The effects of hydrological extremes on former gravel pit lake ecology: management implications

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Abstract

Urban gravel pit lake ecosystems are particularly susceptible to flooding and anthropogenic nutrient loading, and are therefore likely to be significantly affected by the future projections of precipitation extremes. Six shallow ex-gravel pit lakes at Attenborough Nature Reserve, (Nottinghamshire, U.K.), three connected to the nutrient-rich River Erewash and three isolated from it, were monitored from 2005-08 (including the highest and 6th lowest rainfall years of a 40-year record). We aimed to compare lake ecological response to hydrological extremes and to see whether river-connected gravel pits responded differently to those fed mainly by groundwater. Our results showed that flood conditions in the river-connected lakes reduced the maximum phytoplankton biomass achieved and favoured smaller taxa (cryptophytes, *Scenedesmus* spp. and small centric diatoms). Consequently dissolved NO_3-N and SiO_2 maxima were higher during flood years because of the reduced capacity for algal uptake, but dissolved and particulate phosphorus (P) concentrations were lower because increased flushing rates led to more effective removal of sediment-released P from the lake systems. Lakes isolated from the River Erewash responded less clearly to increased rainfall, except for a delay in the timing of the phytoplankton maximum, and a pronounced rise in SiO_2 concentrations after drought conditions. Spatial comparisons also showed that nutrient pollution in the River Erewash and in storm drains feeding into one of the ‘isolated’ lakes (Beeston Pond) led to the existence of a turbid lake ecosystem state through the increased supply of dissolved NO_3-N. The other isolated lakes had lower phytoplankton biomass and extensive aquatic plant coverage, but significantly greater proportions of bloom-forming cyanobacteria (*Anabaena, Aphanizomenon*), because of greater water retention times. Our results show that ex-gravel pit lakes connected to rivers may be more susceptible to ecological disruption from future flooding events and are heavily influenced by river water quality, but may be less susceptible to potentially toxic cyanobacteria blooms which may be favoured in lakes isolated from rivers with long water retention times. Artificial manipulation of urban lake hydrology to increase flushing with water of a higher quality or isolation of lakes from nutrient-rich inflows may be a useful management strategy, but the effectiveness of either approach depends on the ecological quality of the lake and inflowing river. Therefore, managing urban lakes in the face of climate change and increased urbanisation requires a detailed understanding of lake ecology and hydrology.

Keywords: hydrological extremes, urban lakes, gravel pits, eutrophication, water retention time, ecosystem states, shallow lakes, flooding

Introduction

Urban aquatic ecosystems represent a unique management challenge because of the combined effects of altered hydrological regime and nutrient enrichment associated with urbanization. In combination with global climate change, ensuring that urban lakes and wetlands comply with the EU Water Framework Directive (2000/60/EC) is a significant management challenge. Urbanization dramatically alters catchment hydrology by removing natural hydrological buffers to rainfall extremes (Hollis 1975, Walsh et al. 2005). Increased areas of impermeable surfaces and efficient water transport systems rapidly drain urban catchments whilst water extraction for domestic and industrial uses reduces low flows (Paul & Meyer 2001, Walsh et al. 2005). Climate change is likely to exacerbate these effects by reducing summertime precipitation and increasing the intensity of drought and flood events (Kundzewicz et al. 2008, Hansen et al. 2012). The loading of nutrients, suspended sediments, metals and other contaminants is increased in urban streams (Paul & Meyer 2001, Walsh et al. 2005). Lakes and wetlands downstream of urban areas may therefore have a history of high nutrient loading (phosphorus, nitrogen) with associated changes in ecosystem structure and functioning, including a lack of submerged vegetation, high turbidity and high phytoplankton biomass (Scheffer 1998, 2001).

However, in comparison to the extensive literature on the effects of nutrient enrichment, less is known regarding how extreme hydrological change may affect lake structure and functioning. Hydrological extremes alter the fundamental physical properties of lake ecosystems by changing water retention times (WRT), and this has implications for nutrient cycling (phosphorus, P, and nitrogen, N) and phytoplankton biomass (Vollenweider 1976). Empirical evidence shows that a shorter WRT leads to lower total phytoplankton biomass (Brook & Woodward 1956, Paidere et al. 2007, Tolotti et al. 2010), smaller cell sizes (Dickman 1968, Timms & Moss 1984) and favours diatoms and cryptophytes over cyanobacteria (García de Emiliani 1997, Paidere et al. 2007, Reichwaldt & Ghadouani 2012). Zooplankton species tend to be smaller and total biomass lower in lakes with a short WRT (Walz & Welker 1998, Angeler et al. 2000, Obertegger et al. 2007). Heavy precipitation generally enhances total nutrient supply to lakes, but may change the main point of origin (e.g. Weyhenmeyer et al. 2004, Rennella & Quirós 2006, Sokal et al. 2010). For example, enhanced precipitation dilutes point-source nutrient supplies but increases the rate of diffuse-source nutrient transport (e.g. Jones & Elliott 2007, Elliott et al. 2009, Jones et al. 2011).

Ex-gravel pit lakes offer an opportunity to investigate the unique management challenges posed by high nutrient loading and highly variable hydrological regimes in urban environments. River floodplains in many temperate latitudes are rich sources of sand and gravel. Industrial extraction of aggregate has led to the formation of many basins along floodplains which become water-filled and eventually develop into ponds, lakes and wetlands (Hartwright 1974). Ex-gravel pit sites are often located in urban or industrial areas with a history of river channelization and floodplain drainage, and are therefore of high conservation value (e.g. Santoul et al. 2009). The importance of former gravel pit sites to wildlife conservation is recognised by aggregate companies, who often try to restore sites sensitively, and to conservation organisations, with many ex-gravel pits being designated as Nature Reserves (e.g. CEMEX 2013).

This research focuses on six ex-gravel pit lakes at Attenborough Nature Reserve, located within the confluence of the River Erewash and R. Trent in Nottinghamshire (UK), three of which are directly connected to the nutrient-enriched River Erewash, and three which have no surface connection to the river and are largely groundwater-fed. We aimed to determine the extent to which the hydrological management regime (river-connected / not connected) affected lake ecology. In the river-connected lakes, we predicted a larger phytoplankton community compared to the river-isolated lakes due to a high rate of supply of nutrients. We also predicted that the shorter WRT in river-connected lakes may favour small, rapidly reproducing phytoplankton. During our study, anomalously high rainfall dramatically altered the hydrology of the lakes, enabling us to investigate how reduced WRT and increased water depth altered nutrient dynamics and plankton communities. We used these contrasting hydrological conditions to predict how future increases in precipitation variability may affect shallow lakes and the implications of this for their management.

Study site

The Attenborough Nature Reserve (ANR) located approximately 7 km south-west of the city of Nottingham, UK (52° 53’ 59”, 1° 14’ 6”; Fig. 1) is designated a Site of Special Scientific Interest (SSSI) because of its diversity of breeding and overwintering aquatic birds. This study includes six small and shallow gravel-pit lakes within the reserve. During the period of the study (2005-2008), the ‘river-connected’ lakes (Coneries, Tween and Main Ponds) were interlinked in a chain fed directly by the River Erewash, whereas the ‘isolated’ lakes (Clifton, Church and Beeston Ponds) were largely unconnected to surface flows, although during January 2008 increases in water depth in Tween Pond following heavy rain resulted in water overtopping the bund dividing it from Church Pond. Beeston Pond was fed by surface storm drains from the adjacent urban area, supplying small volumes of nutrient-rich water. A small stream enabled water from Beeston Pond to drain into the River Trent. The contemporary configuration of the river-connected lakes was designed to enable the site owners, CEMEX UK Operations Ltd, to transport material on barges from some gravel-pits south-west of the ANR boundary to an aggregate processing plant located along the north-western edge of the Reserve.

There is a long-standing nutrient enrichment problem on the River Erewash, resulting from its location within a mixed urban and agricultural catchment with an industrial legacy (Environment Agency 1995). The River Erewash flows 41 km in a predominantly southerly direction towards the ANR and has a catchment (206 km^2) dominated by Magnesian Limestone with outcrops of Carboniferous Coal Measures, overlying sandstones and mudstones (Natural England 2013). The Erewash Valley underwent intense industrial development during the 19th century including coal mining, although land use in the north of the catchment is mainly for arable agriculture and livestock grazing. High loadings of mine drainage water have reduced since the 1990s, but intense urbanization in the catchment has led to effluent from eight sewage treatment works (STW) forming 70% of the river discharge during periods of low flow (Environment Agency 1995).

Methods

Hydrological data

Mean daily discharge (m^3 day^{-1}) of the River Erewash was calculated from measurements taken at 30 minute intervals, using an Ultraflux UF322 CO ultrasonic flowmeter situated a short distance upstream from where the river enters Coneries Pond (Fig. 1). Periods of missing data (31 October-26 November 2005; 18 February-4 April 2007, 15-25 June 2007 and 26 October 2007-26 January 2008) in the River Erewash record were estimated via linear regression (r^2 = 0.67, p <0.001) of River Trent and River Erewash daily discharge (March 2005-January 2008). Discharge data for the River Trent was obtained from the National River Flow Archive record for Colwick gauging station (www.ceh.ac.uk/data/nrfa/data/station.html?28009). To estimate WRT of the Erewash-connected lake chain, the volume was first calculated from 470 depth measurements, a digital elevation model was constructed (20 m resolution using point kriging in Surfer (version 11)) and surface integration. The WRT was calculated by dividing the volume by the inflow discharge (Vollenweider 1976). Daily rainfall data recorded by the rain gauge at Sutton Bonnington (ca. 9 km south of ANR) was provided by the University of Nottingham, and summed into monthly rainfall data. Daily rainfall data and WRT datasets were smoothed using the 20-day running mean to remove high-frequency variability and to enable comparison at the same temporal resolution. Historic monthly rainfall totals (March 1961-March 2008) were obtained from the Met Office climate records (Met Office 2013).

Clifton and Church Ponds had no surface inflows so calculation of WRT was not possible. As an alternative, water depth was measured from a fixed point in each lake to allow an approximation of hydrological variability. In the connected lakes, spot measurements of water level were made at the six-flap weir forming the outflow from the connected lakes into the River Trent (site MPO on Fig. 1). The average depth was calculated from the measured depth in all six outlets. No depth data were gathered from Beeston Pond.

