THE LIMNOLOGY OF THE EUTROPHIC MERES OF THE SHROPSHIRE-CHESHIRE PLAIN: A REVIEW

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ABSTRACT

The existing literature describing aspects of the distribution, origin, morphometry, hydrology and hydrochemistry of the eutrophic North-West Midlands Meres, together with information on the planktonic, littoral and profundal biotic communities which they support, is reviewed. Characteristic features of the meres are identified, and their influence upon the present-day ecology is discussed. Reference is also made to the historical development of the basins.

I. INTRODUCTION

As a series, the meres of the North-West Midlands are recognised to be among the most important natural freshwaters in Britain (Luther and Rzòska, 1971). Several individual sites are also acclaimed, either for the flora or wildlife they support, or for aspects of their freshwater ecology. However, published information, specifically on the meres or on the related peat-filled sites (the mosses), is still regrettably meagre, although a considerable body of relevant data is scattered in the literature and in unpublished reports and theses. Apart from short general descriptions of the meres (eg Reynolds, 1973a; Reynolds and Sinker, 1976; Savage, 1976), no comprehensive review of the literature has yet been attempted, but Sinker (1962) and Tallis (1973) include many useful references to previous work at (respectively) Shropshire and Cheshire sites.

This paper sets out to summarise the extent of current knowledge relating to the origin, development and present-day ecology of the meres and to identify the underlying characteristics which influence their biology. The account is mostly factual; some personal opinions are given in Section VIII, which also proposes a definition of a mere for the first time.

I have attempted to classify the information in this review by using two type-sizes. The larger type is used to convey the main theme and more descriptive passages. Detailed information which amplifies general comments and conclusions appears in small type. Moreover, literature citations have been grouped at the ends of relevant paragraphs, where long lists in parentheses would otherwise interrupt the flow disproportionately. A glossary of units and notations used in this review is also appended.

II. THE PHYSIOGRAPHIC SETTING OF THE MERES

1. *Structure of the Shropshire-Cheshire Plain*

The Shropshire-Cheshire Plain (Fig. 1) is a well-defined geographical unit, extending from the Mersey estuary to the South Shropshire hills and lying between the Welsh Massif in the west and the Pennines in the east (Ordnance Survey 1:50,000 sheets 108, 109, 117, 118, 126, 127, 137, 138, 139). Over most of its extent the gently undulating Plain lies below 100 m OD, but it is interrupted by several low but prominent hill ridges. The Plain is virtually enclosed by uplands to the east, south
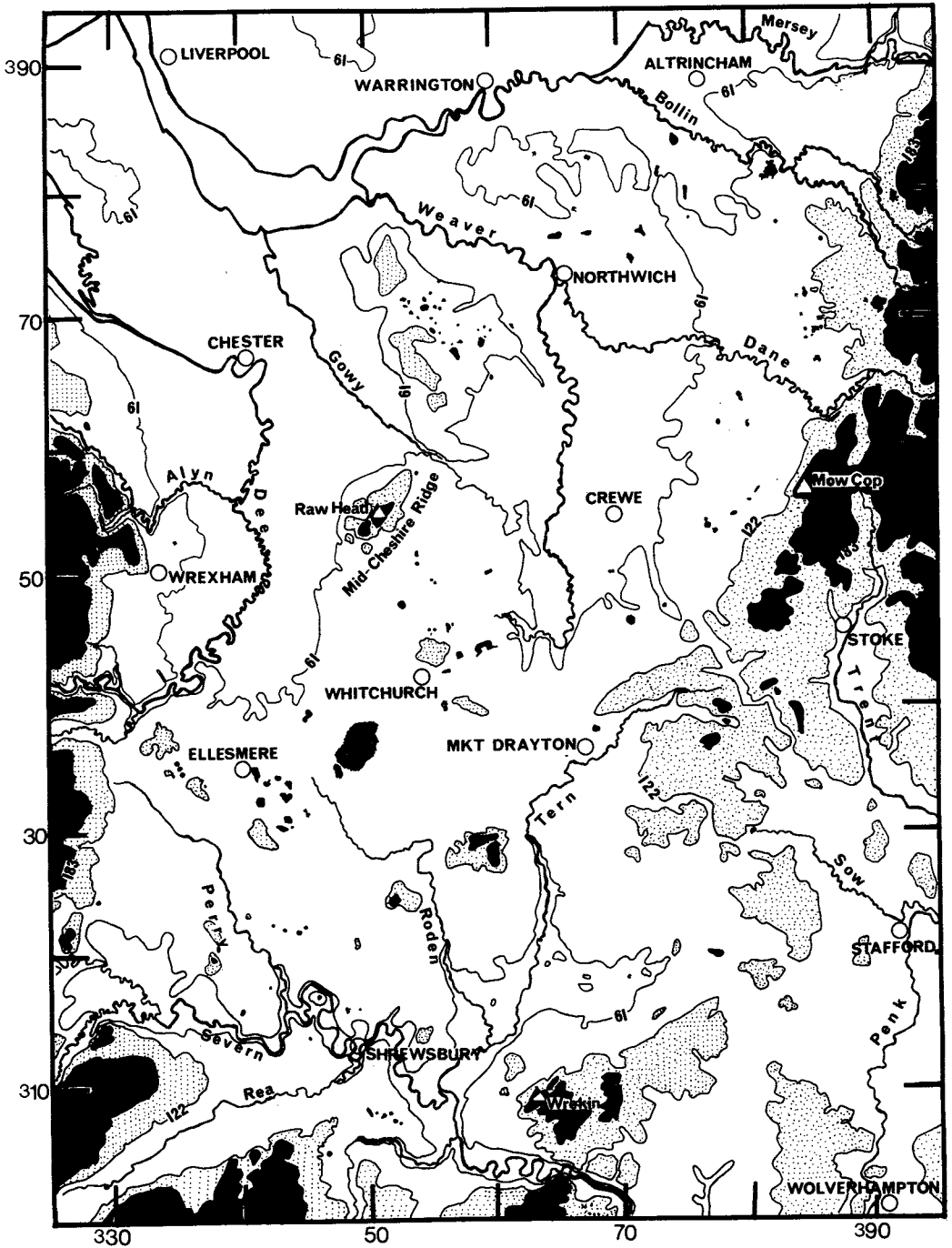
Fig. 1.
The Shropshire-Cheshire Plain. Based on Ordnance Survey.

