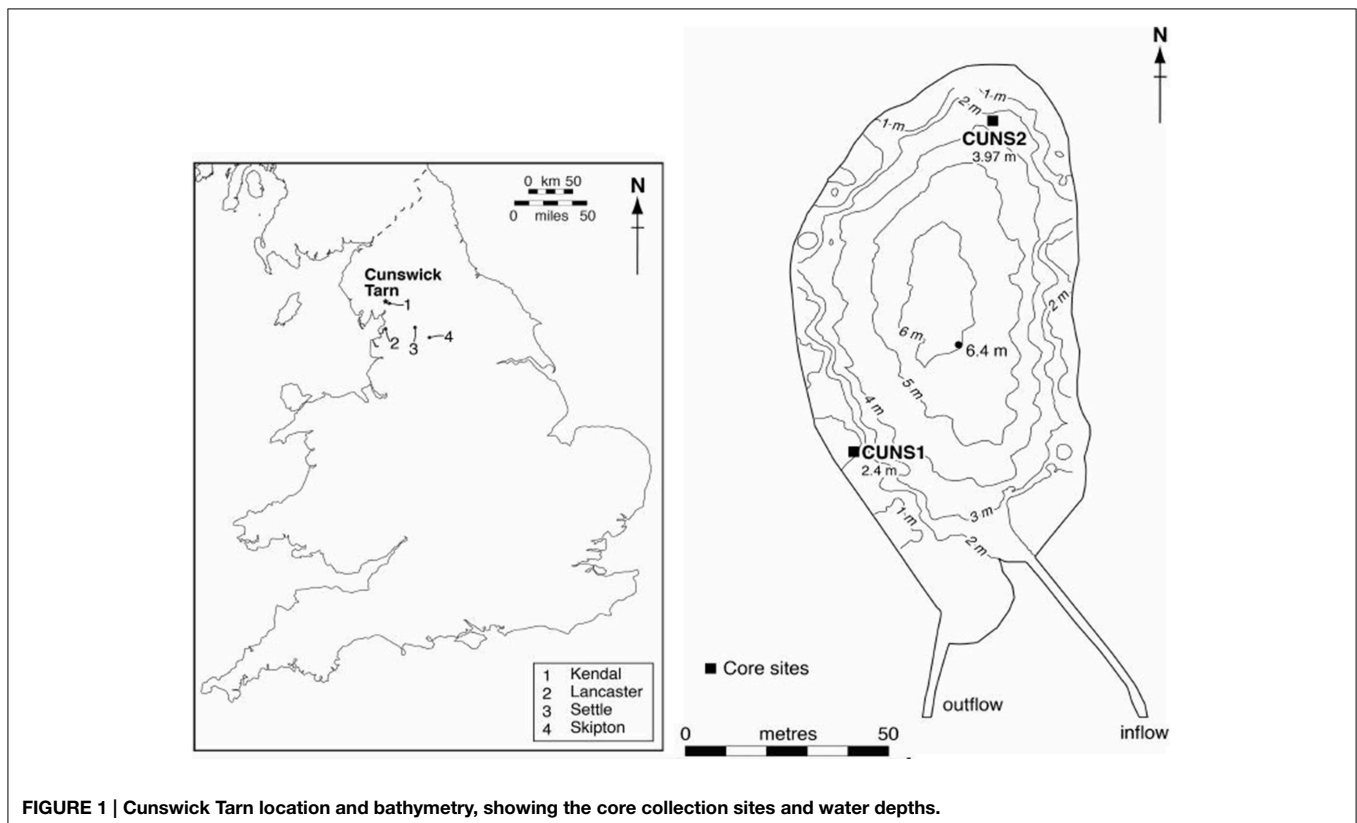


FIGURE 1 | Cunswick Tarn location and bathymetry, showing the core collection sites and water depths.

TABLE 1 | Samples used to create the dating profile of CUNSS2.

Depth (cm)	Sample type	Material	Sample ID
0.5, 3.5, 6.5, 10.5, 13.5, 15.5, 17.5, 19.5, 20.5, 22.5, 23.5, 27.5, 30.5, 40.5, 42.5, 44.5, 46.5	²¹⁰ Pb	Bulk sediment	
75.5	¹⁴ C (AMS)	Terrestrial leaf fragments, <i>Bidens cernua</i> seed	UCIAMS-144613
83.5	¹⁴ C (AMS)	Terrestrial leaf fragments, <i>Betula</i> fruit, stems	SUERC-48875
83.5	¹⁴ C (AMS)	Terrestrial leaf fragments	UCIAMS-144614

Sample ID: Laboratory identifier for radiocarbon samples. (see Appendix 2 in Supplementary Materials for further information on the CUNSS2 profile).

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 CUNSS2 carbonate $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were measured at 5 cm intervals at the Natural Environment Research Council (NERC) Isotope Geosciences Laboratory (Keyworth, UK). Samples were disaggregated in 5% sodium hypochlorite solution (10% chlorox) for 24 h 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 CO₂ for measurement. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are reported as per mil (‰) deviations of the isotopic ratios ($^{18}\text{O}/^{16}\text{O}$, $\delta^{13}\text{C}/\delta^{12}\text{C}$) calculated to the Vienna Pee Dee Belemnite scale using a within-run laboratory standard calibrated against National Bureau of Standards standards. The patterns in $\delta^{18}\text{O}$, and between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, were used to determine changes between open and closed conditions in the lake following Leng and Marshall (2004) and Leng et al. (2006), with consideration to disequilibrium values following *Chara* stem and oospore calcification (Andrews et al., 2004).

Biological Groups

Analysis of chlorophyll and carotenoid pigments followed Moorhouse et al. (2014) and was undertaken at all levels of CUNSS2. Diatom analysis of CUNSS2 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. Identification was carried out with reference to Krammer and Lange-Bertalot (1986, 1988, 1991, 2004). All identifications were to species level excepting *Gomphonema pumilum* and *Gomphonema angustum* (see Kelly et al., 2008) which were aggregated as *Gomphonema angustum* (agg.).

Testate amoebae were analyzed roughly at 2–3 cm intervals throughout the core. Subsamples of 2 cm³ were wet sieved through a 250 μm mesh to remove coarse organic flocs 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, in accordance with Patterson and Fishbein (1989), were quantified to >150 specimens per sample where abundance was permitting. Species and strains were identified according to lacustrine testate amoeba keys (Medioli and Scott, 1983; Kumar and Dalby, 1998) and published scanning electron micrographs (Roe et al., 2010; Patterson et al., 2012). Due to the significant amount of morphological variability in lacustrine testate amoebae (Medioli and Scott, 1983), a strain-based nomenclature was adopted in accordance with other lacustrine researchers (Escobar et al., 2008; Kihlman and Kauppila, 2012; Patterson et al., 2012), in order to include these “ecophenotypes.”

