COMPARATIVE LIMNOLOGY OF WATERS IN A CONIFEROUS FOREST: IS A GENERALISATION POSSIBLE?

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Introduction

The British Isles have several well-known lake districts: the Scottish lochs, Irish loughs, Cumbrian Lake District and the Broads in Norfolk and Suffolk. The West Midland region (including Cheshire, Staffordshire and Shropshire) also has a high concentration of lakes. These lakes (mostly known as meres) share some common features. They are lowland, glacial in origin, with high pH, high Ca content and usually fertile. They appear to be more frequently limited by nitrogen than in other areas. Descriptions of these meres and mosses (raised peat mires developed on former meres) can be found in Lind (1949), Tallis (1973) and Reynolds (1979) but the emphasis has been given on the central and southern parts of the region. Delamere Forest (ca. 970 ha, latitude 53°13'45"N and longitude 2°40'15"W, National Grid Reference (NGR) SJ550706) is located to the north-west of the region and its lakes have had less attention. It is situated on the glacial sand and gravel deposits overlying the Mercia Mudstone Group (mostly Lower Mudstone, but also Northwich Halite and Tarporley Siltstones) in the north Cheshire Plain. The high density of meres and mosses in the Delamere area comes from numerous moraine-hollows formed after the melting of stranded ice-blocks following last glaciation. The main vegetation is of conifers along with some deciduous species (Fairhurst 1988) and the area was designated as a National Forest Park in 1987. It has been managed since the beginning of the 19th century and is a popular tourist area with walking, orienteering, cycling and educational activities. In recent years this forest park has been attracting over half a million people per year.

Besides a large number of existing or now-drained small mosses, the Delamere Forest area bears diverse water-bodies: peat-bog lakes (Black Lake), peatland under restoration (Blakemere Moss), an extremely nutrient-rich acid lake (Delamere Lake), nutrient-poor quarries (Delamere Quarries) and the Ramsar-designated Hatchmere (Figs 1 & 2). Apart from Hatchmere, all these waters have so far been little-studied. A recent study

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FIG. 1. Blakemere Moss. *Top left:* the moss from the east shore. *Top right:* former draining ditches (north-west). *Bottom left:* growth of *Riccia fluitans* and *Lemna* sp. in summer. *Bottom right:* the outlet – less humic water from Hatchmere outlet mixing with darker moss water. Photo: Mike O'Connor.

FIG. 2. *Top:* Hatchmere. *Bottom:* Delamere Lake. Photo: Mike O'Connor.

on Delamere Lake revealed an unusual, apparently fishless acid lake with very high single-species phytoplankton growth, low Cladocera abundance, absence of *Daphnia* and apparent invertebrate predation (Irfanullah 2004).

A study of the limnology of different aquatic habitats in the Delamere Forest area may give us some insight into the waters of a coniferous, temperate forest area, which has so far been largely unexplored. Generally, lakes located in a particular area show some degree of similarity. We, therefore, thought that despite apparent large variability in origin, age, surface area, morphometry, catchment size and hydraulic regime, the waters of Delamere Forest might share some revealing chemical and biological features.

The lakes and streams

Seven water-bodies in the Delamere Forest Park area, namely, Black Lake, Blakemere Moss, Delamere Lake, Delamere Quarry, Hatchmere, Windyhowe Farm Spring and Fir Brook were sampled (see below for national grid references). All these are located at about 75 m above sea level. The aquifer type of this area is classified as Minor with soil having high leaching potential (Groundwater Vulnerability Map, Sheet 16, West Cheshire, National Rivers Authority 1994). Permeability to groundwater is low in the Delamere Forest area in general because of overlying peaty deposits. The main soil type of the forest is Crannymoor (acidic – pH around 3, well-drained with a tendency to droughtiness). Data on groundwater levels and water quality are scarce for this area (ECUS 2001a). A detailed geology of the catchments of the water-bodies described below can be found in British Geological Survey (England and Wales, sheet 109) – Chester, Drift Geology (1965) and Solid Geology (1986). For main vegetation types and land-use patterns consult Ordnance Survey Explorer 267 (2000) and ECUS (2001a, b).

Black Lake

Black Lake is a small (ca. 0.5 ha), isolated peat-bog (NGR SJ537708) surrounded by conifers and apparently formed in a kettle hole on the glacial sand-gravel deposits. It is a Site of Special Scientific Interest and is managed by the Cheshire Wildlife Trust as a nature reserve. At present most of the unvegetated part of the water is shallow (< 0.5 m) although the maximum depth is estimated to be ca. 5 m (Fairhurst 1988). There are signs of one surface inflow (north-east corner) and a surface outflow (south-west corner controlled by a sluice), but both apparently have not been carrying water for some time. The surface water catchment is ca. 11 ha (ECUS 2001a) and the water contains high concentrations of humic compounds. The lake has been subject to human disturbance, e.g. in 1820

it was excavated for making habitats for ducks for shooting (Fairhurst 1988). In the 1920s the lake had a large area of open water which vanished by the 1940s when the whole area was covered with *Sphagnum* spp. (*S. cuspidatum* (Ehrh.) Russ. et Warnst. and *S. recurvum* P. Beauv.) (Lind 1949). Since the late 1960s the lake has had a thick raft of *Sphagnum* (‘*schwingmoor*’) along with other associated vascular bog species and an open water area (Tallis 1973), and in 1970s the raft showed signs of deterioration (Fairhurst 1988). At present (2002–2004), approximately 25 % of the lake area is open water. The lake represents a good example of hydroseral succession and early developmental stages of ‘*schwingmoor*’ and is important for educational purposes (Fairhurst 1988). ECUS (2001a) identified conservation issues and recommended management plans for it. The Environment Agency (North-West Region) has been recording some chemical variables in the winters since 2001 (Environment Agency 2004).