and west, except for the wide gap separating the Pennines from the South Shropshire hills, through which the lowlands are linked to the Trent valley. Elsewhere the hills are breached by the valleys of the Severn, Vyrnwy and Dee to the west, by the Church Stretton fault to the south, and by the Ironbridge Gorge south-eastwards across Wenlock Edge to the lower Severn basin. The predominant drainage is northwards through the Dee, Gowy and Mersey-Weaver systems, but North Shropshire is drained almost exclusively by the southward-flowing tributaries of the Severn. The Trent drains the eastern fringes of the Plain.

Geologically, the Plain is an elongated saucer-shaped depression of mainly carboniferous rocks (limestones, grits, shales and coal measures) which outcrop around much of its perimeter, enclosing a broad basin of younger Triassic rocks of the New Red Sandstone series. The latter include the mottled Bunter sandstones and pebble beds and the overlying sandstones, marls and saliferous strata of the Keuper series, in a well-defined sequence (Edmunds and Oakley, 1947; see also Hains and Horton, 1969). Rhaetic shales and Jurassic mudstones outcrop near Prees, Shropshire. The various strata are faulted and tilted and exposed surfaces have been much eroded, though several escarpments, including the Mid-Cheshire Ridge which bisects the Plain from north to south rising to a maximum altitude of 230 m OD (Raw Head, SJ 508549) and the broken Elysian-Nesscliff Hill axis which divides North Shropshire from north-east to south-west, remain as prominent features.

Elsewhere, however, the solid rock mostly lies buried under a blanket of unconsolidated glacial drift deposited during the Pleistocene ice advances. Ice-sheets entered the Shropshire-Cheshire basin from two main sources; the more substantial of these originated from the Lake District and south-west Scotland passing southwards by way of the Irish Sea and Lancashire Plain ("Irish Sea Ice"), the lesser deriving from North Wales, through the Severn, Vyrnwy and Dee valleys. The drift deposits vary in thickness, from over 100 m (Johnson, 1971) to only 10-20 m in parts of Cheshire. Drift is thin or absent where the ground level exceeds 200 m.

Structurally, the drift deposits are of two major types: (i) heavy, unstratified boulder clay lodgement tills, laid down at the base of an advancing ice sheet; and (ii) resorted silts, sands and gravels, carried out and redeposited by meltwater issuing from the decaying ice fronts, or in englacial channels beneath the ice sheet. The general distributions are shown in Figure 2.