Subfossil cladocerans were analyzed at 3 cm intervals for CUNSS2 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 of *Daphnia pulex* were aggregated to *Ceriodaphnia* and *Daphnia* spp. Morphological plasticity of *Chydorus* remains was interpreted as variability within *Chydorus sphaericus sensu lato*. *Bosmina longirostris* was the only species of *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).

Macrofossil analysis followed Sayer et al. (2010) and was undertaken at every 6 cm of CUNSS2, and for 16 levels of CUNSS1. Macrofossils were identified using a dedicated reference collection of plant and animal parts and relevant publications held at UCL Geography. Where species-level detail was not attainable, remains were aggregated. These included *Daphnia hyalina* agg. ephippia (UK species other than *D. magna* and *D. pulex*), *Potamogeton pusillus* + *berchtoldii* leaf tips (*P. pusillus* and *P. berchtoldii*) and Nymphaeaceae trichoscleroids, i.e., leaf cells (*Nymphaea alba* and *N. lutea*). Molluscs were mostly identified to family or genus level. Owing to morphological plasticity, charophyte oospores were aggregated as *Chara* spp. for numerical purposes. However, morphotypes were also tentatively identified using reference collection material and an oospore key (Haas, 1994). Uncalcified and calcified oospores were counted separately.

Historical presence of fish in CUNSS2 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*.

Historical Evidence

Diagrammatic reconstructions of the macrophyte communities and colonization depths in Cunswick Tarn for the present, the mid-1900s, and the late 1800s/early 1900s were constructed based on (1) the CUNSI and CUNSI2 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).

Statistical Analysis

All data analysis was performed with R version 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 CUNSI2 data owing to the low resolution of the chronology for CUNSI1.

Diatom and testate amoeba data were transformed into percentage abundances and taxa with <5% abundance and less than five 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_{10}) -transformed and normalized with respect to organic matter, respectively. Cladoceran data were transformed into percentage data for principal curves and multivariate regression trees (MRT), and square-root transformed for all analyses. Finally, pigment data were further standardized to abundances between 0 and 1 to reduce the statistical effects of "abundant" pigments (low degradation, high preservation).

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 CUNSI2 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).

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, testate amoebae, cladocerans, macrofossils) for all analyzed levels using age (in years 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), and to test for synchronicity in change across indicators (ecosystem change). 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), $n = 39$ (testate amoebae), $n = 32$ (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).

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 0.05 level (e.g., $1/18 = 0.056$). Therefore, although too liberal, permutation tests were also performed without restrictions.

Results

Core Chronology and Lithostratigraphy

Core CUNSI2 spanned a period of approximately 1260–2009 AD (date of core collection) with highest age uncertainties in the middle section of the core (46.5–75.5 cm; **Figure 2**). The gap in measured ages was unavoidable given the constraints of the time spans of ^{210}Pb (to ca. 150 years from present) and radiocarbon dating (minimum age several hundreds of years). Sedimentation rates (SRs), core carbonate (**Figure 3**), and Ca (Supp. 1 in Supplementary Material) 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 $\rho = 0.97$, $p < 0.001$).

Four carbonate zones were apparent in CUNSI2 (**Figure 3**) and were used as Zones for all Diagrams in Supplementary Materials, and as sections for presentation of biological data results. Zone 1 encompassed the base of the core (92.5 cm; 1250s) to the early 1400s, characterized by relatively low carbonate content (<10%), low variability, and low SR (ca. $0.12 \text{ cm year}^{-1}$). Carbonate and SR were at their lowest values in Zone 2 (ca. 5% and $0.07 \text{ cm year}^{-1}$, respectively), which encompassed the 1400s (72.5 cm) to the 1890s (42.5 cm). Zone 3 (42.5–22.5 cm) encompassed substantial increases in carbonate and SR (to ca. 1 cm year^{-1}), with two carbonate peaks of 36% and 40% (1920s) followed by a rapid decline (ca. 10 years). Slightly lower carbonate (ca. 20–30%)

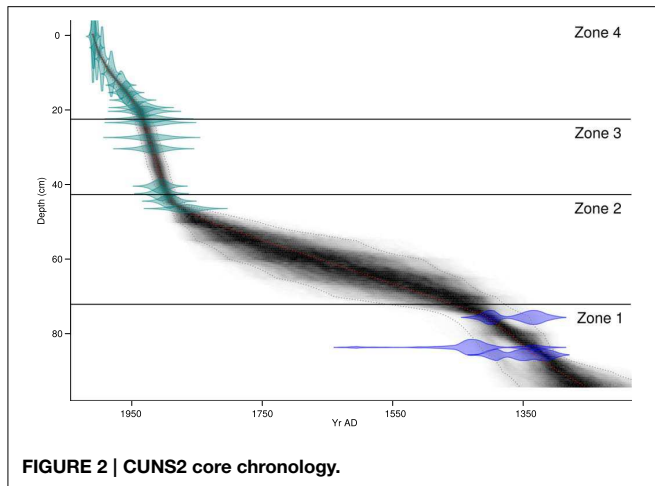


FIGURE 2 | CUNSS2 core chronology.

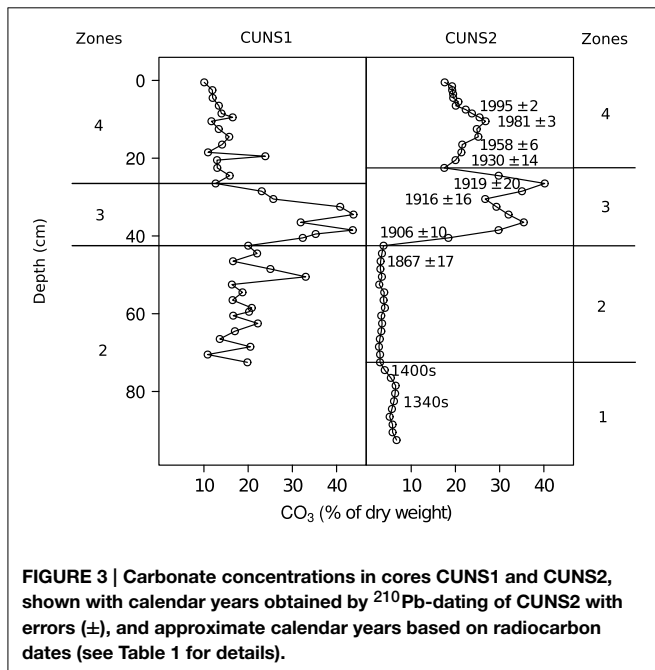


FIGURE 3 | Carbonate concentrations in cores CUNSS1 and CUNSS2, shown with calendar years obtained by ^{210}Pb -dating of CUNSS2 with errors (\pm), and approximate calendar years based on radiocarbon dates (see Table 1 for details).

and SRs (ca. $0.2\text{--}0.5\text{ cm year}^{-1}$) occurred in Zone 4 from the 1930s (22.5 cm) to 2009 (core top).