Blakemere Moss

Blakemere Moss is the largest peatland of Delamere Forest Park (NGR SJ552712, Fig. 1). It was drained in the early 19th century (1815–1823) for the plantation of broad-leaved trees for timber. Because of low productivity these trees were replaced with conifers. The area was restored to peatland in 1994 by cutting down the trees and establishing a sluice gate to retain water, which made it one of the largest wetland reclamation projects in Britain (Forestry Enterprise, personal communication). At present it has a surface area of > 33 ha with an average depth of < 1 m, a maximum depth of 4 m and a surface water catchment of 135 ha. The drift geology of the catchment is a combination of peat and sand-gravel glacial remains. The water retention time of Blakemere Moss is about 94 weeks. The water is extremely dark-brown with high humic content. There are several drainage channels collecting water from the surrounding coniferous forest, and one outlet (Fig. 1). The extensive boggy part on the western part of the lake is mainly made up of rush and *Sphagnum* spp. *Lemna* sp. grows near the bank on stagnant water along with *Riccia fluitans* L. and *Callitriche* sp. This lake supports populations of gull and water-fowl. No data were found on the water quality of this moss.

Delamere Lake

The small lake situated on the east edge of the Delamere Forest Park is unofficially called Dead Lake by the owners of part of the site (Forest Enterprise), but in this account we refer to it as Delamere Lake (NGR SJ559709, Fig. 2). The surface area of the lake is ca. 1.8 ha, the mean depth 1.7 m, and the surface water catchment 19 ha mainly covered with coniferous trees. Residence time of this lake was estimated at ca. 53 weeks.

The western half of the lake is within the Delamere Forest Park area and the eastern half is owned by the adjacent farm (Windyhowe Farm).

This lake is man-made. The available information suggests that sometime between the late 1930s and early 1940s a culvert was blocked and a part of the forest flooded quickly, giving rise to Delamere Lake (Lind 1949; Forest Enterprise, personal communication). At present there is no clear inlet or outlet, hence the lake entirely depends upon precipitation, surface run-off and diffuse soil and ground-water seepage. There are no submerged plants in the lake, only some small beds of rush (*Juncus bulbosus* L.) and yellow flag iris (*Iris pseudacorus* L.) in the shallower eastern edge of the lake. The detailed limnology of this lake has been described in Irfanullah (2004).

Delamere Quarries

Delamere Quarries (owned by Tarmac Central Limited) are two interconnected artificial lakes originating from gravel extraction (NGR SJ563696). These were used for about 40 years starting in 1950. They have a total surface area of ca. 12.1 ha (older southern part, ca. 3.4 ha and relative recent northern part, ca. 8.7 ha), and are quite deep (10–14 m) according to the owner. There is no surface inlet and they are mainly fed by precipitation and surface run-off as they are located in an area with little ground-water permeability. The surface water catchment is ca. 80 ha and 54 % of it is grassland (mainly a golf-course), 22 % is mixed forest, 15 % is open water and 9 % is arable land. The southern lake is connected to a forest drainage stream controlled by a sluice-gate. Residence time of these lakes together is about 9 years. Although the water is clear, it lacks submerged macrophytes owing to the absence of sufficient littoral zone, and has only sparse reed- and rush-beds. No data were found on the water quality of this lake. Only the southern lake (henceforth the Delamere Quarry or Quarry) was sampled.

Hatchmere

This lake (NGR SJ553722, Fig. 2) is the most extensively studied lake of this area (Lind 1949; Gorham 1957; Tallis 1973; Reynolds 1979; Moss et al. 1994) and is presently owned by Cheshire Wildlife Trust. It is small (4.7 ha) and shallow (maximum depth ca. 3.5 m) (Fairhurst 1988). Its surface water catchment area is ca. 222 ha of which 34 % is grassland, 25 % conifers and 13 % arable land (ECUS 2001b). The drift geology of this area is diverse; along with sand and gravel (ca. 75 %) it includes alluvium, boulder clay, peat and solid areas without deposits. The extent of peat around it indicates that the lake was formerly about twice the current size. The lake and its surrounding woodland (total 13.27 ha) is designated

as a Site of Special Scientific Interest, and being a part of the Midland Meres and Mosses it is also designated as a Ramsar site. The north and west shores of the lake are surrounded by acidic heath and bog communities and the peaty area to the west edge contains pockets of *Sphagnum* spp. The lake has one inlet coming from the north-west and a second one from the east from Flaxmere (NGR SJ557724), and one outlet meeting the outlet of Blakemere Moss just outside the north-east corner of the latter (Fig. 1). However, it has been suggested that this lake could be principally fed through groundwater and has a water retention time of 21 weeks (Moss et al. 1993). The water has a strong yellow tint because of dissolved organic compounds. The Environment Agency (North-West Region) has been recording some of its chemical variables since 1994 (Environment Agency 2004).

The lake has an extensive belt of reeds (*Phragmites australis* (Cav.) Trin. ex Steud.) along with narrow-leaved cattail (*Typha angustifolia* L.) and patches of yellow water-lily (*Nuphar lutea* (L.) Sibth. & Sm.), but no submerged plants have been recorded at least since 1987 (Fairhurst 1988; ECUS 2001b). The mixed fish community includes bream (*Abramis brama* L.), carp (*Cyrinus carpio* L.), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.), roach (*Rutilus rutilus* L.), rudd (*Scardinius erythrophthalmus* L.) and tench (*Tinca tinca* L.). Water-birds include mainly coot (*Fulica atra* L.), mallard (*Anas platyrhynchos* L.) and mute swan (*Cygnus olor* Gmelin). The lake is a popular site for angling, walking, picnicking and bird watching. Recently, conservation issues in Hatchmere were identified and suggestions were made for its management (ECUS 2001b).