Limnological sampling and laboratory methods

Lakes were sampled every four weeks between March 2005 and March 2008 from a central point with physical and chemical parameters (temperature, conductivity, pH) measured using a YSI 650 Sonde. Water samples from the River Erewash were taken simultaneously at the 'Erewash inflow' site (Fig. 1) for chemical analysis. Depth-integrated and river water samples were analysed for soluble reactive (SRP-P) and total phosphorus (TP-P), silica (SiO_2) and ammonium (NH_4-N) using standard colorimetric techniques (Mackereth et al. 1978, Eaton et al. 1995), and nitrate (NO_3-N), chloride (Cl^-), magnesium (Mg^{2+}), calcium (Ca^{2+}), sodium (Na^+) and potassium (K^+) using ion chromatography (Metrohm Basic 792 ion chromatography system) following filtration through a Whatman GF/C filter paper (1.2 μm pore size) for dissolved parameters. Total alkalinity was determined using titration according to Golterman et al. (1979). Filtration was also used to provide quantitative estimates of total suspended solids (TSS). Total phytoplankton biomass was estimated by spectrophotometric chlorophyll-*a* analysis (Jeffrey & Humphrey 1975). A subsample of the depth-integrated lake water sample was fixed with Lugol's iodine for phytoplankton identification using a Zeiss Invertoskop inverted microscope at 400 × magnification. At least 300 cells from a subsample of known volume were identified to genus, or species level where possible, with reference to Prescott (1954), Bellinger (1992) and John et al. (2002), and scaled to the number of cells per millilitre. Diatoms were identified to genus level, except centric species (e.g. *Cyclotella* spp., *Stephanodiscus* spp.) which were grouped as either 'large centric' (>5 μm diameter) or 'small centric' diatoms (<5 μm) to improve the accuracy of biovolume estimates. Phytoplankton biovolumes were estimated by measurement and approximation of the cell to 3-dimensional shapes (e.g. Wetzel & Likens 1991, Hillebrand et al.

1999; see Cross 2009 for dimensions). Zooplankton were sampled by duplicate vertical tows of a 250 μm mesh fixed to a weighted bucket and preserved with a methanol-sucrose solution before counting. Where possible, a minimum of 100 zooplankters were identified and enumerated from subsamples. Identification of cladocerans was to species level using Scourfield & Harding (1966), whereas copepods were classified as either calanoid or cyclopoid using Harding & Smith (1974).

Data Analysis

Three 12-month hydrological periods were defined based on total precipitation data, representing dry, wet and intermediate conditions (see below). A one-way ANOVA with Bonferroni correction for multiple comparisons was used to compare limnological variables among hydrological periods in each lake. Non-normally distributed variables were $\log_{(x+1)}$ transformed prior to analysis. Multivariate analyses were used to summarise changes in the plankton communities and since detrended correspondence analysis (DCA) axis 1 scores were >2, correspondence analysis (CA) was used to ordinate the phytoplankton and zooplankton datasets (ter Braak & Prentice 1988). Rare species were down-weighted and diagrams used Hill's Scaling. Sample scores for the growth seasons only (May-September each calendar year) were extracted and plotted separately. Canonical correspondence analysis (CCA) was used to determine the effect of abiotic variables on the phytoplankton and zooplankton communities, for both individual hydrological periods and all periods combined. Separate analyses were undertaken for Erewash-connected and isolated lakes. Forward selection of variables and a 1000 permutation Monte Carlo test under a reduced model was used, with variables considered significant if $p \leq 0.05$. Day of year was used as a covariable. The significance of the first ordination axis and all canonical axes was assessed using Monte Carlo tests. Water depth data from Church Pond was used for Beeston Pond as data was not originally collected but the response of both lakes to rainfall events appeared to be consistent. All multivariate analyses were performed using CANOCO 4.5 (ter Braak & Šmilauer 2002). Spearman's rank correlation

(r_s) was used to examine the correlations between hydrological variables and identify temporal trends. All univariate analyses were performed using SPSS 17.

To investigate the effect of hydrological change on lake P dynamics, a simple Vollenweider-type model was used to model in-lake TP for the connected lakes at monthly intervals in order to investigate the effect of changing hydrology on TP concentrations (e.g. Søndergaard et al. 1999). The model was in the form $TP_{(lake)} = L/z(\rho+\sigma)$ (Brett & Benjamin 2008), where L was TP loading (mg m^3 $month^{-1}$); z, mean depth; ρ, lake flushing rate (defined as Q/V_L, where Q is inflow volume [m^3] and V_L is lake volume [m^3]) and σ, in-lake TP loss coefficient (defined as $\sqrt{(z/Q)}/t_q$; where t_q is hydraulic residence time (months) calculated as V_L/Q (Vollenweider 1976).

Results

Precipitation

Total annual precipitation (starting in March each year) was 537 mm in 2005-06, 635 mm in 2006-07 and 766 mm in 2007-08 (Fig. 2), and trends in daily rainfall increased marginally during the study period ($r_s = 0.13$, $p < 0.001$). The seasonal distribution of rainfall changed substantially. During the first 12 months of monitoring (from March 2005) monthly total rainfall ranged between 15 and 72 mm, with the highest monthly totals in autumn (September-November 2005). Rainfall was more variable in 2006, with low rainfall from March-August 2006, but a series of precipitation events in September 2006 increased the monthly total to 64 mm. The highest rainfall occurred in 2007 (June-August, with 137 mm falling in June alone). Based on this annual total, the hydrological and limnological data were structured into three hydrologically different periods: 2005-06 (referred to the ‘dry period’), 2006-07 (‘intermediate period’) and 2007-08 (‘wet period’). Compared to the Met Office historic record for Sutton Bonnington (1961-2007) the total rainfall for the March 2007-08 period was the wettest, 2006-07 the 15th wettest and 2005-06 the 42nd wettest (6th driest) on record.

Lake WRT

Erewash-connected lakes: The WRT were longer in the dry period (mean: 15.9 days) than the intermediate and wet periods (12.3 and 11.7 days respectively) (Fig. 3a). Mean WRT during the intermediate and wet periods were not significantly different ($p > 0.05$), but the variance in WRT was. During the wet period, WRT were <5 days in June-July 2007, whilst during the same months in the intermediate period, the 20-day mean WRT were more than twice as long. Estimated 20-day mean WRT and rainfall were weakly but significantly correlated during the study period ($r_s = -0.480$, $p < 0.001$). Increases in water depth were generally synchronous with declines in WRT, and whilst water depth mostly varied by <10 cm, extreme rainfall events caused water depth to increase by up to 50 cm.

Erewash-isolated lakes: Water depths in the isolated lakes were greater during the wet period than the dry and intermediate periods, and were generally greatest in the winter of each year (Fig. 3b). Water depth varied little between the summer of the dry and intermediate periods, but increased by 15-20 cm during the summer of the wet period. The most significant increase in water depth was during the winter of 2006 and 2007 in Clifton Pond. Water depth data were not available for Beeston Pond, but the response to precipitation patterns appeared, from field observations, to be consistent with that observed in Church Pond.

Water chemistry

Erewash-connected lakes: Water chemistry of the connected lakes differed among hydrological periods (Fig. 4). In wetter conditions, conductivity, pH (Table 1) and annual mean and maximum TP (Fig. 4a) and SRP (Fig. 4b) declined and TSS increased (Table 1). Trends were more subtle for NO_3-N (Fig. 4c), but annual maxima were generally highest in the wet period. NH_4-N was similar among hydrological periods (Fig. 4d), and SiO_2 concentrations were less variable during wetter hydrological periods (Fig. 4e). Dissolved N:TP ratios (Fig. 4f) were similar among hydrological periods. Modelled TP predicted lower values than observed in the field, except during the wet period, when there was good agreement (Fig. 5).

Erewash-isolated lakes: Concentrations of nutrients were lower in the isolated lakes compared to the connected lakes. Within the isolated lakes group, Beeston Pond had the highest concentrations (Fig. 4, a-e). Conductivity, pH and TSS (Table 1) were not clearly affected by the different hydrological conditions, and no clear differences were observed in nutrient concentrations either, with the exception of increases in SiO_2 concentrations in Church and Clifton Ponds during the intermediate period.

Phytoplankton

Erewash-connected lakes: No significant differences were recorded in mean chlorophyll-*a* concentrations among hydrological periods in the Erewash-connected lakes. However, annual maxima (in the summer) declined when the WRT was shorter (Fig. 6). The wet period resulted in disruption to the seasonal phytoplankton periodicity with chlorophyll-*a* concentrations being markedly lower during late summer (July-August), in comparison to the dry and intermediate periods. The phytoplankton community was generally dominated by chlorophytes, diatoms and cryptophytes, and distinct differences in the composition of the summer phytoplankton communities were observed during the different hydrological conditions (Fig. 7a & b). Cryptophytes (*Cryptomonas* sp. and *Rhodomonas* sp.), small *Scenedesmus* spp. and small centric diatoms dominated the phytoplankton community during the wet period whereas larger coenobial chlorophytes, such as *Pediastrum* sp. and *Coelastrum* sp. were abundant during the dry and intermediate period. Cyanobacteria were more abundant during the dry and intermediate periods, including species from the genera *Oscillatoria*, *Aphanizomenon*, and *Microcystis* in comparison to the wet period where there were only occasional occurrences of *Microcystis* spp. CCA showed that hydrological variables (minimum WRT and rainfall) were significant explanatory variables of the phytoplankton community in all hydrological periods

(Table 3). No nutrient variables were related to phytoplankton community variance during the dry period, but P and N availability were identified as significant during the intermediate and wet periods.