CUNSS1 followed a similar carbonate pattern to CUNSS2, allowing cross-correlation to estimate the chronology of CUNSS1 (Figure 3). A CUNSS1 parallel for CUNSS2 Zone 1 was not appropriate owing to the brevity of the CUNSS1 sequence and differences in carbonate concentration in this core section. The zone limits for CUNSS1, therefore, are Zone 2: core base to 42.5 cm (base to ca. 1890s), Zone 3: 42.5–26.5 cm (1890s–1930s), and Zone 4: 26.5 cm to top (1930s–2008) (Figure 3). Higher carbonate concentrations than in CUNSS2 were found in Zone 2 (ca. 20% vs. ca. 5%), and similar carbonate peaks ($>40\%$) occurred in Zone 3.

CUNSS2 carbonate $\delta^{18}\text{O}$ could not be measured for most of Zone 2 owing to insufficient carbonate (data not shown). Therefore, only 14 samples were analyzed, five of which were in

Zones 1 and 2 and had highly variable $\delta^{18}\text{O}$ out of equilibrium with rainfall (-3 to -6‰), indicating a hydrologically closed system (Leng and Marshall, 2004; Leng et al., 2006). The uppermost nine samples ranged between -6 and -7‰ and were in equilibrium with rainfall, indicating that CUNSS2 Tarn became a hydrologically open system between the 1890s and 1900.

CUNSS2 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 (Supp. 1 in Supplementary Material). Ranged between 0 and 1 for simplicity, the lowest concentrations occurred before the 1530s (0.5–0.6) and between the 1530s and the 1890s (0.4–0.45). Rapid increases occurred in the early 1900s coincident with increases in Ca, with concentrations between 0.55 and 0.8. From the 1930s to 2009, concentrations increased consistently from 0.7 to 1 (Supp. 1 in Supplementary Material).

Zone 1: ca. 1250–1400 (CUNSS2 Only; No Diatom Data)

Pigments of algae, higher plants, and cyanobacteria were low in Zone 1 (Supp. 2 in Supplementary Material). 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 sulfur 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 (Supp. 2 in Supplementary Material).

The testate amoeba community (Supp. 3 in Supplementary Material) in this zone included moderate abundances of *Diffflugia oblonga* (Ehrenberg, 1832) strain “oblonga” (ca. 15–30%), often associated with organic rich substrates (Kihlman and Kauppila, 2012), and *Centropyxis aculeata* (Ehrenberg, 1832) strain “aculeata” (ca. 10–25%). Lesser proportions consisted of *Arcella vulgaris* (Ehrenberg, 1830) (ca. $<10\%$), *Centropyxis constricta* (Ehrenberg, 1843) “aerophila” and the oligotrophic indicator *Cyclopyxis kahli* (Deflandre, 1929) (Schönborn, 1967; Wall et al., 2010). The eutrophic indicator species *Cucurbitella tricuspidis* (Carter, 1856) (Medioli and Scott, 1983) was also present in small amounts ($<5\%$).

Remains of pelagic cladocerans at the base of the core were relatively abundant, and declined slightly toward the upper end of the zone (e.g., *Bosmina longirostris*/spp. 42% to $<10\%$) (Supp. 4 in Supplementary Material). Other filter-feeding and/or pelagic species included *D. 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. 5 in Supplementary Material). Oblong

Plumatella sp. statoblasts were particularly abundant in Zone 1 compared to the rest of the core (Supp. 6 in Supplementary Material). Mollusca were largely absent with the exception of Sphaeriidae.

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 in Supplementary Material). Benthic species (e.g., *Pseudostaurosira brevistriata* ca. 50–60%) dominated the CUN2 diatom record at the latter end of the Zone (three samples counted), forming 60–80% of the community (Supp. 7 in Supplementary Material). Periphytic taxa formed 10–30% of the community and included *Gomphonema angustum* and *Amphora pediculus*, while planktonic species accounted for <5% (Figure 4). *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 testate amoeba taxa (Supp. 3 in Supplementary Material) included gradual increases in *Cucurbitella tricuspis* (to ca. 23%), before rapidly declining in the mid nineteenth century, and decreases in *Diffflugia oblonga* “oblonga.” *Centropyxis constricta* “aerophila” and *Arcella vulgaris* increased in abundance, while *Cyclopyxis kahli* remained in lesser proportions.

Diversity and total abundance of cladocerans were at their lowest in Zone 2, and pelagic taxa were rare (Supp. 4 in Supplementary Material, Figure 4). 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 CUN2 (Supp. 8 in Supplementary Material), planktonic *Ceriodaphnia* spp. ephippia were abundant ($n > 1000 \times 100 \text{ ml}^{-1}$) at the beginning of Zone 2 (ca. 1400–1500s), followed by consistent decreases to the upper end of the zone ($n < 100 \times 100 \text{ ml}^{-1}$).

In CUN2 Zone 2, there were fewer plant macrofossils of both terrestrial and aquatic origin compared with Zone 1 (Supp. 5 in Supplementary Material). Whilst species composition was similar, Charophyta differed as *Nitella* spp. were absent and *C. hispida* agg. dominated. In CUN1, there were high abundances of calcified *Chara aspera* oospores in Zone 2, which was not recorded in CUN2 (Supp. 9 in Supplementary Material, Figure 4). One other submerged macrophyte species, *Potamogeton praelongus* (CUN1), occurred in this Zone. Floating-leaved macrophyte remains included Nymphaeaceae trichoclereids (leaf cells), occurring in CUN1 and CUN2 at slightly higher abundance than in Zone 1, and increasing substantially toward the end of Zone 2 in CUN1 (Supps 5, 9 in Supplementary Material). Only *N. alba* seed remains were recorded, although *N. lutea* occurred in the Tarn in the early 1800s (Baker, 1885). *Potamogeton natans* seeds occurred throughout this Zone (CUN1). Mollusc remains were more diverse and abundant in Zone 2 compared with Zone 1 (Supp. 6 in Supplementary Material, Figure 4). In CUN2, the Sphaeriidae dominated the record (maximum of $n = 50\text{--}100 \times 100 \text{ ml}^{-1}$) whereas in CUN1 several different taxa became more abundant toward the latter part of the Zone (*Bithynia leachi/tentaculata*, *Planorbis* cf. *albus*, *Valvata* cf. *macrostoma*) (Supp. 8 in Supplementary Material).