The streams

Samples were also collected from two flowing waters adjacent to the forest. Windyhowe Farm Spring (henceforth the Farm Spring; NGR SJ562707), emerges from the middle of the adjacent pasture on the east of Delamere Lake. It has no connection with the lake and is entirely covered with *Apium nodiflorum* (L.) Lag. It contributes to a nearby stream, Fir Brook, which was also sampled (NGR SJ562706; adjacent to a railway bridge). This section of Fir Brook is connected to the outlet of Delamere Quarry, but no surface connections currently exist with another stream called Fir Brook, a forest drainage system (NGR SJ566694), on the south-east of the Quarry.

All these sites were visited on 20 November 2002 (autumn), and 21 January (winter), 15 April (spring), 7 July (summer) and 6 October 2003 (autumn) for collecting water samples, and phytoplankton and zooplankton samples were also collected from the standing waters on the same dates. All samples were collected around midday.

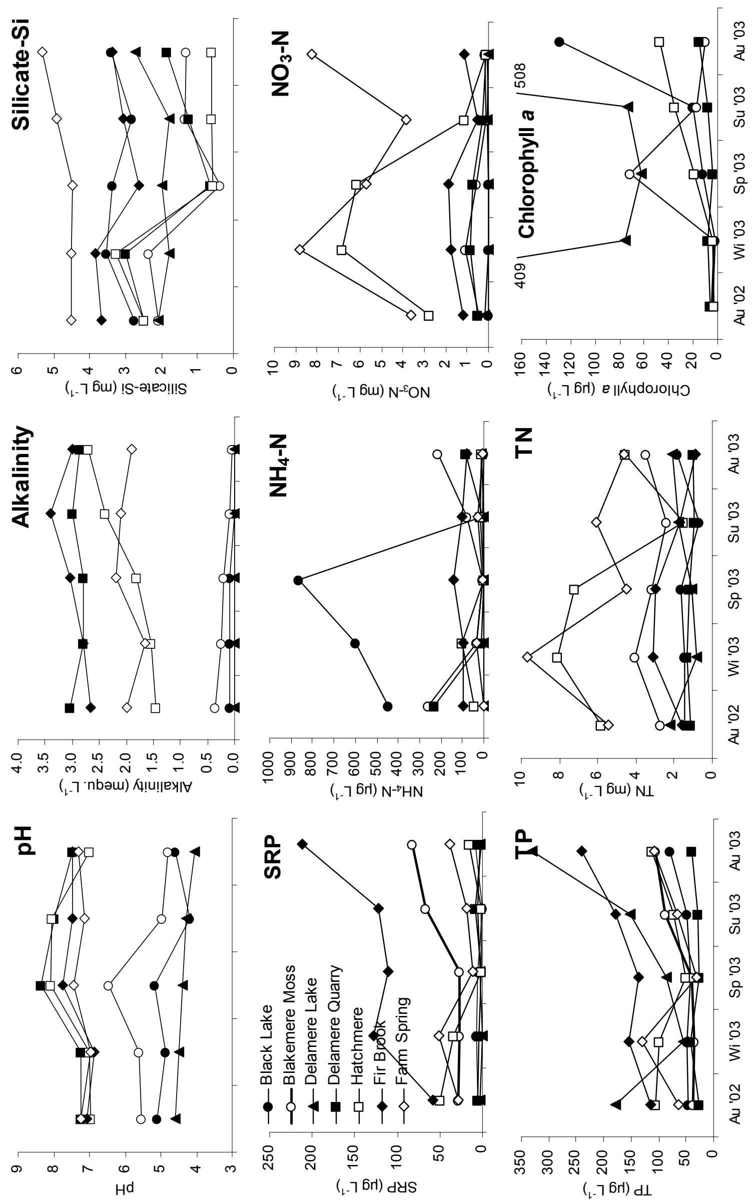


FIG. 3. Dynamics of pH, alkalinity, silicate-Si, SRP, NH_4-N, NO_3-N, TN, TP and chlorophyll *a* concentrations in Black Lake, Blakemere Moss, Delamere Lake, Delamere Quarry, Hatchmere, Fir Brook and Farm Spring in autumn 2002 and winter, spring, summer and autumn of 2003. In SRP and TP graphs, concentrations shown for Blakemere Moss are $\times 10^{-1}$.

Water chemistry

The pH (Jenway 3310 pH Meter) of the lake waters in Delamere Forest was mostly low (Figs 3 & 4). Alkalinity (Mackereth et al. 1989) and conductivity (Jenway 4010 Conductivity Meter) of the lake waters separated the lakes into two major groups corresponding to their acidic and alkaline pH regimes (Figs 3 & 4). Oxygen concentration (YSI 550DO Instrument), however, was low in Black Lake (mean ± SEM, 7.7 ± 1.1 mg L^{-1}); others ranged from 9.2 to 11.6 mg L^{-1} but were not significantly different among the lakes. In peatlands, low pH can be maintained in a number of ways: uptake of cations and release of H^+ by *Sphagnum*, decomposition of peat, release of organic acids, and sulphide oxidation ultimately producing sulphuric acid (Charman 2002). We presume that low pH in Black Lake and Blakemere Moss is predominantly maintained by dissolved organic carbon (DOC) and associated organic anions from the peaty and/or forested catchment (Schindler et al. 1992; Kortelainen & Saukkonen 1995). For Delamere Lake, the source of DOC is the coniferous vegetation. Higher pH in the rest of the study sites along with high (Delamere Quarry and Fir Brook) and moderate (Hatchmere and Farm Spring) alkalinity indicate that these waters are predominantly fed by groundwater. Earlier studies also showed that weathering of $CaCO_3$ in the glacial drift deposits (sand and gravel) can increase the bicarbonate concentrations in groundwater of this area (Gorham 1957).