Erewash-isolated lakes: Chlorophyll-*a* concentrations were significantly higher during the intermediate period in Church Pond (Fig. 6). Wet conditions delayed the onset of the chlorophyll-*a* maxima in Church and Clifton Ponds by up to two months. Chlorophyll-*a* concentrations varied little among all three hydrological periods in Beeston Pond. Church and Clifton Ponds had markedly higher relative abundances of cyanobacteria (*Aphanizomenon* sp. in Clifton Pond and *Microcystis* and *Anabaena* sp. in Church Pond) than the Erewash-connected lakes. In contrast, phytoplankton in the third isolated site, Beeston Pond, was similar to the connected lakes with abundant diatoms (*Aulacoseira* and other, generally small, centric diatoms), cryptophytes (*Cryptomonas and Rhodomonas* sp.) and chlorophytes (*Ankyra*, *Scenedesmus*, *Coelastrum* and *Pediastrum*). Growth season communities did not show any clear differences associated with hydrological period, although there was a significant skew towards more positive axis 2 scores in Church Pond, associated with a large number of *Euglena* sp. during November 2007. Hydrological variables (depth and rainfall) were only identified by CCA as significant drivers of the phytoplankton community when all periods were grouped together (Table 3). However, variables associated with silica availability (SiO_2 and Si:SRP) were significant in all hydrological periods.

Zooplankton

Erewash-connected lakes: Zooplankton biomass was generally lowest in the wet period (Fig. 8). Maximum abundances of zooplankton occurred during July and September during all three hydrological periods, and the dominant taxa were small *Daphnia* (mostly *D. hyalina*) and *Bosmina* (*B. longirostris*) with cyclopoid copepods, with the latter increasing in density during the dry and intermediate periods (Fig. 9). Hydrological variables were only selected by the CCA as significant explanatory variables of the zooplankton community during the wet period (Table 3).

Erewash-isolated lakes: Mean abundances of zooplankton responded in different ways among hydrological periods, with highest abundances occurring in the wet period in Beeston Pond and the intermediate period in Church and Clifton Ponds (Fig. 8). Daphnids (*D. hyalina*) and cyclopoid copepods were common in all isolated lakes, but the community composition was more diverse in Clifton Pond (Fig. 9) with larger bodied daphnids (*D. pulex* and *D. cucullata*), calanoid copepods and macrophyte-associated taxa (*Eurycercus lamellatus* and *Chydorus ovalis*) being present. *D. cucullata* was also frequent in Beeston Pond. There was no obvious pattern of zooplankton community change in association with hydrological conditions during the dry and intermediate years, but depth and rainfall were both identified by CCA as significant explanatory variables during the wet period (Table 3).

Discussion

Importance of river connectivity for determining ecosystem state

The major consequence of river connectivity in the lakes of the ANR is the absence of aquatic macrophytes from the river-connected lakes and associated changes in the structure and functioning of these lakes (Jeppesen et al. 2000) compared to the groundwater-fed lakes. The Erewash-connected lakes had higher nutrient concentrations and conductivity than the groundwater-fed lakes Church and Clifton Pond. Sewage effluent derived from the eight STWs along the length of the River Erewash (Vane et al. 2010) maintained the Erewash-connected lakes in a hypertrophic, turbid state (mean SRP-P >320 µg L^{-1}; NO_3-N, >4 mg L^{-1}) and devoid of submerged macrophytes (Scheffer 1998, 2001). Seasonal patterns in TSS concentrations in the Erewash-connected lakes indicate that most of the turbidity derives from the high biomass of phytoplankton (chlorophyll-*a* concentrations >279 µg L^{-1}; Secchi depths <30 cm) but may be supplemented by particulates from the river during periods of high flow (Cross 2009). Despite declines in nutrient concentrations in these lakes since the early 1990s (when annual mean SRP-P and NO_3-N were 1500 μg L^{-1} and 7 mg L^{-1} respectively; Sayer & Roberts 2001) reflecting improved tertiary treatment methods at the STW (Severn Trent Water, pers. comm.), there have been no significant improvements in the ecological quality of the lakes.

In comparison to the Erewash-connected lakes, Church and Clifton Ponds existed in the clear-water state (Secchi depths >2 m), with lower nutrient concentrations and lower chlorophyll-*a* concentrations (typically 60-80 μg L^{-1}) (Scheffer 1998, 2001). Macrophyte surveys conducted in 2005 and 2007 indicated 80-90% aquatic macrophyte coverage (predominantly *Elodea canadensis* and *Potamogeton pectinatus*). Nutrients may have been supplied to both lakes by shallow groundwater movements from the River Erewash and Erewash-connected lakes because of the permeable gravels that form the lake basins, but this was not significant compared to the effects of surface river inflows observed in the Erewash-connected lakes and Beeston Pond. Although isolated from the River Erewash, Beeston Pond exists in a turbid state with no submerged macrophytes, but with substantially lower TP-P and SRP-P concentrations than the Erewash-connected lakes. This may be a consequence of high concentrations of NO_3-N (James et al. 2005). Comparison of the Erewash-connected lakes and Beeston Pond reveals similar concentrations of NO_3-N, which is probably derived from polluted urban runoff draining into the lake via a storm drain (which may also have increased ion concentrations due to dissolution of the concrete drain walls; e.g. Davies et al. 2010). Concentrations of NO_3-N in the Beeston Pond inflow were reported by Cross (2009) to regularly exceed 6 mg L^{-1}, particularly during the winter months. This finding supports other evidence that suggests nitrogen pollution is the key variable that limits the growth of aquatic macrophytes (and therefore regulates ecosystem state) in shallow lakes (James et al. 2005). As NO_3-N is predominantly supplied from external sources, and the rate of supply is enhanced during the flood conditions, isolation of ex-gravel pit lakes from surface inflows may be an effective strategy for maintaining the vegetated, clear water state.

Our analyses support the idea that the presence or absence of aquatic macrophytes is an important determinant of shallow lake functioning. Thus, the phytoplankton biomass in Beeston Pond (no macrophytes) was consistently higher than Church Pond (with macrophytes), despite similar TP concentrations, suggesting that other mechanisms such as zooplankton grazing were important in restricting phytoplankton biomass in lakes with plants (Jeppesen et al. 1999, Blindow et al. 2000). Our zooplankton analyses also show that there was a more diverse zooplankton community with larger body sizes in the macrophyte-dominated lakes, most probably because they were able to find refuge from predators in the vegetation (Timms & Moss 1984). These buffer mechanisms were not present in the turbid lakes, where a more direct relationship between TP concentrations and algal biomass is observed. Therefore, much greater maximum phytoplankton biomass was achieved in the Erewash-connected lakes than in Beeston Pond because of the higher mean TP concentrations. Overall, these observations indicate that realisation of potential phytoplankton biomass is influenced by ecosystem structure (i.e. vegetated or not vegetated; Scheffer 1998) which in turn may be influenced by river-connectivity and the supply of NO_3-N.

Separating the effects of hydrology and nutrient enrichment

The three contrasting hydrological periods allow a direct comparison of how similar gravel-pit lakes with different hydrological connectivity respond to changes in rainfall intensity. Lakes connected to the River Erewash displayed increased flushing rates. The consequences of the increased flushing rates were generally consistent with our expectations. We observed dilutions of major ions and reduced conductivity, increased turbidity through enhanced supply of particulate matter, reduced dissolved and particulate P and higher maxima of NO_3-N and SiO_2. The phytoplankton biomass declined (Brook & Woodward 1956, Dickman 1968, Reynolds et al. 2012) and the proportion of cryptophytes, small *Scenedesmus* spp. and small centric diatoms increased. Increases in the NO_3-N and SiO_2 concentrations may be explained by the lower phytoplankton biomass, because when retention times are longer, phytoplankton blooms can significantly deplete the in-lake concentrations of these nutrients (Reynolds 2006). The persistence of NO_3-N and SiO_2 suggests that phytoplankton are being continuously washed out of the lake chain, whilst the nutrients are being continuously supplied. The contrasting observation of lower phosphorus concentration might seem at odds with this idea, but may be explained with the assistance of the Vollenweider model which substantially underestimates TP concentrations in the dry years (Fig. 5). This is because of the release of phosphorus from lake sediments which supplements the lake P budget during the summer months (e.g. Søndergaard et al. 2001, 2003). During flood conditions, P released from the sediments will be rapidly flushed through the lake system (Spears et al. 2007), which explains the better match between modelled and observed TP concentrations during the flood. The flushing of P and continued supply of Si caused Si:P ratios to increase during the wet period, theoretically favouring an increased abundance of high Si:P species dominating the diatom community (e.g. *Synedra* and *Nitzschia*) (Kilham et al. 1986). However, our data show that centric diatoms were more abundant, which typically favour low Si:P ratios (Kilham et al. 1986). This may reflect the physical effect of very rapid flushing favouring the smaller diatoms because of their potential to reproduce rapidly (Reynolds & Descy 1996) rather than compete for Si and P, both of which remained in excess of limiting concentrations during the wet period.

The response of the isolated lakes to increased rainfall was an increase in water depth, partly through direct runoff and precipitation and partly through increased groundwater inputs. Rapid groundwater movements through the permeable gravel floodplain probably contributed to the fast response of the groundwater-fed lakes to rainfall events. In contrast to the river-connected lakes, there were few marked differences in lake parameters among each hydrological period. Increased Si concentrations during the intermediate hydrological period may have been associated with internal cycling in the lakes due to the dissolution of diatom frustules (Wetzel 2001). A possible explanation for the observed increase is that high productivity during the summer of the intermediate period may have increased pH sufficiently to enhance Si dissolution (Rippey 1983). The slight increase in Si concentrations during the wet hydrological period may have been initiated by aquifer recharge and increased transport into the lakes (LaBaugh et al. 1995). The most noticeable biological response was that the summer phytoplankton bloom appeared to be delayed in Church and Clifton Ponds, which could have been a combination of direct dilution and of the lower light availability during the rainy conditions (e.g. Dokulil 1994). Other differences between hydrological periods were relatively minor, suggesting that extreme rainfall events influence river-connected lakes to a greater extent than groundwater fed ones.