The stratigraphy of the drifts has been investigated at a number of localities and a comprehensive interpretation of the glacial chronology is at last emerging, though it is still incomplete (see Gemmel and George, 1972). Wills' (1950) differentiation between the "older" and "newer" drifts, whose basal layers were defined by the presence of lodgement tills (the Lower and Upper Boulder Clays, respectively) separated by an assortment of sand and gravel deposits (collectively referred to as the "Middle Sands"), were believed to correspond with two supposed major glaciations. Earlier chronological interpretations are also consistent with two or more glacial incursions having taken place [Peake (1961), Poole and Whiteman (1961), Boulton and Worsley (1965)].

It is clear, however, that much of the "newer drift" surface of the Shropshire-Cheshire Plain can be ascribed to the last glacial stage of the British Pleistocene, now known as the Devensian (Mitchell *et al*, 1973). The type locality (or stratotype) is Four Ashes Quarry, Wolverhampton (in the district once settled by the Devenses

☐ Boulder clay
■ Sand, gravel
▥ Drift -free

FIG. 2.
The superficial drifts of the Shropshire-Cheshire Plain. Based on Geological Survey.

tribe of ancient Britons). Stratigraphical examination of the site (eg Shotton, 1967; Morgan, 1973) has revealed a full sequence of the Devensian deposits, overlying an Ipswichian interstadial horizon. Its dominant features are a Late-Devensian Irish Sea till superimposed upon a series of Middle Devensian gravels incorporating numerous lenses of organic silts and peat which have been variously dated to be between 30,000 and 40,000 radio-carbon years in age. The latter deposits formed when the area was ice-free, and correlate closely with deposits outside the region, notably at Upton Warren and Fladbury in the lower Severn Valley (see Shotton and Strachan, 1959; Coope, Shotton and Strachan, 1961), laid down in relatively milder Middle-Devensian period (the Upton Warren Interstadial). Deeper lenses near the base of the gravel layers are apparent correlatives of the Chelford Interstadial, dated from wood-fragments from peat located in Middle Sands at Farm Wood Quarry, Chelford (60,800-63,000 radio-carbon years before present: Simpson and West, 1958).

The stratigraphic description of Four Ashes necessitated a complete revision of previous interpretations of glacial chronology in the north-west Midlands (Worsley, 1970). The Church Stretton-Wolverhampton limit, previously said to mark the maximum extent of the "older" Irish Sea drifts (Wills, 1950), in fact approximates to the zenith of the last Devensian ice advance. The ice sheet traversed the solid rock of the Long Mynd and Wenlock Edge to an altitude of 240 m OD or more (Pocock and Whitehead, 1948).

This advance is dated by the presence of marine mollusc shells in Upper Irish Sea boulder-clay deposits near Sandiway, which yielded a radio-carbon date of 28,000 years BP (Boulton and Worsley, 1965). Moreover, this may have been the only Devensian glaciation of the region, since there is no certain evidence, either at Chelford or Four Ashes, to confirm earlier Devensian glacial incursion into the Shropshire-Cheshire basin. Apart from the brief flourishing of a subarctic flora

during the Chelford and Upton Warren Interstadials, however, the climate must have remained generally cold until after the Late Devensian maximum.

Nevertheless, there remain many structural features of the drift which indicate that major time sub-divisions exist within the Late Devensian: the presence of many till lenses and fragments in middle sands, identified by Evans and Arthurton (1973), suggest that the dating of the drifts is oversimplified. Some idea of the complicated nature of drift depositional processes can be gained from published case studies in regions which are still glaciated today, for instance, Boulton's (1970) work on Svalbard glaciers. More significantly, the undulating Plain is interrupted by abrupt moraine belts of low, steep-sided hillocks of poorly-sorted ablation till (laid down locally at ice fronts at their zenith or during long periods of relative stagnation) interspersed with stratified outwash deposits. The most significant belt is the complex bilobate system which straddles the Plain along the Wrexham-Whitchurch-Bar Hill line (see Fig. 3). Smaller analogues occur elsewhere: the features of the Kingsley-Sandiway moraine are especially distinctive.