Dissolved organic carbon (DOC)

Colour (absorbance at 440 nm – Cuthbert & del Giorgio 1992) of the standing waters in Delamere Forest indicated the presence of high concentrations of DOC. The estimated means were: Black Lake, ca. 300 mg Pt L^{-1}; Blakemere Moss (Fig. 1), > 1000 mg Pt L^{-1}; Delamere Lake, > 50 mg Pt L^{-1} and Hatchmere, ca. 100 mg Pt L^{-1}. Coniferous forests and peatlands are important sources of DOC (mainly as humic and fulvic acids). Water with colour ≥ 50 mg Pt L^{-1} can have > 50 % organic carbon of allochthonus origin and with > 200 mg Pt L^{-1} it can be > 90 % (Meili 1992). The humic water in Delamere Lake is apparently a result of sub-surface run-off from the coniferous forest to the lake as shown by the leachates from soil samples from the catchments (see below, also Hongve 1999). In Black Lake, in addition to this, peat deposits are important in maintaining a humic condition. The water colour of Hatchmere is also influenced by the forest coverage in the catchment and the peaty lake margin. In Blakemere Moss, the very high humic content in the water is probably owing to high decomposition of the reflooded peaty bottom, rather than solely from inputs from the terrestrial sources through drainage systems.

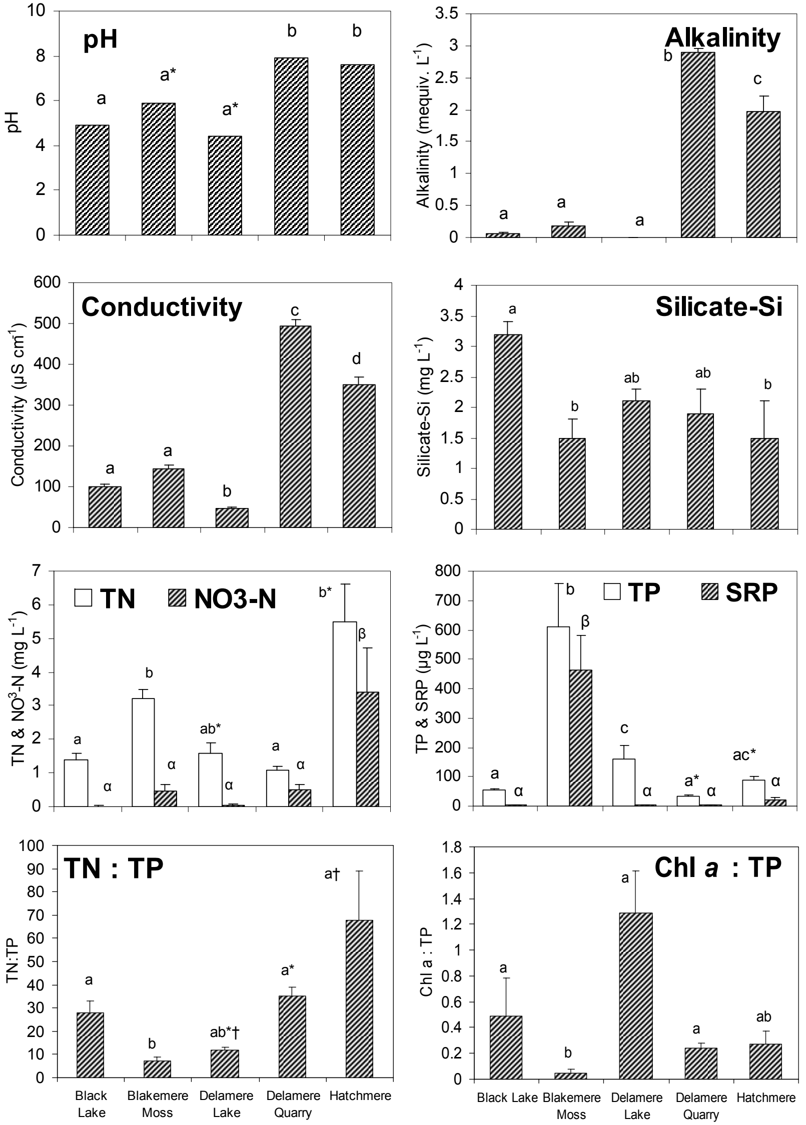


FIG. 4. Overall means (+SEM, n=5) of chemical variables in Black Lake, Blakemere Moss, Delamere Lake, Delamere Quarry and Hatchmere (2002 & 2003). Bars of same variable with different small letters (either Roman or Greek (NO_3-N and SRP) or with '*' or '†' are significantly (P<0.05) different from each other (one-way ANOVA followed by Tukey test). TN : TP and chlorophyll *a* : TP ratios are by mass.