Comparisons among the lake types also offer insights into how the combination of nutrients and hydrology may affect lake ecology. The phytoplankton communities of the Erewash-connected lakes differed markedly from the two isolated sites (Church, Clifton), whereas phytoplankton of the third isolated site, Beeston Pond, was more similar to the Erewash-connected sites. The functional classification of freshwater phytoplankton of Reynolds et al. (2002) categorises phytoplankton communities based on the tolerance of phytoplankton species to different environmental factors, and was used to explore the contrasting phytoplankton communities among the lakes of the ANR. The small centric diatoms and *Synedra* found throughout the Erewash-connected lakes and Beeston Pond are typical of functional group D (associated with shallow, enriched and turbid lakes and rivers, and tolerant of flushing). *Pediastrum*, *Coelastrum* and *Scenedesmus* were also abundant in these lakes and are typical of functional group J (shallow and enriched ponds and rivers, and sensitive to settling into low light; Reynolds et al. 2002). Some phytoplankton genera found were also typical of river systems (centric diatoms, *Actinastrum*, *Chlamydomonas*, *Pediastrum*, *Monoraphidium* and *Scenedesmus*), due to their adaptations to highly flushed conditions (e.g. rapid cell reproduction and ability to effectively intercept light; Reynolds & Descy 1996). These observations suggest that a combination of the turbid ecosystem state initiated by the nutrient loading, and low WRT caused by surface inflows, create a phytoplankton community typical of well-flushed hypertrophic lakes, since their small size and rapid growth rates enables them to both exploit the abundance of nutrients (Jensen et al. 1994) and overcome the washout of cells (Reynolds 2006).

In contrast, the phytoplankton community in groundwater-fed Church and Clifton Ponds had a much greater prevalence of cyanobacteria (*Aphanizomenon*, *Microcystis* and *Anabaena* sp.) and was representative of the functional groups Y (small enriched lakes), G (short, enriched water columns) and J (shallow, enriched ponds) (Reynolds et al. 2002). Therefore, whilst phytoplankton abundance was lower in the isolated lakes, the community composition favoured species that are potentially toxic and problematic for water quality (Pitois et al. 2001, Paerl & Paul 2012). Cyanobacteria are known to favour lakes with a long WRT and low N:P ratios and it is likely that this combination of factors explains their prevalence and periodical surface blooms (e.g. in 2006) in Church and Clifton Ponds (Smith 1983, Reichwaldt & Ghadouani 2012). Periods of lower flow in the Erewash-connected lakes also resulted in increased relative abundances of *Oscillatoria* and *Aphanizomenon* supporting the idea that WRT is an important factor in determining whether cyanobacterial populations (and hence blooms) will form. The increased availability of N during the wet period was associated with a brief increase in chlorophyll-*a* concentration and abundance of *Euglena* in Church Pond, also supporting the importance of NO_3-N in structuring the phytoplankton community.

Implications for management

Urban ex-gravel pit lakes represent a significant management challenge, because of their susceptibility to flooding and urban pollution. However, because they are created artificially, there are unique opportunities to manage their hydrological connectivity to achieve the most favourable ecological outcome. Our data clearly illustrate that lakes isolated from river inflows were in a significantly better ecological condition, with lower nutrient concentrations and phytoplankton biomass and dense aquatic plant coverage, and therefore they provide the best habitat for wetland birds within Attenborough Nature Reserve (Nottinghamshire Wildlife Trust, pers. comm.). However, one of the consequences of hydrological isolation is that it may favour the development of cyanobacterial blooms because of the lower WRT and lower N:P ratios. It is likely that N:P ratios in our isolated lakes were particularly low because the lakes were once connected to the River Erewash (in the 1980s), and there is recycling of P from the lake sediments. Therefore, for sites where there is no prior eutrophication issue complete hydrological isolation may be a good option. The further advantage of hydrological isolation is that, as our data illustrate, flood events influence their ecology to a lesser extent and so they may be more resilient to future climate change.

An alternative management option is to retain hydrological connectivity to the river system. Overcoming internal P loading is a significant challenge for restoring shallow lakes and meeting the requirements of the Water Framework Directive. In many cases, sedimentary P release maintains high P concentrations for several decades after external supplies are reduced (Jeppesen et al. 1991, Søndergaard et al. 2001, 2003). Manipulating the hydrological regime of highly eutrophic lakes may help reduce the effects of internal P release (e.g. Spears et al. 2007), reduce the abundance of (potentially toxic) cyanobacteria and promote the re-establishment of vegetation, suggesting it may be an option for the restoration of urban shallow lakes. Altering the hydrological regime may be difficult unless appropriate infrastructure (e.g. flow controls, weirs) are available. Promoting flushing at the end of the summer, when in-lake concentrations of P are highest and there is the greatest threat of cyanobacteria blooms developing, would be a particularly effective regime. This approach depends on the availability of water of a better quality than that in the lake. Our data show that water with low NO_3-N and suspended sediment concentrations would be most effective for promoting vegetation growth. However, because many urban rivers are heavily degraded (Paul & Meyer 2001) river water of sufficient quality may not be available. This suggests that urban lake restoration should be accompanied by effective catchment-scale plans to reduce sediment and nutrient loading to urban streams and rivers (Walsh et al. 2005).

Our analyses indicate that the ecology of river-connected lakes is substantially altered by hydrological changes. Although during flood events the changes we observed were potentially beneficial to lake management, the effects of droughts may severely degrade urban lakes, particularly when internal P loading and WRT is high. In urban catchments, with rapid drainage, water extraction and a lack of buffering wetlands, the increasing frequency of droughts due to climate change will make urban lakes vulnerable to toxic cyanobacteria and loss of ecosystem services, such as biodiversity and amenity value. However, the question remains whether it is better to use gravel pits for conservation, as opposed to other ecosystem services. For example, gravel pits may be important flood retention areas, and when connected to rivers may be important lentic areas for the settling of particulates from rivers and the processing and removal of nutrients by algal uptake and sedimentation (Hansson et al. 2005). As such, on a catchment scale they have the potential to be significant carbon sinks.

Ultimately, the ability of ex-gravel pit lakes to provide valuable ecosystem services in the context of increasing urbanisation and climate change requires a clear understanding of their interactions with other surface water systems. Actively managing lake hydrology (by promoting connection to, or isolation from, rivers) may help mitigate the effects of climate change and urbanisation, but the appropriate strategy is dependent on the ecological condition of both the river and the lake itself.

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Table 1. Physical and chemical parameters recorded in lakes of the Attenborough Nature Reserve, for each hydrological period. Data are shown as minimum and maximum values with the median in parentheses (cond., conductivity).

Lake / Period		**pH**	**Cond. (ms cm^{-1})**	**TSS (mg L^{-1})**
Coneries	Dry	7.67 (8.59) 9.89	0.71 (0.98) 1.26	3.4 (14.8) 61.3
	Int.	7.20 (8.83) 9.40	0.77 (0.96) 1.18	5.3 (21.0) 43.0
	Wet	7.60 (8.34) 9.19	0.53 (0.93) 1.19	4.4 (15.2) 44.0
Tween	Dry	7.81 (8.73) 10.18	0.72 (0.98) 1.21	6.4 (8.3) 32.5
	Int.	8.32 (8.66) 9.68	0.82 (0.90) 1.18	4.7 (10.3) 34.4
	Wet	7.60 (8.44) 9.21	0.47 (0.91) 1.09	6.4 (14.7) 66.0
Main	Dry	8.10 (9.00) 10.42	0.72 (0.98) 1.18	5.6 (16.2) 40.0
	Int.	8.40 (8.70) 9.77	0.79 (0.87) 1.20	7.3 (21.7) 38.0
	Wet	7.31 (8.55) 9.09	0.47 (0.86) 1.01	8.0 (17.0) 57.0
Beeston	Dry	7.07 (8.29) 9.15	0.45 (0.58) 0.80	2.6 (8.8) 28.0
	Int.	8.49 (8.76) 8.99	0.53 (0.65) 0.79	2.0 (15.6) 20.8
	Wet	7.95 (8.56) 9.07	0.54 (0.61) 0.71	3.3 (14.0) 67.0
Church	Dry	7.54 (8.42) 9.40	0.34 (0.54) 0.59	1.4 (4.6) 12.0
	Int.	8.13 (8.83) 9.79	0.50 (0.57) 0.77	3.5 (8.3) 36.5
	Wet	7.48 (8.54) 9.21	0.54 (0.56) 1.09	1.7 (7.6) 23.2
Clifton	Dry	8.05 (8.73) 9.46	0.40 (0.59) 0.66	2.0 (4.2) 13.8
	Int.	8.44 (8.65) 9.36	0.58 (0.66) 0.71	3.2 (5.2) 28.8
	Wet	7.82 (8.35) 8.91	0.58 (0.62) 0.73	0.9 (4.4) 20.8

Table 2. Phytoplankton species recorded in lakes of the Attenborough Nature Reserve and abbreviations used in Fig. 7.

CHLOROPHYTES			
A. anc	*Ankyra ancora* (G. M. Smith) Fott	P. dup	*Pediastrum duplex* Meyen
A. falc	*Ankistrodesmus falcatus* (Corda) Ralfs	P. sim	*Pediastrum simplex* Meyen
A. han	*Actinastrum hantzchii* Lagerheim	Ped	*Pediastrum* sp.
A. jud	*Ankyra judyaii* (G. M. Smith) Fott	Pter	*Pteromonas* sp.
C. acu	*Closterium acutum* var. *variable* (Lemmerman) Willi Kriger	S. abu	*Scenedesmus abundans* (Kirchner) Chodat
C. mic	*Coelastrum microporum* Nägeli in A. Braun	S. arc	Scenedesmus arcuatus (Lemmerman) Lemmerman
Chl	*Chlorella vulgaris* Beijerinck	S. bic	*Scenedesmus bicaudatus* Dedusenko
Chlmy	*Chlamydomonas* spp.	Sc2 / Sc4 Sc8	*Scenedemus communis* E. H. Hegewald
Chloroc	*Chlorococcum* sp.	Schro	*Scroderia robusta*
Clos	*Closterium* sp.	Sele	*Selenastrum* sp.
Cosm	*Cosmarium* sp.	Sf2 / Sf4 Sf8	*Scenedesmuc falcatus* Chodat
Cruci	*Crucigeniella rectangularis* (Nägeli) Komárek)	So2 / So4	*Scenedesmus opoliensis* P. G. Richter
Dictyo	*Dictyosphaerium* sp.	T. inc	*Tetraedron incus* (Telling) G. M. Smith
E. ele	*Eudorina elegans* Ehrenburg	T. min	*Tetraedron minimum* (A. Braun) Hansgrig
Gflag	Small green flagellated species (unidentified)	T. reg	*Tetraedron regulare* Kützing
Larg	*Lagerheimia* sp.	T. tri	*Tetraedron triangular* Korschikoff
M. con	*Monoraphidium contortum* (Thuret) Komárková-Legnerova	Te	*Tetrastrum elegans* Playfair
M. pus	*Micratinium pusillum* Fresenius	Tet	*Tetraedron* sp.
P. bor	*Pediastrum boryanum* var. *longicorne* Reinsch	Tetrad	*Tetradesmus* sp.
		Uloth	*Ulothrix* sp.
DIATOMS			
Asteri	*Asterionella* sp.	L/c	Large centric diatom (>5 µm diameter)
Aula	*Aulacoseira* spp.	Merid	*Meridion* sp.
Cocc	*Cocconeis* sp.	Navic	*Navicula* sp.
Cymb	*Cymbella* sp.	Nitzs	*Nitzschia* sp.
Diatoma	*Diatoma* sp.	S/c	Small centric diatom (<5 µm diameter)
Fragil	*Fragilaria* sp.	Spenn	Small pennate diatom
Gyros	*Gyrosigma* sp.	Syned	*Synedra* sp.
		Tabell	*Tabellaria* sp.
CYANOPHYTES			
A. aeq	*Anabaena aequalis* (Kützing) Bornet et Flahault	Micrs	*Microsystis* sp.
A. flaq	*Aphanizomenon flos-aquae* (Linneaus) Ralfs ex Bornet et Flahault	O. arg	*Oscillatoria arghardii* Gormont
An. flaq	*Anabaena flos-aqaue* (Lyngbye) Brébisson Bornet et Flahault	O. lim	*Oscillatoria limnetica* Lemmerman 1900
Aphon	*Aphoncapsa* sp.	O. red	*Oscillatoria redekei* Goor 1918
Chroco	*Chroococcus* sp.	Osc	*Oscillatoria* sp.