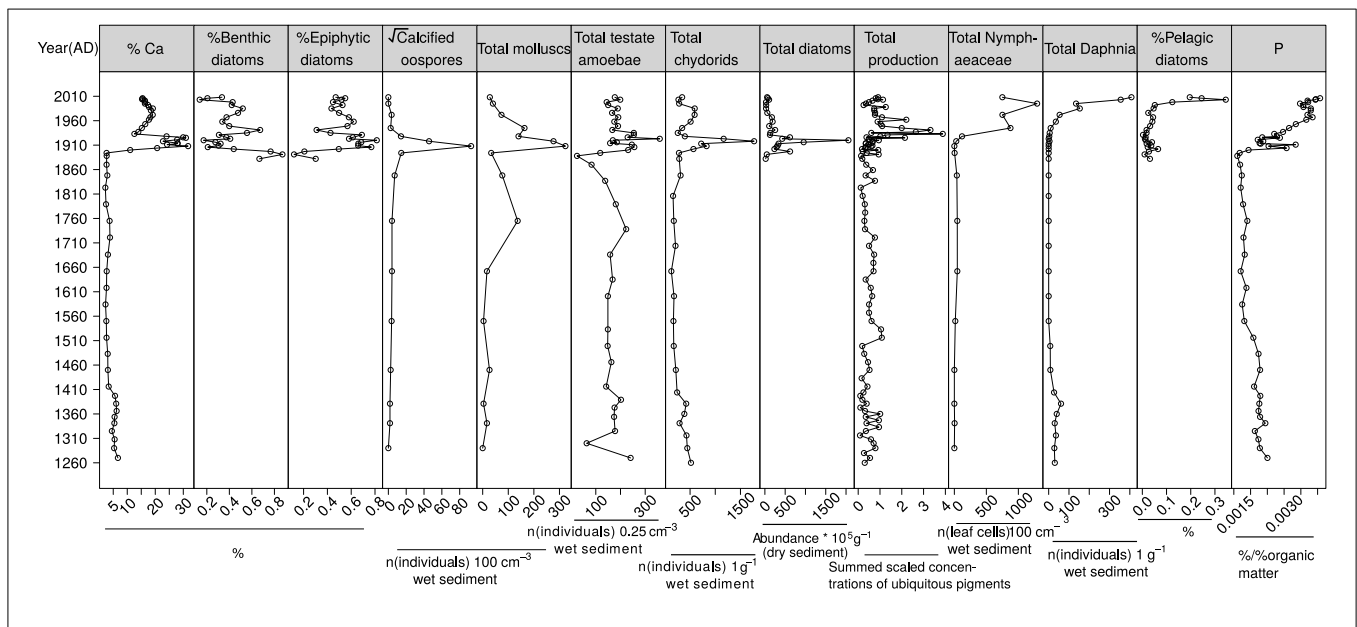


FIGURE 4 | Summary plot of CUN2 Ca, P, and key absolute and relative abundance changes of biological groups against time.

Zone 3: ca. 1890–1930

The CUN2 Zone 3 pigment assemblage remained largely similar to Zone 2 with low biomarker concentrations of cyanobacteria (zeaxanthin, canthaxanthin) and cryptophytes (alloxanthin), and purple sulfur bacteria (okenone) below the limit of detection (Supp. 2 in Supplementary Material). Consistent increases toward the top of the Zone occurred in chlorophyte (lutein, pheophytin *b*) and diatom (diatoxanthin) pigments. Increases in biomarkers of all algae (chl *a*, β -carotene) occurred abruptly at the end of the sequence around the 1920s. In the CUN1 and CUN2 macrofossil record, *Gloeotrichia* cf. *pisum*, a nitrogen-fixing colonial cyanobacterium, increased approximately three-fold in abundance throughout the zone (Supps. 4, 9 in Supplementary Material). The proportion of periphytic diatoms in the CUN2 record increased from ca. 40 to 70%, dominated by *G. angustum* and *A. pediculus*. (Supp. 7 in Supplementary Material). Throughout Zone 3, diatoms were more abundant than in the other zones (Figure 4). Persistence of the nutrient-sensitive *Cymbella microcephala* suggested relatively low nutrient concentrations (Schneider et al., 2000) (Supp. 7 in Supplementary Material).

The most substantial and rapid changes in the testate amoeba community occurred in this zone with peaks (at ca. 50%) in *Arcella vulgaris* and *Centropyxis aculeata* “aculeata,” taxa often associated with low oxygen environments (Roe et al., 2010; Drljejan et al., 2014). The proportions of *Diffflugia oblonga* “oblonga” and *Cucurbitella tricuspis* (to ca. <5%), *Cyclopyxis kahli* and *C. constricta* “aerophila” decreased further. While species diversity was at a minimum in this zone, maximum absolute concentrations increased almost 10-fold (Figure 4).

Cladoceran abundances were highest in Zone 3 (Figure 4). Benthic taxa remained dominant, however community composition changed toward 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 (Supp. 4 in Supplementary Material). Ehippia of pelagic cladoceran taxa were largely absent or rare in CUN1 and CUN2 (Supps. 4, 8 in Supplementary Material).

Two macrophyte phases within Zone 3 were identified in the cores (Supps. 5, 9 in Supplementary Material). Oospores attained maximum abundances in the first phase (CUN1 $n = 2698 \text{ ml}^{-1}$ and CUN2 $n = 8707 \times 100 \text{ ml}^{-1}$; Supps. 5, 9 in Supplementary Material; Figure 4) 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 (CUN1 $< 400 \text{ ml}^{-1}$, CUN2 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. 6, 8 in Supplementary Material; Figure 4).

Zone 4: ca. 1930–2000s

Diatom, cyanobacteria, and cryptophyte pigment concentrations in CUN2 increased substantially from the 1930s to maximum abundances in the 2000s (Supp. 2 in Supplementary Material), indicative of increasing eutrophication (Leavitt, 1993; McGowan et al., 2005). In contrast, biomarkers of all algae (chl *a*, β -carotene) peaked around the 1930s followed by declines to concentrations similar to the early 1900s (Figure 4). 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) (Supp. 7 in Supplementary Material). Okenone reappeared in the pigment record and increased from the 1980s, coinciding with a decrease in *G. cf. pisum* (Supps. 2, 5, 9 in Supplementary Material) and an increase in the proportion of planktonic diatoms such as *Aulacoseira* spp. and *Stephanodiscus hantzschii* indicative of eutrophication (Reynolds et al., 2002; Negro and de Hoyos, 2005) from ca. 5% to ca. 30% (Supp. 7 in Supplementary Material; Figure 4).