Nutrient regimes

Water

Different waters in the Delamere Forest area showed considerable fluctuations in available and total nutrient concentrations over the study period (Fig. 3) (NO_3-N, NH_4-N, soluble reactive phosphorus (SRP as PO_4-P): Mackereth et al. 1989; soluble reactive silicon (henceforth silicate-Si): Golterman et al. 1978; total nitrogen (TN) and total phosphorus (TP): Johnes & Heathwaite 1992). Most distinctive of these were high concentrations of NO_3-N and TN in Hatchmere; NH_4-N in Black Lake; SRP and TP in Blakemere Moss and TP in Delamere Lake. Comparisons of different chemical variables among different standing waters showed significantly higher NO_3-N and TN in Hatchmere, and SRP and TP in Blakemere Moss (Fig. 4). NH_4-N concentrations were not significantly different among the lakes. Of the running waters Farm Spring had very high NO_3-N concentrations giving very high TN (Fig. 3). TN : TP ratios suggested that all the studied lakes were P-limited (Fig. 4), except Blakemere Moss (N-limited) and Delamere Lake (either co-limited, or absence of N/P-limitation) (where N-limited at ratio < 9, P-limited at ratio > 22.6, by mass).

Soil

Deep soil cores (30–40 (–50) cm) were collected from Delamere Lake and Black Lake catchments and used to extract readily leachable compounds (Irfanullah 2004). The concentrations in extracts (mg or µg L^{-1}) were converted into mg L^{-1} kg^{-1}, interpreted as an amount of nutrient present in the first one litre of water passed through one kg dry soil. These values, however, should only be used as indicative values of soil chemical contents rather than actual concentrations. Low pH (mean 3.6) and high readily leachable SRP (mean ± SEM, 5 ± 2 mg L^{-1} kg^{-1}), NH_4-N (5 ± 3 mg L^{-1} kg^{-1}), NO_3-N (11 ± 2 mg L^{-1} kg^{-1}) and DOC (8 ± 3 g Pt L^{-1} kg^{-1}) concentrations were recorded in Delamere Lake catchment soils (30–40 cm core, top 20–30 cm organic layer, n = 6). Soil extracts from the Black Lake catchment (50 cm core, top 40 cm organic layer, n = 3) also contained high SRP (0.6 ± 0.1 mg L^{-1} kg^{-1}), NH_4-N (8 ± 3 mg L^{-1} kg^{-1}), NO_3-N (16 ± 12 mg L^{-1} kg^{-1}) and DOC (7 ± 1 g Pt L^{-1} kg^{-1}) concentrations. Overall DOC content was positively correlated with SRP (r = 0.589, P < 0.01), NH_4-N (r = 0.483, P < 0.05) and NO_3-N (r = 0.729, P < 0.001) concentrations in the soil extracts. NO_3-N was positively correlated with NH_4-N (r = 0.518, P < 0.05).

Undisturbed peatlands are relatively nutrient-poor systems (Charman 2002). When disturbed by harvesting and drained for agriculture and afforestation, oxidation and decomposition cause considerable nutrient release (Heathwaite 1990; Holden et al. 2004). Despite its history of human interference, Black Lake is now an example of an actively growing peat bog with low nutrient concentrations and with occasional high NH_4-N peaks indicating mineralisation. Blakemere Moss, on the other hand, represents a disturbed peatland because of its long history of drainage, and then recent re-flooding. Humic waters often show high concentrations of P; mostly SRP possibly associated with humic matter rather than entering as dissolved free inorganic forms (Rask et al. 1986; Meili 1992). High TP and SRP concentrations in Blakemere Moss followed similar patterns (SRP was 63 % of TP) suggesting a release of much SRP from the decomposing peat. High, readily exportable nutrient concentrations from the soil samples of the forested catchment suggested that significant amounts of nutrients can get into the lakes through surface run-off and sub-surface percolation (Kortelainen & Saukkonen 1998).

The catchment of Hatchmere bears several farms. Historically it has thus been subject to animal waste discharge and silage effluent through the north-west inflow (Fairhurst 1988; ECUS 2001b). A number of initiatives were taken to decrease the nutrient input in the lake vicinity in the late 1990s, but since then it has still shown irregular high levels of nutrient enrichment, especially of NO_3-N (ECUS 2001b). The overall fertility of this lake is probably a result of the land-use pattern in its catchment. Fertilisation of the surrounding pasture may also explain the very high nitrogen concentrations (mainly NO_3-N) in Farm Spring. Reasons for low nutrient concentrations in the Quarry are not clear, but are probably due to the relatively small catchment (mainly golf course) for surface run-off and nutrient-poor groundwater. Moreover, being a deep system, though with a long residence time, this lake apparently has a very low internal P loading. Fir Brook is mainly receiving water from the peaty area west to the Quarry, from a roof-tiles factory and only to a smaller extent from the catchment of Farm Spring. Its very high SRP concentrations are probably because of the factory.

Meres in Cheshire are often N-limited (Reynolds 1979; Moss et al. 1994; James et al. 2003). Nutrient limitation in the present sites, however, is different. Land use in the surface catchment, drift geology and lake history can explain the TN : TP ratios in most cases. Although the ratio showed co-limitation or absence of N/P limitation in Delamere Lake, bioassays suggested that this lake was N-limited (Irfanullah 2004). Because of very high phytoplankton growth all year round, such potential limitation is of minor importance in controlling algal growth in this lake.

Phytoplankton and primary production

Phytoplanktonic chlorophyll *a* concentrations (acetone extraction method; Talling & Driver 1961) in Black Lake, Blakemere Moss and Delamere

Lake fluctuated considerably (Fig. 3). Delamere Lake showed the highest chlorophyll *a* concentrations (Fig. 5). In terms of phytoplankton growth Delamere Lake not only showed very much higher biomass than any other lake, but its species composition and their relative abundance were also distinct (Irfanullah 2004; Table 1, Fig. 5). Cryptomonads were the only group common in all lakes. While a single chlorophyte was dominant in Delamere Lake (*Dictyosphaerium pulchellum* Wood), chrysophytes and dinoflagellates were abundant in Black Lake. Diatoms were more abundant in the alkaline ones. Cryptophytes were dominant in Blakemere Moss. Cyanobacteria were rarely seen and only in the alkaline lakes. The higher pH lakes showed greater species richness than the acid ones (Table 1). There were no significant correlations among either annual means or winter values of total nutrients (TN and TP) and chlorophyll *a* concentrations with any chemical variables.