Meris	*Merismopedia* sp.	Spir	*Spirulina* sp.
EUGELENOPHYTES		**CRYPTOPHYTES**	
E.acu	*Euglena acus* Ehrenburg 1830	Crypt	*Cryptomonas* spp.
Eugl	*Euglena* sp.	Rhod	*Rhodomonas* spp.
P. cau	*Phacus caudatum*	**CHRYSOPHYTES**	
Phac	*Phacus* sp.	Dinob	*Dinobryon* sp.
T. bac	*Trachelomonas bacillifera* Playfair 1915	Mallo	*Mallomonas* sp.
Trach	*Trachelomonas* sp.		

(Table 2 contd.)

Table 3. CCA of the phytoplankton communities in lakes of the Attenborough Nature Reserve. Hydrological variables are shown in **bold**. Abbreviations: hydro.; hydrological, Int.; intermediate, env; environmental, cum.; cumulative, temp.; temperature, min.; minimum.

Hydro. period	**Significant env. variables**	**Correlation with axis 1**	**Eigenvalues**		**Cum. % species – environment variance**		**Monte Carlo significance test *F* (*p*)**	
			Ax. 1	Ax. 2	Ax. 1	Ax. 2	1st axis	All axes
Erewash-connected lakes								
All	TP	0.526	0.086	0.067	20.4	36.4	3.210	1.754
	NO_3-N	-0.407					(0.001)	(0.001)
	SiO_2	-0.342						
	Na^+	0.314						
	K^+	0.375						
	Mg^{2+}	0.233						
	Temperature	0.344						
	Dissolved O	0.345						
	pH	0.559						
	Min. WRT	**-0.037**						
Dry	Na^+	-0.114	0.151	0.125	34.5	63.2	2.072	1.746
	TSS	-0.600					(0.005)	(0.001)
	pH	-0.467						
	Min. WRT	**0.423**						
Int.	TP	-0.437	0.144	0.123	25.5	47.2	2.299	1.961
	NO_3-N	0.281					(0.001)	(0.001)
	NH_4-N	0.396						
	K^+	-0.176						
	Secchi	0.626						
	Rainfall	**-0.613**						
Wet	NO_3-N	0.245	0.108	0.094	25.1	47.0	1.721	1.644
	DIN:SRP	-0.113					(0.08)	(0.001)
	Temperature	-0.356						
	Dissolved O	-0.637						
	Min. WRT	**0.076**						
Erewash-isolated lakes								
All	TSS	-0.472	0.133	0.111	21.6	39.7	3.284	1.920
	Si:SRP	0.256					(0.001)	(0.001)
	K^+	0.260						
	Ca^{2+}	0.449						
	Alkalinity	0.283						
	Temperature	-0.540						
	Dissolved O	0.078						
	Depth	**0.417**						
	Rainfall	**0.072**						
Dry	SiO_2	-0.133	0.263	0.169	38.8	63.8	2.273	1.722
	Na^+	-0.391					(0.005)	(0.001)
	Alkalinity	0.177						
	Secchi	-0.684						
Int.	TP	0.103	0.217	0.191	23.2	43.5	1.978	1.878

	DIN:SRP	-0.437					(0.002)	(0.001)
	Si:SRP	-0.293						
	Secchi	0.138						
	Temperature	0.411						
	pH	0.758						
Wet	SiO_2	0.210	0.176	0.139	44.5	79.7	2.124	1.725
	Na^+	0.729					(0.001)	(0.001)
	Temperature	0.171						

(Table 3 contd)

Table 4. Zooplankton species recorded in lakes of the Attenborough Nature Reserve and abbreviations used in Fig. 9.

CLADOCERA	
Alon	*Alona* sp.
B. cor	*Bosmina coregoni* (Baird) s. str.
B. lon	*Bosmina longirostris* (O. F. Müller)
C. meg	*Ceriodaphnia megalops* Sars
Cerio	*Ceriodaphnia* sp.
Chyd	*Chydorus ovalis* (Kurz)
D. cuc	*Daphnia cucullata* Sars s. str.
D. cur	*Daphnia curvirostris* (Eylmann)
D. hya	*Daphnia hyalina* (Leydig)
D. hy(g)	*Daphnia hyalina* var. *galeata* Sars
D. hy(l)	*Daphnia hyalina* var. *lacustris* Sars
D. lon	*Daphnia longispina* (O. F. Müller)
D. pul	*Daphnia pulex* (De Geer)
E. lam	*Eurycercus lamellatus* (O. F. Müller)
S. cry	*Sida crystallina* (O. F. Müller)
S. muc	*Scaphelobris mucronata* (O. F. Müller)
COPEPODS	
Calan	Calanoid copepods
Cyclo	Cyclopoid copepods

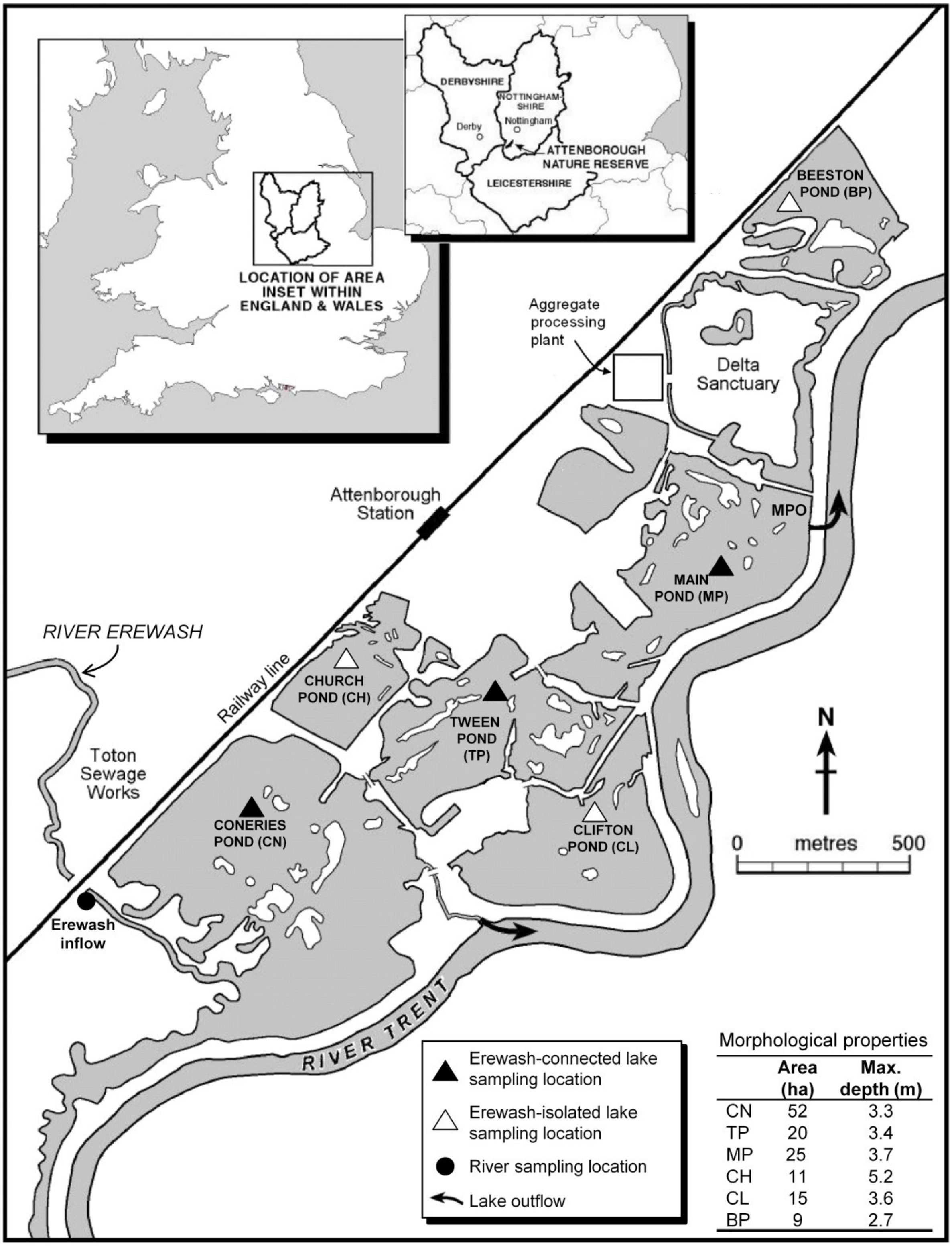
Table 5. CCA of the zooplankton communities in lakes of the Attenborough Nature Reserve. Hydrological variables are shown in **bold**. Abbreviations: hydro.; hydrological, Int.; intermediate, env; environmental, cum.; cumulative.