Boulton and Worsley (1965) demonstrated considerable differences, both in the relative erosion of the land forms, and in the extent of leaching from the upper drift horizons, occurring on either side of the Wrexham-Bar Hill moraine belt. Moreover, surface drifts of Welsh provenance overlie Irish Sea deposits in the area west of Shrewsbury. These represent the most recent "Little Welsh Advance" (Wills, 1950) which has been roughly correlated with the Wrexham stage of the Irish Sea ice-front (Peake, 1961). There is some evidence that the two fronts met in the Ellesmere District (Worsley, 1970; Shaw, 1972). The original explanation of Boulton and Worsley, that the Wrexham-Bar Hill system represented the limit of "newer drift", is now obviously redundant, but a correct interpretation has yet to be resolved. Three possibilities can be advanced. It may represent (a) a later end moraine, of the type suggested by Boulton and Worsley (1965), (b) a retreat moraine, or (c) some pre-existing feature overridden by the Late Devensian advance (eg Poole, 1968). The latter possibility raises several objections: the "freshness" of its ice-contact land forms seems inconsistent with a further phase of glacial erosion, and the "Little Welsh" deposits, which overlie Irish Sea drifts to the south would then need to be rather younger than the Wrexham moraine. Thus, the latter is more likely to be Late Devensian in age. As Beales (1976) has pointed out, the differences between possibilities (a) and (b) are mainly ones of definition. Peake (1961) recognised at least four end moraines of Irish Sea drift in the Ellesmere district. The most northerly (the "Flintshire Maelor") moraine forms the present divide between the Dee and Severn catchments, whereas the other three are each bordered by outwash deposits flattening out into lake-like depressions, which drain southwards. Peake considered the complex to have been formed by a re-advance, with a succession of stagnation episodes in a slow general recession from south to north.

Gemmel and George (1972) critically considered the evidence then available and concluded that the Wrexham-Bar Hill moraine belt represented a long equilibrium phase in the recession of the Late Devensian glaciation, before the ice finally wasted away northwards. Boulton and Worsley's (1965) field obvservations indicate that this would have occurred significantly later than the initial retreat from the Wolverhampton limit. Being nearer its sources of glacial flow, a contemporaneous re-advance of Welsh ice remains plausible. Moreover the broad tract of irregular hummocky drift bordering the Pennine foothills in east Cheshire (the "Marginal
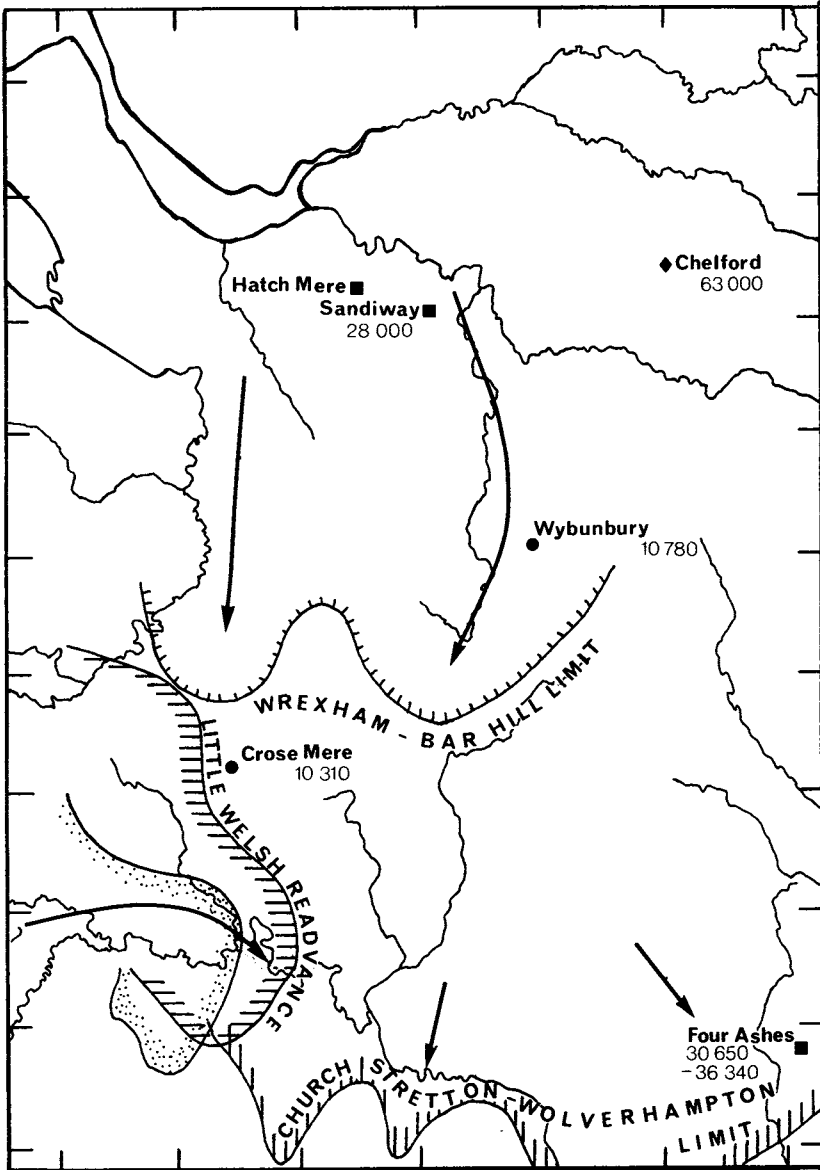
FIG. 3.
Sketch map to show approximate ice front limits and principal Early (◆) Mid- and Late-Devensian (■) and Flandrian (●) radio-carbon dates (years before present). Based on Fig. 3 of Gemmel and George (1972), with later information added.