The species composition and abundance of phytoplankton in Delamere Lake were unusual for an acid lake (e.g. Findlay et al. 1999). Despite high total nutrient concentrations, other lakes did not show very high phytoplankton productivity as in Delamere Lake. High DOC concentrations can reduce phytoplanktonic photosynthesis by decreasing light availability in the water column, and also by making trace elements and P less available by combining with them. This may explain the low phytoplankton growth in polyhumic Black Lake and Blakemere Moss. However, the greatest phytoplankton growth in these lakes was dominated by cryptophytic and chrysophytic flagellates, which may prevail in humic waters because of their ability to migrate in the water column. Light absorption by DOC may also cause relatively low phytoplankton growth in Hatchmere despite very high nutrients, and in summer also due to P-limitation. In Delamere Quarry, on the other hand, the phytoplankton crop was always low because of low internal and external nutrient loadings.

Zooplankton and grazing

In all the lakes of the Delamere Forest area rotifers were the dominant zooplankters, except Blakemere Moss (high *Bosmina longirostris* (O.F. Müller) in summer only, maximum 245 L^{-1}) (Table 1, Fig. 5). Large-bodied cladocerans were rarely seen and only in Hatchmere. In other lakes chydorids or bosminids were the main cladocerans (Table 1). Adult Copepoda were low in density, so were nauplii. Moderate chlorophyll *a*: TP ratios in most of the lakes indicate low grazing pressure on the phytoplankton (Fig. 4).

The assemblage of rotifers and small cladocerans in all the studied lakes in Delamere Forest is consistent with other studies on acid lakes (Fryer 1980; Havens 1990; Siegfried 1991; Fischer & Frost 1997). In addition to the ability of these species to survive at low pH, high reproduction rate

Table 1. Occurrence of phytoplankton and zooplankton species in Delamere Lake (Delamere, from two years' data 2001–03), Black Lake (Black), Blakemere Moss (Blake), Delamere Quarry (Quarry) and Hatchmere (Hatch) (2002 & 2003). A = abundant (> 75 %), D = dominant (50–74 %), C = common (25–49 %), O = occasional (10–24 %), R = rare (< 9 %); estimated for phytoplankton and rotifer species from the relative densities and for cladocerans and copepods from absolute density (no. L^{-1}). Rare phytoplankton species in the Quarry also included species of *Ankistrodesmus*, *Tetraedron* and *Euglena*, Hatchmere included *Actinastrum*, *Coelastrum*, *Closterium*, *Crucigenia*, *Pediastrum,* unidentified green flagellate (Chlorophyceae), *Gomphosphaeria* and *Oscillatoria* (Cyanobacteria).

Phytoplankton	Black	Blake	Delamere	Quarry	Hatch
Cyanobacteria					
Small unicellular taxa				R	R
Euglenophyceae					
Phacus longicauda			R		
Trachelomonas (1–2 spp.)				O	R
Cryptophyceae					
Chroomonas acuta				R	R
Cryptomonas erosa	O	D	O	R	R
C. ovata		R	O	R	R
Chlorophyceae					
Chlorogonium (?) sp.			R		
Dictyosphaerium pulchellum			A		R
Monoraphidium griffithii			R		R
Scenedesmus (1–2 spp.)	O			R	O
Chrysophyceae					
Dinobryon divergens			R	C	O
Mallomonas sp.		O			
Synura cf. *sphagnicola*	C	R			
Bacillariophyceae					
Asterionella formosa				C	R
Pennate – (**Cocconeis, Eunotia, Fragilaria*, *Pinnularia*)		R*			R
Tabellaria flocculosa				R	
Cyclotella (1–3 spp.)				O	O
Aulocoseira sp.					O
Dinophyceae					
Peridinium cf. *inconspicuum*	O		R		

Table 1. Continued…

Zooplankton	Black	Blake	Delamere	Quarry	Hatch
Rotifera					
Anuraeopsis fissa	O	R	R	R	
Asplanchna sp.		O		R	R
Brachionus angularis			R	R	R
B. urceolaris	R		R		
Filinia sp.					R
Keratella cochlearis	C		R	D	A
K. quadrata	O	D	A	R	R
Lecane (1–2 spp.)	R		R		
Lepadella ovalis	R	R	R	R	
Mytilina sp.		R			
Notholca (2 spp.)				R	
Polyarthra sp.		O		O	O
Synchaeta sp.	R	R	R	R	
Trichoceras sp.		R	R	R	R
Cladocera					
Alona guttata			R		
Bosmina longirostris	R	D		R	
Ceriodaphinia quadrangula					R
Chydorus sphaericus			R		
Daphnia longispina					R
D. pulex					R
Scapholeberis mucronata			R		
Copepods					
Nauplii	C	C	R	O	O
Adults	R	R	R	R	R

exceeding predatory losses (Havens 1990; Yan et al. 1991), lack of competition from larger grazers (Siegfried 1991; Locke & Sprules 2000), and low or selective predation by invertebrate predators (Havens & DeCosta 1985; Havens 1991) can also be important in determining their occurrence and abundance. In the present study, small Cladocera were low in density in most of the lakes. Interestingly, *Bosmina longirostris*, one of the most common acid species, was absent from Delamere Lake despite its presence in other lakes of this area. Larger cladocerans such as *Daphnia* were never seen in the acid lakes. So it is possible that the abundance of rotifers in these lakes was owing to the lack of competition from viable cladoceran populations. Much higher densities of rotifers in Delamere Lake were probably a direct result of the very high grazable phytoplankton crop in addition to the absence of large cladocerans.