Hydro. period	**Significant env. variables**	**Correlation with axis 1**	**Eigenvalues**		**Cum. % species – environment variance**		**Monte Carlo significance test *F* (*p*)**	
			Ax. 1	Ax. 2	Ax. 1	Ax. 2	1st axis	All axes
Erewash-connected lakes								
All	NO_3-N	0.492	0.177	0.100	51.0	79.7	22.302	6.970
	SiO_2	0.199					(0.001)	(0.001)
	Na^+	-0.145						
	Ca^{2+}	0.138						
	Alkalinity	-0.339						
	Secchi	0.766						
	pH	-0.601						
	Rainfall	**-0.104**						
Dry	Alkalinity	-0.064	0.189	0.108	60.9	95.7	13.452	10.482
	Secchi	0.841					(0.001)	(0.001)
	Temperature	-0.078						
Int.	TP	-0.556	0.282	0.105	63.3	86.9	26.740	13.547
	NO_3-N	0.321					(0.001)	(0.001)
	Si:SRP	0.555						
	Mg^{2+}	-0.608						
	Ca^{2+}	0.821						
	Alkalinity	-0.104						
	Secchi	0.872						
Wet	NO_3-N	0.441	0.205	0.119	40.9	64.7	10.942	6.590
	SiO_2	0.088					(0.001)	(0.001)
	NH_4-N	0.695						
	DIN:SRP	-0.120						
	Si:SRP	-0.261						
	Cl^-	0.098						
	Mg^{2+}	-0.506						
	Dissolved O	-0.556						
	pH	-0.523						
	WRT	**-0.045**						
	Rainfall	**-0.151**						
Erewash-isolated lakes								
All	NH_4-N	0.287	0.216	0.177	32.5	59.3	9.233	3.983
	Cl^-	-0.043					(0.001)	(0.001)
	K^+	-0.479						
	Mg^{2+}	-0.120						
	Ca^{2+}	0.169						
	Secchi	-0.018						
	Temperature	-0.120						
	pH	0.076						
	Depth	**-0.452**						
Dry	SiO_2	-0.669	0.620	0.359	56.2	88.7	14.870	10.675
	Cl^-	0.341					(0.001)	(0.001)

	Alkalinity	-0.419						
	Secchi	0.762						
	Temperature	-0.232						
Int.	K$^+$	-0.740	0.263	0.175	49.6	82.6	4.896	3.975
	Mg^{2+}	-0.096					(0.012)	(0.001)
	Depth	**0.113**						
Wet	Ca^{2+}	0.105	0.372	0.146	54.5	75.9	6.491	3.563
	Temperature	-0.448					(0.001)	(0.001)
	Depth	**-0.538**						
	Rain	**-0.474**						

(table 5 contd)

Cross, McGowan, Needham and Pointer Figure 1



Morphological properties

	Area (ha)	Max. depth (m)
CN	52	3.3
TP	20	3.4
MP	25	3.7
CH	11	5.2
CL	15	3.6
BP	9	2.7

Fig. 1. The Attenborough Nature Reserve, a summary of lake morphology, locations of sampling sites and abbreviations used in other figures.

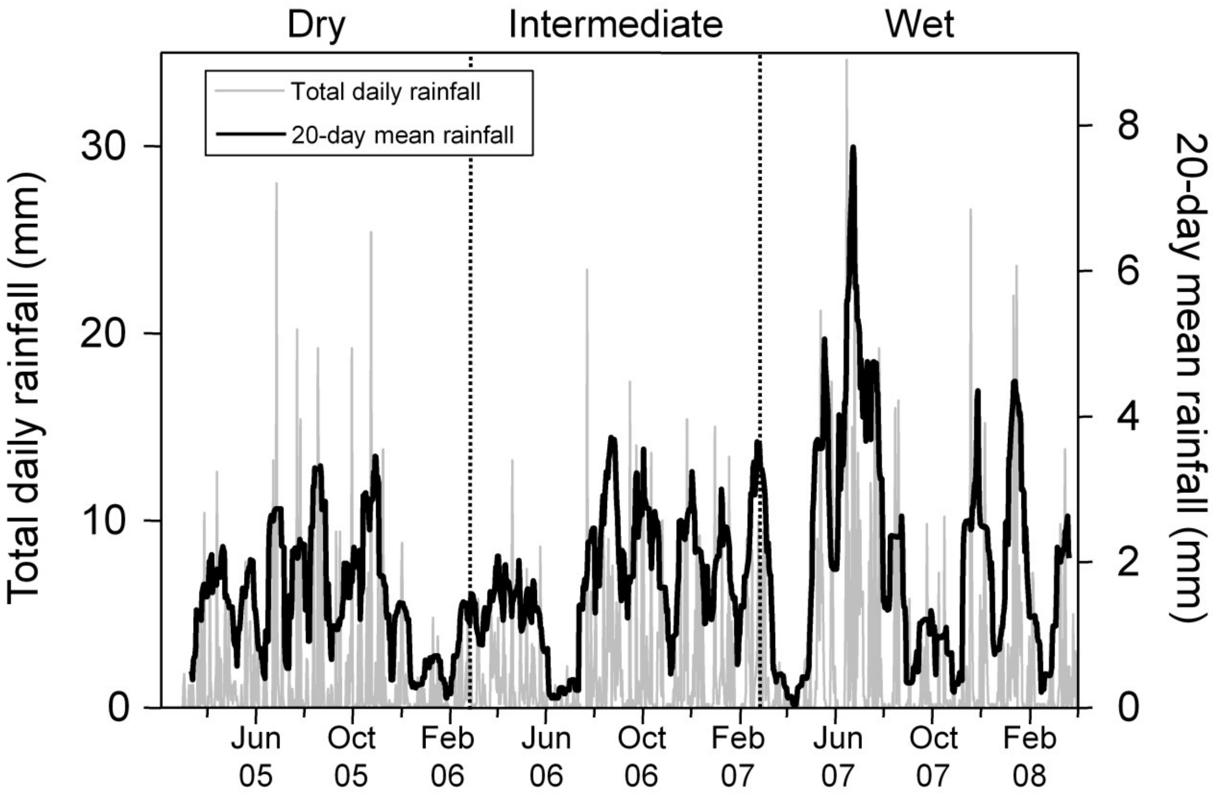


Fig. 2. Total daily rainfall and 20-day mean rainfall for the period March 2005-March 2008, recorded at Sutton Bonnington, Nottinghamshire.

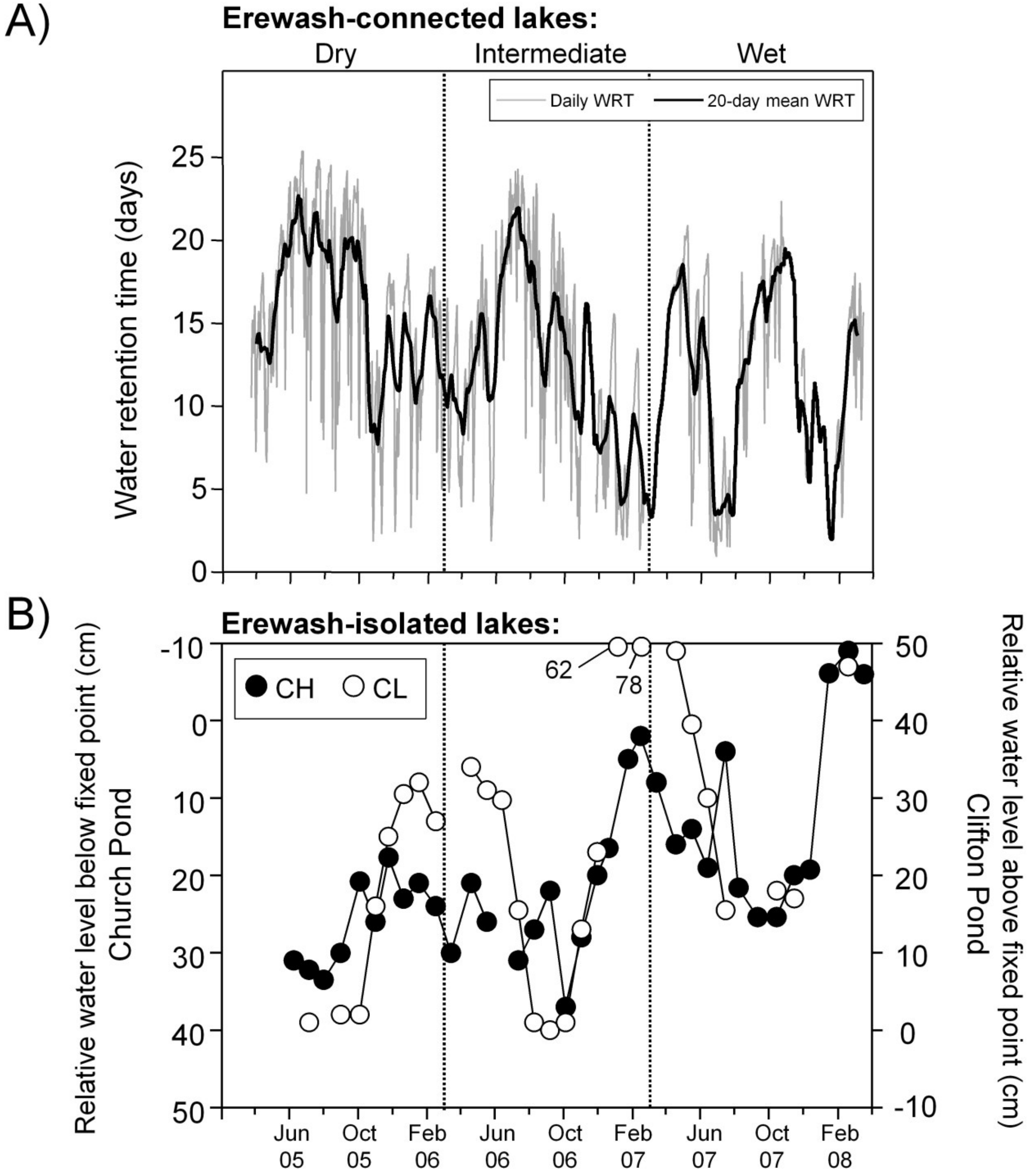


Fig. 3. A – Daily water retention time (WRT) and 20-day mean WRT in the Erewash-connected lakes; **B –** Water depth relative to fixed points in the Erewash-isolated lakes Church (CH) and Clifton (CL) Pond.