Remains of pelagic cladocerans, *Daphnia* spp. in particular, increased consistently from the 1930s to the 2000s in the macrofossil (CUN1, CUN2) and cladoceran records (CUN2) (Supps. 4, 8 in Supplementary Material). *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 ubiquitous species (*Alonella nana*), filter feeders (*Sida crystallina*) and sediment-associated species (*Leydigia leydigi*) (Supp. 4 in Supplementary Material).

A substantial increase occurred in the relative abundance of *Diffflugia oblonga* “oblonga” in the 1930s (Supp. 3 in Supplementary Material), corresponding with increases in core organic matter. In contrast, relative abundances of *Arcella vulgaris* and *Centropyxis aculeata* “aculeata” decreased. Some recovery in the uppermost part of the core was evident for the aforementioned species with modest increases also in *Cucurbitella tricuspis* (to ca. 9%) in the 1990s. Species diversity and concentrations (Figure 4) 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. 5, 9 in Supplementary Material). In CUN1, oospore numbers fell two-three orders of magnitude from maximal abundances in Zones 2 and 3, while CUN2 numbers fell to levels comparable with Zone 1. Nymphaeaceae trichosclereids increased to >3 times their previous abundance (CUN1, CUN2). Linear-leaved *Potamogeton* remains persisted in the core record (CUN2). 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* (CUN1) 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 6, 8 in Supplementary Material).

Constrained Analyses

Ca and P were correlated with between 10 and 37% of the CUN52 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, testate amoebae, 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.

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 years) will necessarily be more precise than those for macrofossils (median age gap 40 years). 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 (Figure 5). 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 (Figure 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 testate amoebae around 1516 (Figure 5).

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), testate amoebae (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) (Figure 5). The highest frequency of splits occurred between the 1900s and 1930s. The most important pigment splits are indicated by solid lines (Figure 5).

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 (<0.001 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 (Figure 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 (Figure 6).

TABLE 2 | RDA-based correlations and *p*-value of Ca and P over biological data.

Group	<i>n</i>	%VarExp		Cyclic <i>p</i>		Free <i>p</i>	
		Ca	P	Ca	P	Ca	P
Pigments	54	23	37	0.39	0.02*	0.001***	NA
Cladocerans	18	27	30	0.22	0.06 ⁺	0.002**	0.002**
Testate amoebae	18	13	15	0.88	0.55	0.02*	0.009**
Macrofossils	15	26	20	0.13	0.40	0.002**	0.003**

⁺lowest value attainable with given *n*(samples). The stars refer to standard significance denotations.

Discussion

Cunswick Tarn proved particularly suited for detailing bottom-up effects of eutrophication owing to the absence of fish and their top-down influence throughout the core record. 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 (Figure 5). The two main changes were (1) an abrupt shift between two different benthic phases in the early 1900s (low *Chara* + organic sediment to high *Chara* + marl sediment), and (2) the erosion of benthic primary production pathways as the Tarn became increasingly eutrophic in the mid-late 1900s. 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.

Drivers of Ecosystem Change

Hydrology

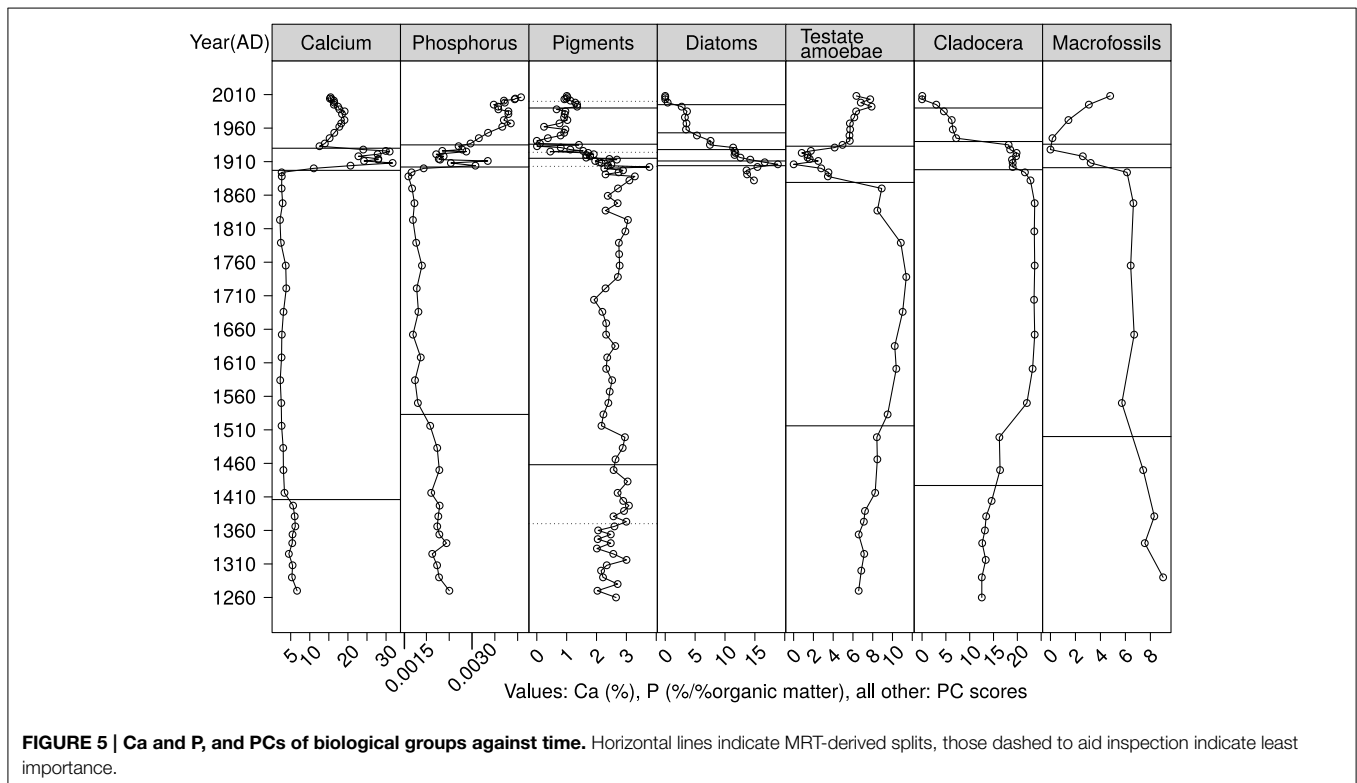
The first substantial changes in Ca, P, and ecosystem structure occurred following lake drainage in the 1890s, corresponding to a period of intensifying land management in the area following land enclosures and attempts at drainage of local lakes (Otley, 1830; Walker, 1955; Cousins, 2013). Both lake 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 (Supps. 5, 9 in Supplementary Material), as well as of epiphytic diatoms and macrophyte-associated molluscs (Figure 4) 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 CUN2 by a shift from a dominance of the *Chara hispida* group to the more shore-line associated, 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 CUN1, the location of which was 1.5 m shallower than that of CUN2 (Figure 1). Secondly, CUN1 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.