Although less frequent, species like *D. catawba* Coker and *D. pulex* (De Geer) can flourish in acidic waters (Siegfried 1991; Arnott & Vanni 1993). Daphnids can also flourish in polyhumic acid waters (*D. longispina* O.F. Müller, Salonen et al. 1992). In a pH-manipulated lake mesocosm experiment in Delamere Lake, *D. pulex* appeared at ambient pH (mean pH 4.3) as well as in elevated pH enclosures (pH 6 and pH 8) along with large number of *Chydorus sphaericus* (O.F. Müller). *D. pulex* density, however, decreased in the subsequent weeks in the ambient pH enclosures. So it is possible that low pH in Delamere Lake is severe enough to hinder

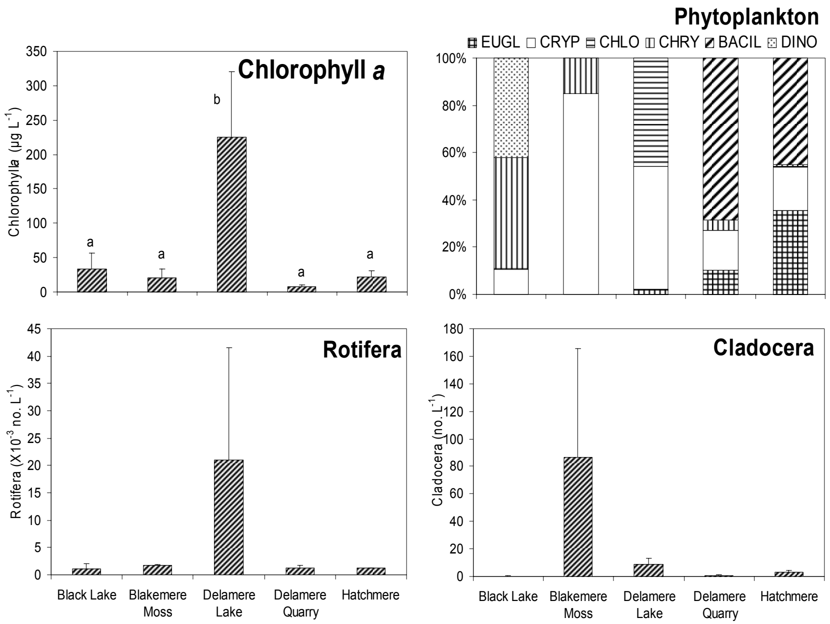


FIG. 5. Overall mean (+SEM, n = 3) chlorophyll *a* concentrations, percentile densities of phytoplankton classes (EUGL, Euglenophyceae; CRYP, Cryptophyceae; CHLO, Chlorophyceae; CHRY, Chrysophyceae; BACIL, Bacillariophyceae; DINO, Dinophyceae) and densities of rotifers and cladocerans in Black Lake, Blakemere Moss, Delamere Lake, Delamere Quarry and Hatchmere (2002 & 2003). Phytoplankton and rotifer values for Delamere Lake are from open-water communities. Means with different small letters are different at $P < 0.05$ level (one-way ANOVA followed by Tukey test).

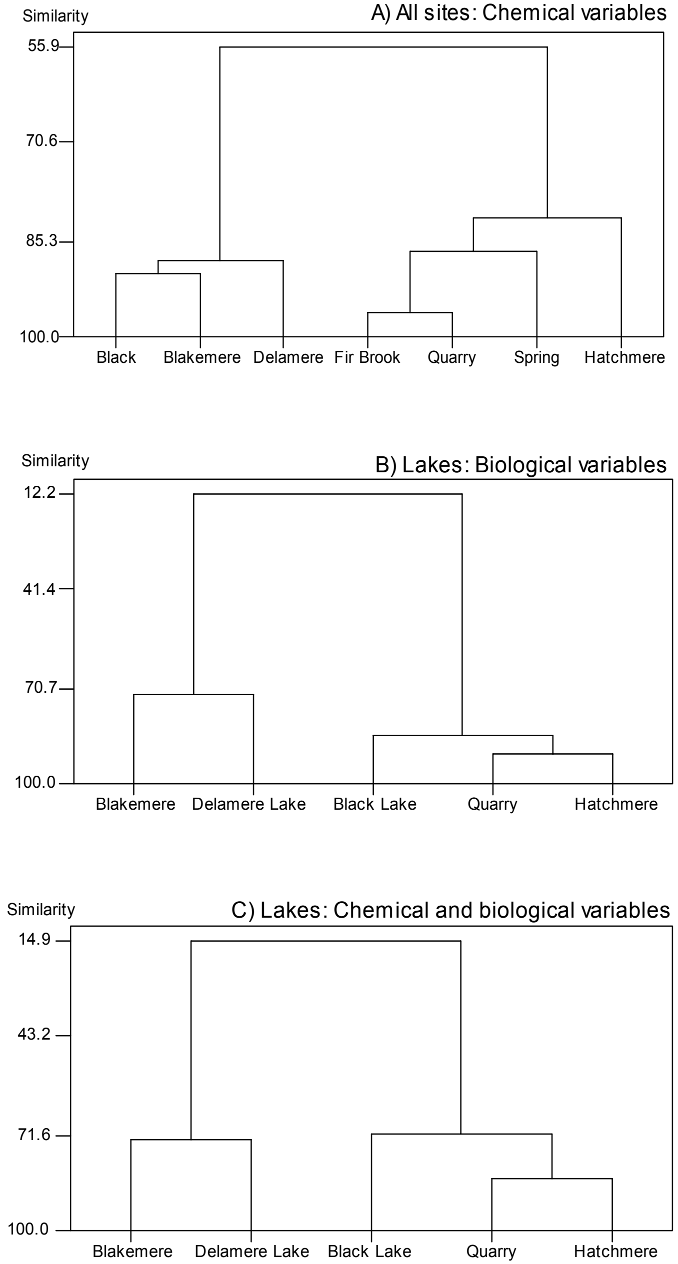
reproduction in *Daphnia*, consequently maintaining a low population (Irfanullah 2004).