Cross, McGowan, Needham and Pointer Figure 4

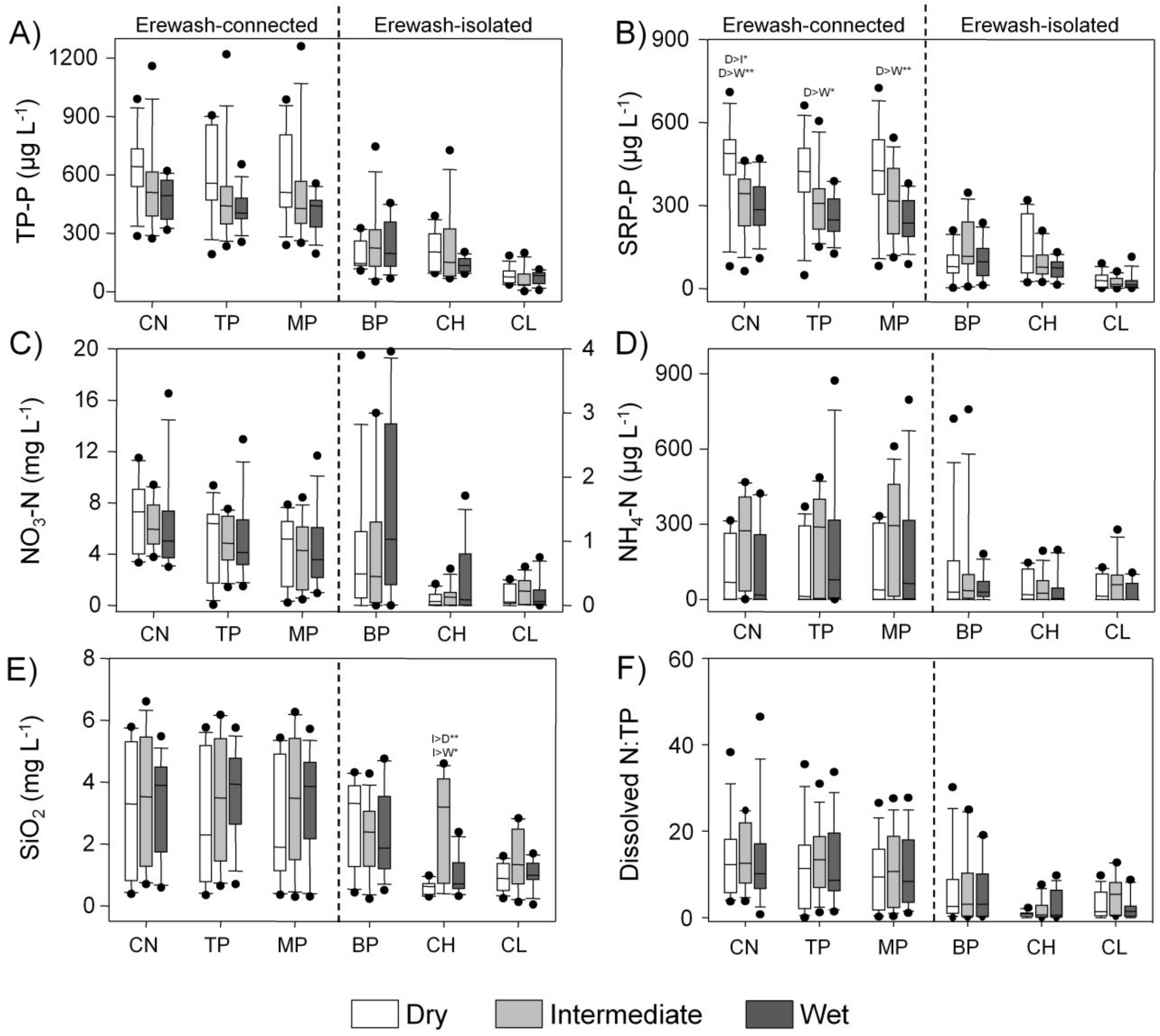


Fig. 4. Box-plots of chemical parameters recorded during each hydrological period in the lakes of the Attenborough Nature Reserve. For abbreviations see Fig. 1. **A –** total phosphorus; **B –** soluble reactive phosphorus; **C –** nitrate (right-hand axis for Erewash-isolated lakes); **D –** ammonium; **E –** silica; **F –** total dissolved N (NH_4-N + NO_3-N):total phosphorus ratio. Significant pairwise differences between hydrological periods (D, dry; I, intermediate; W, wet) for each lake are indicated by * (*p* <0.05) or ** (*p* <0.01). The direction of difference is indicated by >.

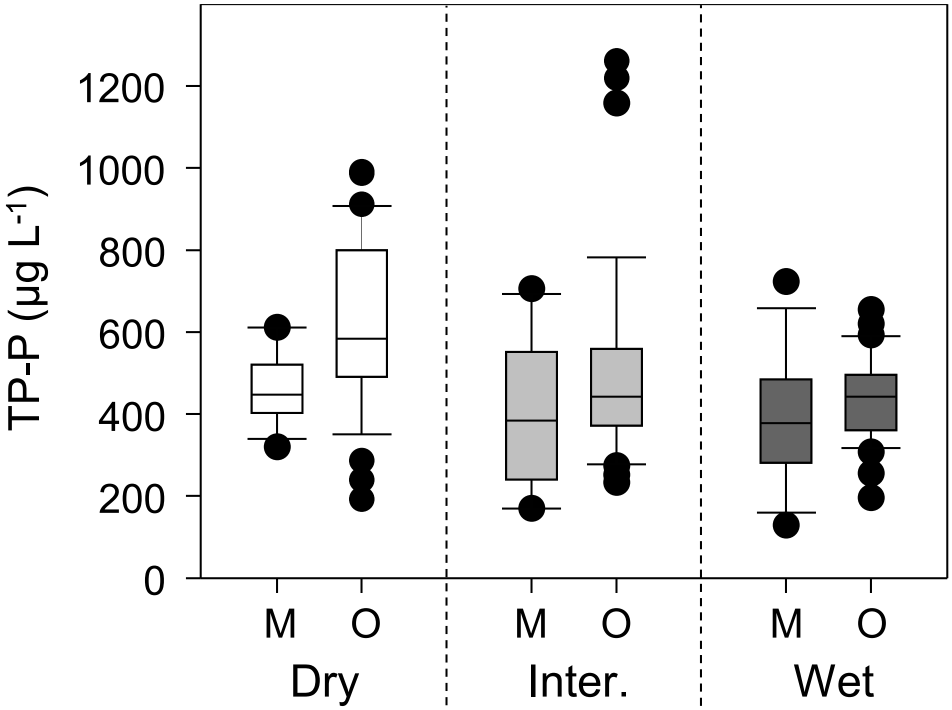


Fig. 5. Box-plots comparing TP concentrations in the Erewash-connected lakes predicted by a Vollenweider-type model (M) and values observed in the field (O) for each hydrological period. (Inter. = intermediate).

Cross, McGowan, Needham and Pointer, Figure 6

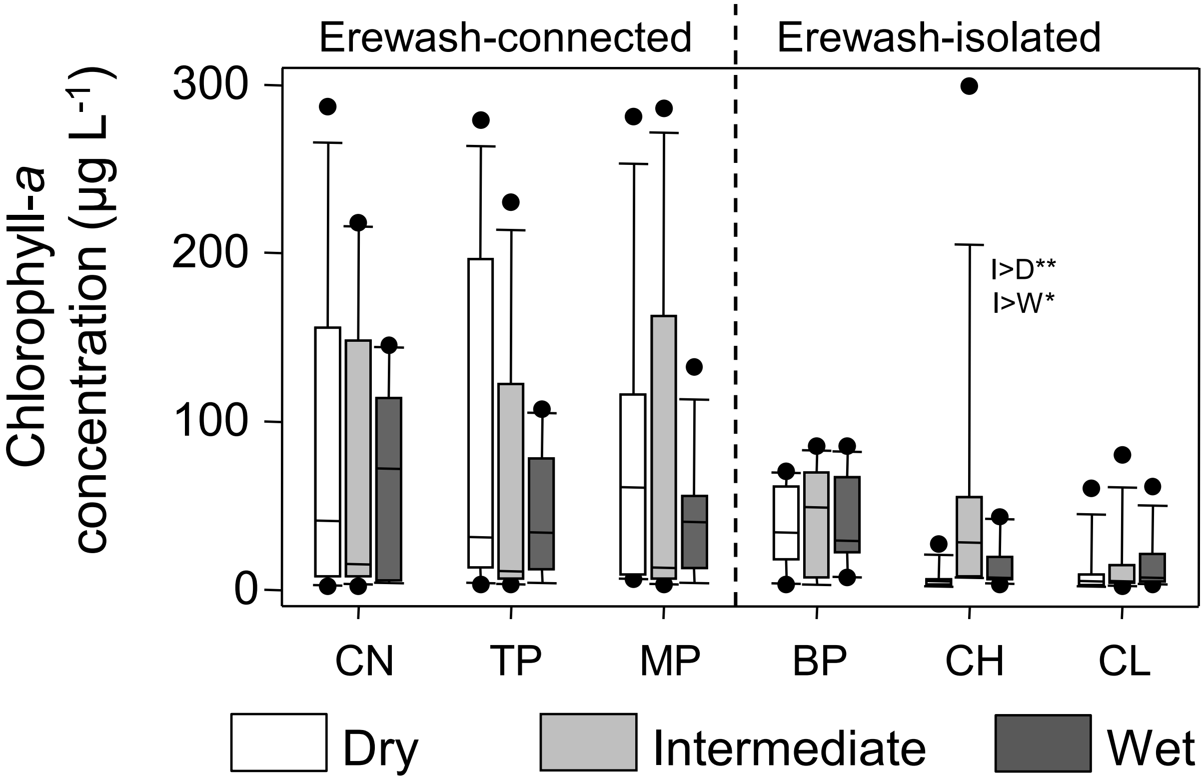


Fig. 6. Box-plots of chlorophyll-*a* concentrations recorded during each hydrological period in the lakes of the Attenborough Nature Reserve. Significant pairwise differences between hydrological periods (D, dry; I, intermediate; W, wet) for each lake are indicated by * (p <0.05) or ** (p <0.01). The direction of difference is indicated by >.