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,



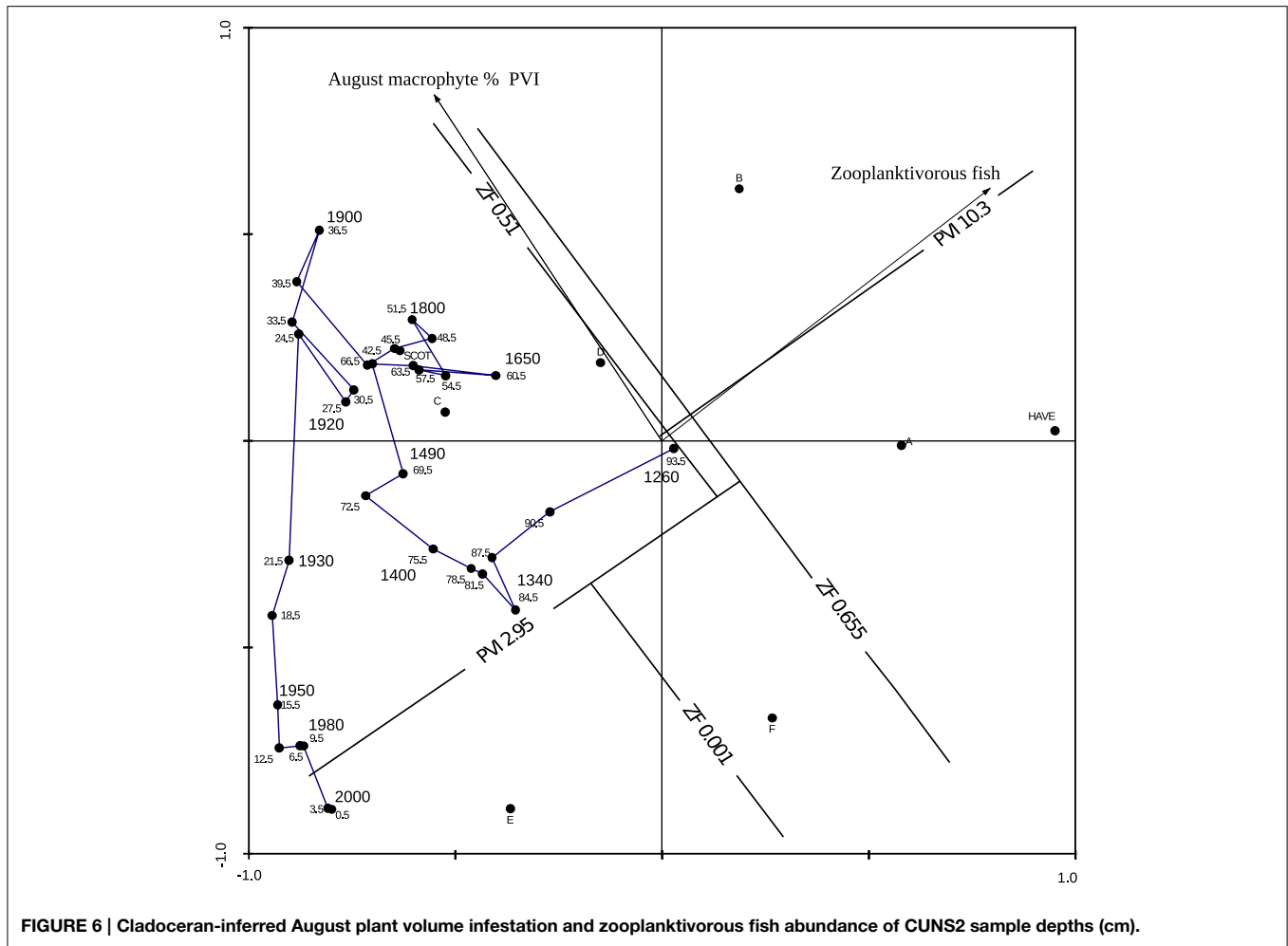


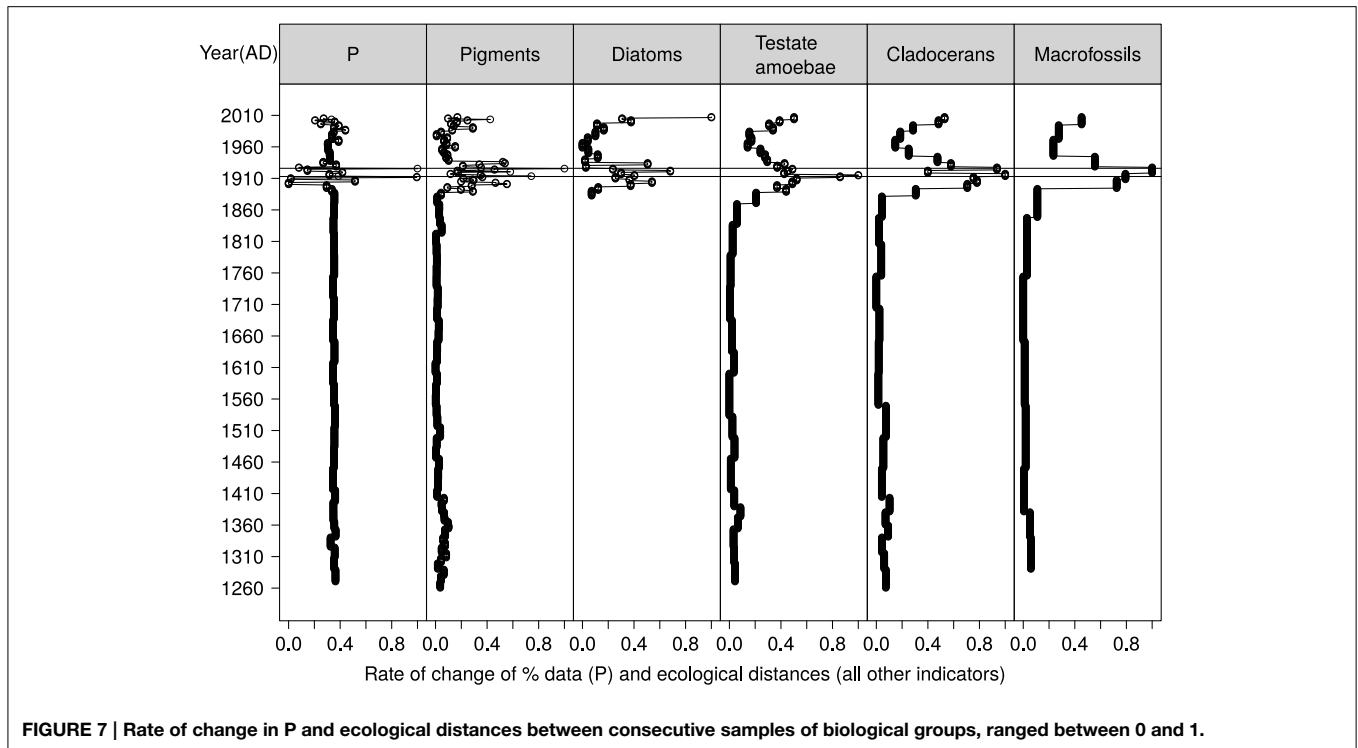
FIGURE 6 | Cladoceran-inferred August plant volume infestation and zooplanktivorous fish abundance of CUNSW2 sample depths (cm).