We do not have fish or invertebrate predator data for the studied lakes except Delamere Lake and Hatchmere. Low Cladocera density in Hatchmere could be explained by the high biomass of a mixed fish community and a lake bottom lacking submerged vegetation (Moss et al. 1993). In contrast, Delamere Lake was apparently fishless and dominated by phantom midge larvae (*Chaoborus flavicans* (Meigen)). Thus, *Chaoborus* predation was another possible reason for the lack of both small and large cladocerans in Delamere Lake. But mesocosm experiments confirmed that *Chaoborus* predation alone cannot control zooplankton in this lake (Irfanullah 2004). It was thus suggested that low reproduction in *Daphnia* caused by low pH may help invertebrate predation (mainly *Chaoborus*) to control the *Daphnia* population. The absence of larger cladocerans in all, and few small cladocerans in most of the acid lakes in Delamere Forest area requires further study to understand the distribution of these species in acid lakes and the factors controlling it.

High chlorophyll *a* : TP ratio in Delamere Lake suggested low grazing pressure as also understood from its zooplankton composition. A mesocosm study in Delamere Lake also suggested that absence of efficient grazers is one of the main reasons causing profuse algal growth in Delamere Lake (Irfanullah 2004). Zooplankton composition can also explain the lower ratios in other lakes, except Blakemere Moss. In Blakemere Moss, high concentration of TP (mostly SRP) was mainly responsible for low chlorophyll *a* : TP ratio, rather than high grazing pressure.

A pattern?

A series of cluster analyses (the distance between two clusters was determined as single linkage and was measured as Euclidean distance, MINITAB 13.20) was used to calculate the similarities among the studied water-bodies. Despite large variations in surface area, catchment size, depth, residence time, humic contents, nutrient concentrations and primary productivity, the waters of Delamere Forest can be divided into two major groups on the basis of chemical features (Fig. 6A). The first group (Black Lake, Blakemere Moss and Delamere Lake) is characterised by low pH and humic water associated with a 100 % coniferous forested catchment or a peaty catchment or both, which are also the potential sources of high nutrient concentrations. The second group (Delamere Quarry, Hatchmere, Fir Brook and Farm Spring) is a more diverse group with circumneutral pH, < 40 % forested catchment and groundwater supply from inorganic glacial deposits. High chemical closeness between Delamere Quarry and Fir Brook is because this stream receives water from the Quarry. Farm



Spring and Hatchmere showed similarities due to the agricultural activity in the catchment.

Biologically the lakes showed different groupings (Fig. 6B), which were similar to the cluster patterns when both chemical and biological variables were considered (Fig. 6C). Despite very high phytoplankton biomass and a unique community structure, Delamere Lake grouped with Blakemere Moss. The similarity level between these two lakes (biological, and chemical–biological variables cluster analyses) was about 15 % less than the cluster analyses of chemical variables, suggesting distant similarities between them. In contrast, Delamere Quarry and Hatchmere showed similar levels in cluster analyses of chemical and/or biological variables (around 80 % similarity). The clustering of Black Lake with Delamere Quarry and Hatchmere was unexpected, and apparently no particular variable influenced such strong similarity (85 %, biological variables only). But, when all the variables were considered, Black Lake showed 15 % less similarity with the high pH lakes. Strong influence of biological variables on overall (chemical and biological) cluster analyses suggests that water quality cannot necessarily explain the overall biological patterns in these lakes.

Concluding remarks

Delamere Forest has long been drained for forestry. A recent survey has revealed about 130 former mosses in this area (English Nature, personal communication). Both Blakemere Moss and Delamere Lake are sites representing failed attempts in transforming infertile land to forest. Damage was considerable in Blakemere Moss, which was a vast well-established peatland. Restoration of drained peatlands involves increasing the water-table, but even heavily disturbed peatland can show regeneration potential if managed efficiently (Girard et al. 2002). Recent flooding of Blakemere Moss has resulted in some positive signs as peat mosses have appeared at its western edge. Black Lake, on the other hand, is a good example of a resilient peat-bog surviving much past disturbance. Delamere Lake has never been a peat-bog, and at present there is no sign of peat formation. This lake shows some characteristics of meres (small, potentially fertile and maintained principally by groundwater flow;

FIG. 6 *(opposite)*. Similarities among Black Lake, Blakemere Moss, Delamere Lake, Delamere Quarry, Hatchmere, Farm Spring and Fir Brook following cluster analyses of their A) chemical variables (pH, alkalinity, conductivity; and oxygen, SRP, NH_4-N, NO_3-N, TP, TN and silicate-Si concentrations); B) biological variables (chlorophyll *a* concentrations, and densities of phytoplankton classes, individual rotifer species, cladocerans, adult copepods and nauplii) and C) both chemical and biological variables for lakes only. Similarity (%) level of each cluster is indicated.

Reynolds 1979), but is an artificial lake originated from damming and not occupying a hollow in glacial drift deposits. Despite some similarities with other waters of the catchment, it remains an unusual system with extraordinary features. The catchment of an individual lake may explain the functionings of the lake in concern, but generalisation is not always possible, even among ecosystems with largely similar catchments in the same area.

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