Cross, McGowan, Needham and Pointer: Figure 7

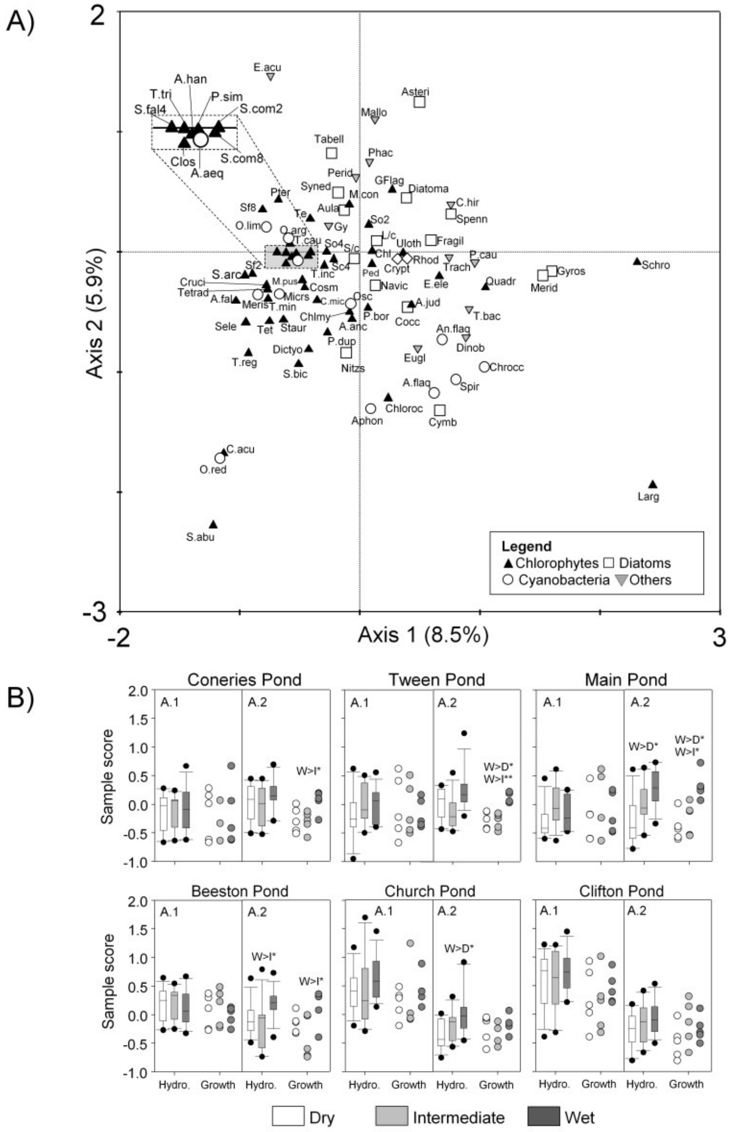


Fig. 7. A – Correspondence analysis (CA) of the phytoplankton community of the lakes of Attenborough Nature Reserve. For abbreviations see Table 2. Percentage variance explained by each axis is shown in parentheses. **B** – Box-plots of sample scores for each hydrological period ('Hydro.') and growth season (May-September; 'Growth') for each axis (A.1, axis 1; A. 2, axis 2). Significant pairwise differences between hydrological periods (D, dry; I, intermediate; W, wet) for each lake are indicated by * (*p* <0.05) or ** (*p* <0.01). The direction of difference is indicated by >.

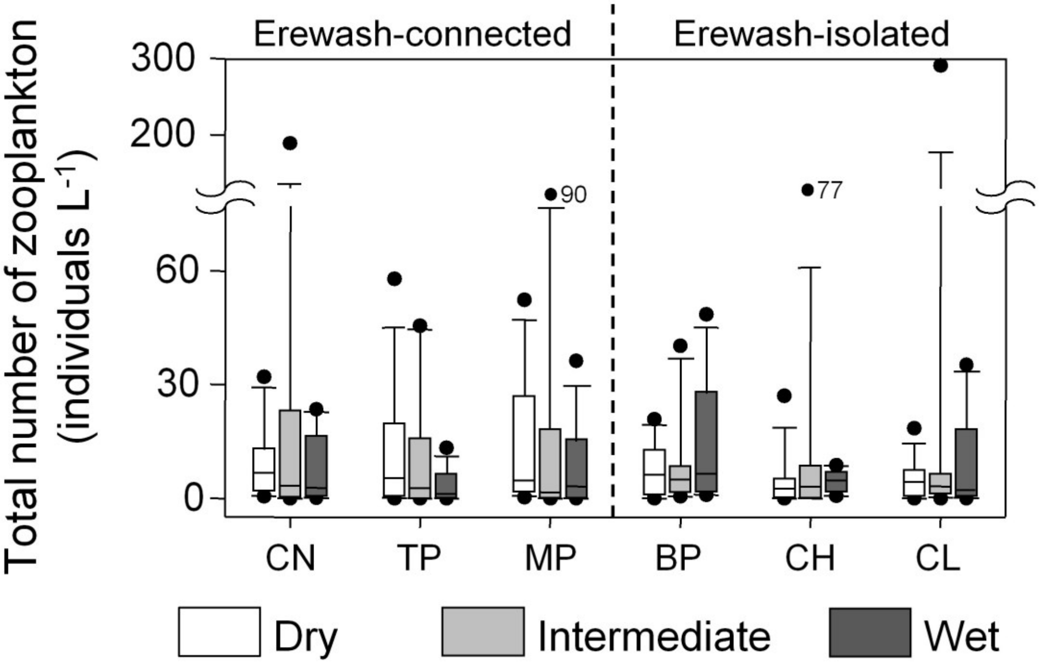


Fig. 8. Box-plots of zooplankton abundance recorded during each hydrological period in the lakes of the Attenborough Nature Reserve.

Cross, McGowan, Needham and Pointer: Figure 9

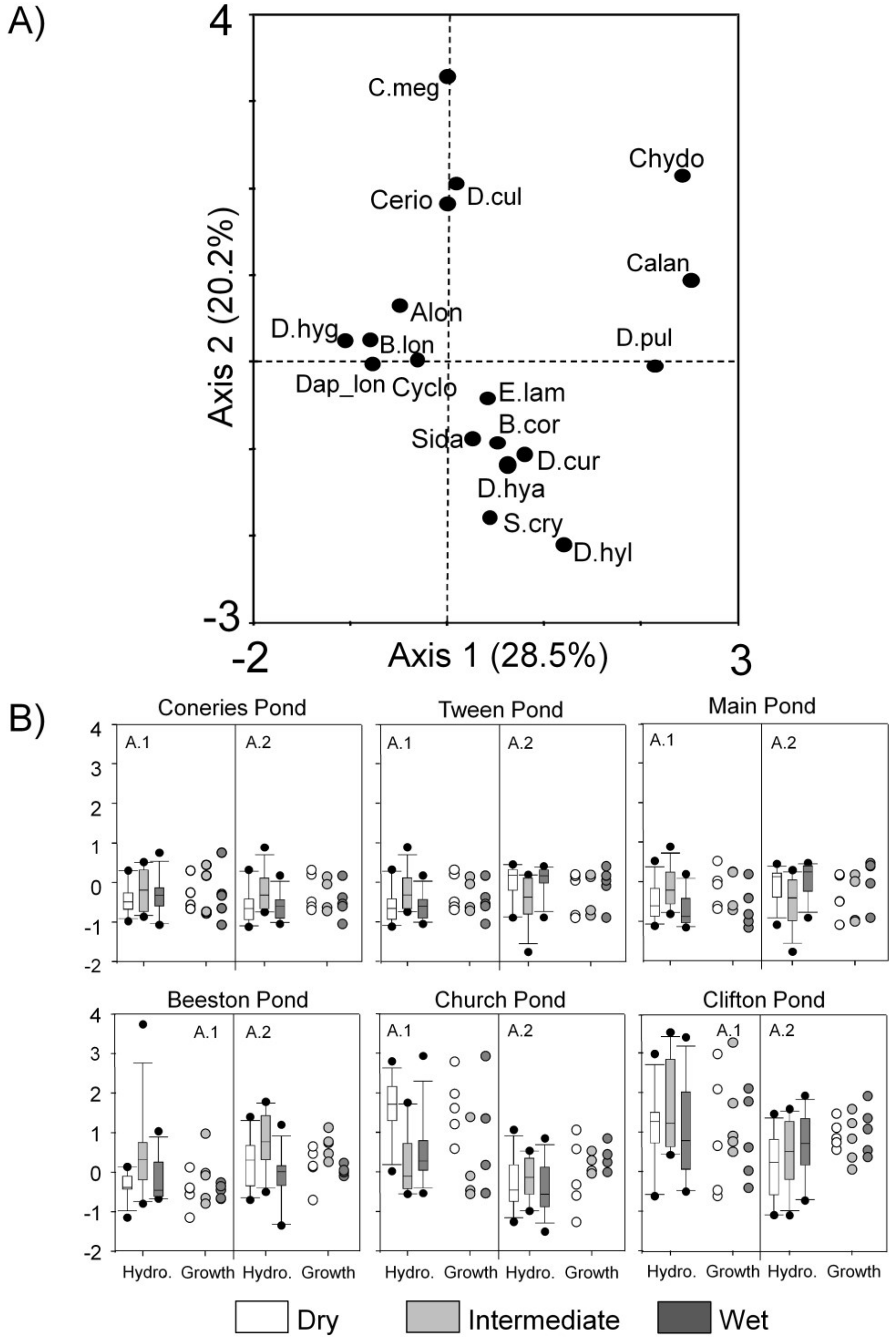


Fig. 9. A – Correspondence analysis (CA) of the zooplankton community of the lakes of Attenborough Nature Reserve. Percentage variance explained by each axis is shown in parentheses. For abbreviations see Table 4. **B** – Box-plots of sample scores for each hydrological period ('Hydro.') and growth season (May-September; 'Growth') for each axis (A.1, axis 1; A. 2, axis 2).