coprecipitation of Ca with P, and sediment stabilization owing to dense growth (Otsuki and Wetzel, 1972; Kufel and 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 (Figure 7).

The first major ecological shift in the Cunswick record 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 (Figure 6), support ideas of self-stabilizing 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 (Figure 4). Also importantly, these numerical changes were synchronous with strictly qualitative ecosystem change as seen in the multivariate analyses of cladocerans, diatoms, and testate amoebae (Figure 5), all of which were transformed to remove effects of total abundance. Indirect effects of high macrophyte biomass, such as local anoxia at the sediment level (Lindholm et al., 2008), may have contributed to the increase in *Arcella vulgaris* and *Centropyxis aculeata* “aculeata” during this time (Roe et al., 2010; Drljepan et al., 2014).

The importance of plant biomass responses as buffers to eutrophication were further supported by the lack of association between P and Ca in CUNSW2, which argues against significant chemical defenses against eutrophication via coprecipitation (see also Hobbs et al., 2005; Hutorowicz and Dzedzic, 2008). Further, the second abrupt change in the core record in the 1930s (Figure 7) corresponded to the breaking down of marling, substantial declines in macrophyte biomass (Figure 6),



particularly that of charophytes (Figure 4), 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 marked point of change in the pigments, diatoms, testate amoebae, and cladocera occurred in the 1990s (Figures 5, 7). Increases in eutrophic indicators such as *Cucurbitella tricuspis* (Medioli and Scott, 1983) (Supp. 3 in Supplementary Material), and planktonic diatoms (Supp. 7 in Supplementary Material), cryptophytes (Supp. 2 in Supplementary Material) and *Daphnia* spp. (Figure 4) (e.g., Bos and Cumming, 2003; Davidson et al., 2007) together with Nymphaeaceae, combined with associated declines in concentrations of ubiquitous pigments, all support the idea of a larger change in ecosystem structure toward pelagic shallow lake ecology (McGowan et al., 2005). Reciprocally, major declines in cladoceran-inferred PVI (Figure 6) and reductions in macrophyte species richness from 9 to 4 between the 1980s and the early 2000s (Wiik et al., 2014) support the idea of a substantial decline in benthic production.

Given the modest concentrations of TP in the lake currently ($56 \mu\text{g L}^{-1}$), and increasing P concentrations toward the core top, the decoupling between marling and P loading following the 1930s likely occurred at very low TP concentrations and opened up a “slippery slope” toward 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 (Krause and King, 1994; Krolikowska, 1997; Hargeby et al., 2007), 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 and $220 \mu\text{g L}^{-1}$ (Pelechaty et al., 2004, 2013). There are also charophyte-dominated clear marl lakes with intermediate and variable TP, including Polish Lakes Jasne (TP 30–50) and Słone (TP 10–74) (Peczula et al., 2014; Pukacz 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 dissolved organic carbon (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; Peczula et al., 2014).

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 twentieth century, particularly since the 1950s (Pitcairn and Fowler, 1995), which in part reflects increases in nitrogen-rich fertilizer 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. 5, 9

in Supplementary Material), suggestive of modest eutrophication (Laugaste and Lessok, 2004) under conditions of nitrogen limitation (Vis et al., 2008; Hudon et al., 2009).

Concentrations of *Gloeotrichia* colonies 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. Further, total nitrogen has been shown to display significant controls over testate amoebae populations (Patterson et al., 2012; Ju et al., 2014) in addition to P (Roe et al., 2010), and increasing N availability could be contributing to the 1920s shift in community composition toward a diiflugid-dominated assemblage. The transition in algal and testate amoeba indicators corresponded with shifts toward 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.

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 (Figure 6), an abundance of pelagic cladocerans, and relatively high concentrations of cyanobacterial pigments (Supps. 2, 4 in Supplementary Material; Figure 4). The presence of considerable concentrations of purple sulfur 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 oligotrophic indicators *Alonella exigua* (Whiteside, 1970; De Eyto et al., 2003) and *Chydorus piger* (Whiteside, 1970; Bos and Cumming, 2003), the oligotrophic indicator testate amoeba *Cyclopyxis kahli* (Schönborn, 1967; Wall et al., 2010), and the low concentration of Nymphaeaceae trichosclereids.

Warmer climate can promote primary production, thereby effecting carbonate precipitation (Mullins, 1998; Miroslaw-Grabowska and Niska, 2007), and favoring high relative abundances of plankton (Jeppesen et al., 2012) as well as high thermal stability, strong stratification, and hypolimnetic anoxia (Viner, 1985; Foley et al., 2012). While the aforementioned were inferred in the “MCA” core record, 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 that 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 (Guiot 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.

Land Clearance and DOC

Cunswick Tarn lies in a shallow depression in the landscape and would naturally have been surrounded by alder (*Alnus glutinosa*) carr habitat with shading willows in the margin. Under such conditions it is strongly possible that the lake margins would have been heavily shaded, resulting in reduced macrophyte development and periodic local oxygen depletion. 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 (Figure 6) and the disappearance of okenone (Supp. 2 in Supplementary Material). 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 growth 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.

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 being required to achieve both Good ecological status and Favorable 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 river basin management plans as part of the WFD, 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 ($Z_{\text{mean}} < 3$ m) and shallow ($Z_{\text{mean}} 3\text{--}15$ 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 designations (SSSI); the Tarn is currently identified as a naturally eutrophic water body, which is in strong disagreement with the palaeolimnological data.

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 deposition 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 zone (Figure 8). 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 (Figure 3; Supp. 9 in Supplementary Material) suggestive of charophyte-dominated marl benches (Jones et al., 2011). The relatively low levels of calcite deposition likely reflected the localized 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 (Figure 8). The observation is not completely unexpected, considering that biomass responses to nutrient loading as a self-stabilizing method in *Chara* lakes inherently imply that these characteristics are a symptom of eutrophication. Indeed, particularly dense (and in some cases tall) growth of charophytes has been observed in lakes subject to considerable nutrient loading (Pelechaty 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; Praeger, 1906; Spence, 1982), which was also indicated in the early record of Cunswick Tarn.

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 thirteenth to eighteenth 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

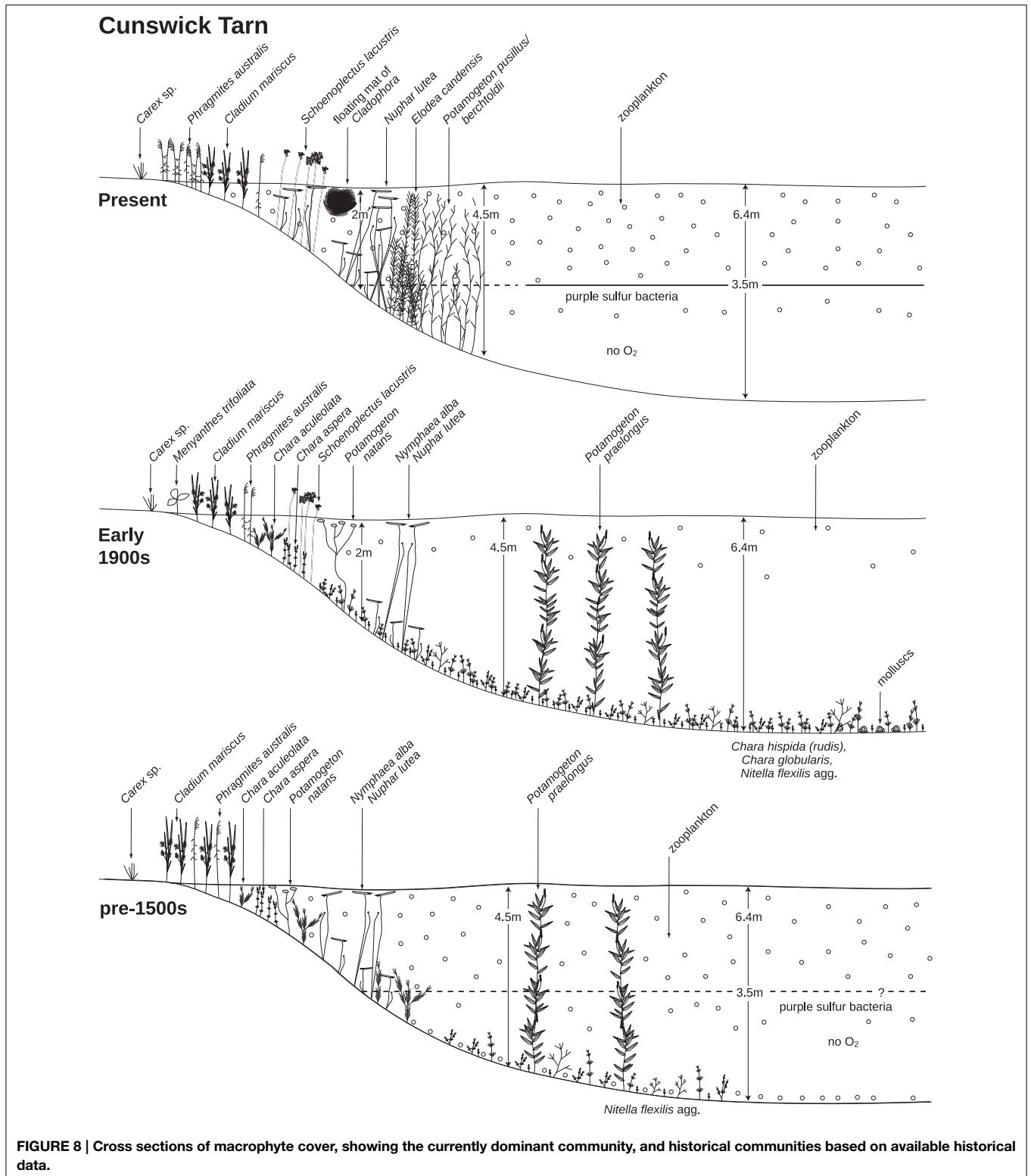
where fish manipulation is irrelevant. Unless nutrient availability for phytoplankton is restricted, charophytes will not be able to recolonize the Tarn. The most likely sources of nutrients to the Tarn are in the north where a drain pipe leads directly into the lake, and high nutrient concentrations have been measured in the inflow (December TP $44 \mu\text{g L}^{-1}$). Streams in the east woodland are likely to contribute less (December TP $14\text{--}20 \mu\text{g L}^{-1}$). Until 2015, the feeding of artificially high populations of ducks in the lake margins was a further major nutrient source. 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 et al., 2010). In this respect, the erosion occurring at the north end of Cunswick Tarn, exacerbated by the duck feeding, is particularly damaging and should be prevented. High external DOC and suspended sediment loads lead to anoxic sediments unfavorable 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, this kind of management could also be seen as interference with natural succession of trees in the lake surrounds. It is therefore a judgment 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) (with the caveat that “natural” succession in this context does not account for grazers prior to major human influence). Considering the large-scale, centennial-scale 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.

Conclusion

Biological community shifts in Cunswick Tarn demonstrated synchronicity 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, testate amoebae, 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 colonization 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.



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 characterized 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 attain sufficient levels of photosynthesis for intensive, whole-lake scale authigenic

carbonate precipitation, and that macrophyte cover could be 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 (ca. $56 \mu\text{g L}^{-1}$) in Cunswick Tarn currently. Importantly, the association of high benthic biomass and calcite deposition with 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.

Author Contributions

The majority of this publication is the direct result of a PhD by EW, which was supervised and guided by HB, CS, SC, and TD. EW undertook all palaeolimnological analyses, taught variously by HB, CS, SMG, and TD, excepting testate amoebae which are part of a PhD by SP, and diatoms which were part of an undergraduate dissertation by LS. All fieldwork was undertaken by EW and a combination of HB, CS, TD, and LS among others. GS offered crucial guidance during statistical analysis of the data during EW's PhD, and also contributed to the design and execution of statistical methods particular to this publication. EW wrote the manuscript, and all other authors contributed essentially to the interpretation and wording of components falling within their expertise.

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Supplementary Material

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fevo.2015.00082>

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