Belt" of Evans *et al*, 1968; see also Tallis, 1973) must also have been formed between the main ice sheet and the peripheral ice downwasting from the hills during a prolonged early stage in the melting of the Irish Sea ice. Modifications to the course of the Alyn River, described by Peake (1961), may also have occurred at this time.

These considerations underline the need to resolve the events towards the end of the Late Devensian period. At present, the maximum extent of the ice sheet cannot

be dated with certainty. The maximum to the east of the Pennines occurred about 18,000 years ago (Mitchell *et al*, 1973), but on the Isle of Man, organic deposits post-dating the Late Devensian glaciation have an age of nearly 19,000 radio-carbon years. Synchronous maxima cannot therefore be assumed. The subsequent retreat stages of the Late Devensian ice front in the Shropshire-Cheshire basin also remain obscure. Several sites in western Britain were ice-free and had begun to lay down organic deposits before 14,500 BP (Pennington, 1975). Morgan's (1973) geological investigations in south Staffordshire, which included the dating of organic sediments at Stafford (13,500 BP), suggest that the area was not free of ice before 16,000 BP, though the wealth of fossil ice wedges and polygons indicate that cold, periglacial conditions persisted for some long period after the ice front had retreated further northwards. The existence of such conditions would be consistent with the proposed Wrexham-Bar Hill stagnation and "Little Welsh" advances.

In contrast, the final wasting of ice from much of Cheshire must have been relatively rapid, apart from the temporary halts such as the one represented by the Kingsley-Sandiway Moraine (Worsley, 1970). The minimum age of these features presumably approximates to the date of the lowermost organic sediments encountered at the base of Blelham Bog, Cumbria, and other sites in Western Britain (14,300-13,000 BP; see Pennington, 1975) and predates the lower pollen assemblage zones of Crose Mere, Shropshire, which Beales (1976) has correlated with Bølling deposits in the Blelham Bog sequence (Pennington and Bonny, 1970). This suggests that the Ellesmere District was ice-free before 12,000 BP.

Other evidence consistent with a more or less rapid wastage in the post-Wrexham period may be cited. In Cheshire, thin spreads of supraglacial sand and gravel originated through the *in situ* downwasting and fragmentation of ice (Evans *et al*, 1968). For a time, a substantial meltwater lake was ponded-up between the retreating ice front and the Wrexham-Bar Hill Moraine, with its level regulated at about 100 m by the Adderley Gap; sandy outwash deltas built out into the lake at Heaton Moor and Rudheath (see Evans *et al*, 1968), and from the Kingsley-Sandiway Moraine to form the distinctive topography of the Delamere Forest (Worsley, 1970). Similar, though smaller, meltwater impoundments regulated by topographic features evidently occurred near Madeley, Staffs. (Yates and Moseley, 1957), Ellesmere (Peake, 1961) and at Venus Bank and Eyton-on-Severn (Lake Buildwas: Shaw, 1972). However, the existence of a widespread late-glacial Lake Lapworth, initially regulated at 90 m OD (ie covering much of north Shropshire) and whose overspill across Wenlock Edge reputedly cut the Ironbridge Gorge and diverted the flow of the Severn southward to the Bristol Channel for the first time (Wills, 1924), has been questioned by Shaw (1972). Fast current-bedded englacial stream deposits near Shrewsbury, levelled at 45·7 m OD (similar to the valley floor at Ironbridge), suggest that the Gorge was already open when Irish Sea ice still covered north Shropshire.

2. *The distribution of meres*

More than sixty open water meres and pools exceeding 1 ha in area and over 200 peat-filled mosses occupy hollows occurring in the drift surface of the Plain. With one exception (Danes Moss, $\sim$150 m OD), their surfaces stand below the 120 m contour. The distribution is neither uniform nor random, most of the sites occurring in distinct local groupings (see Fig. 4). Major clusters are centered
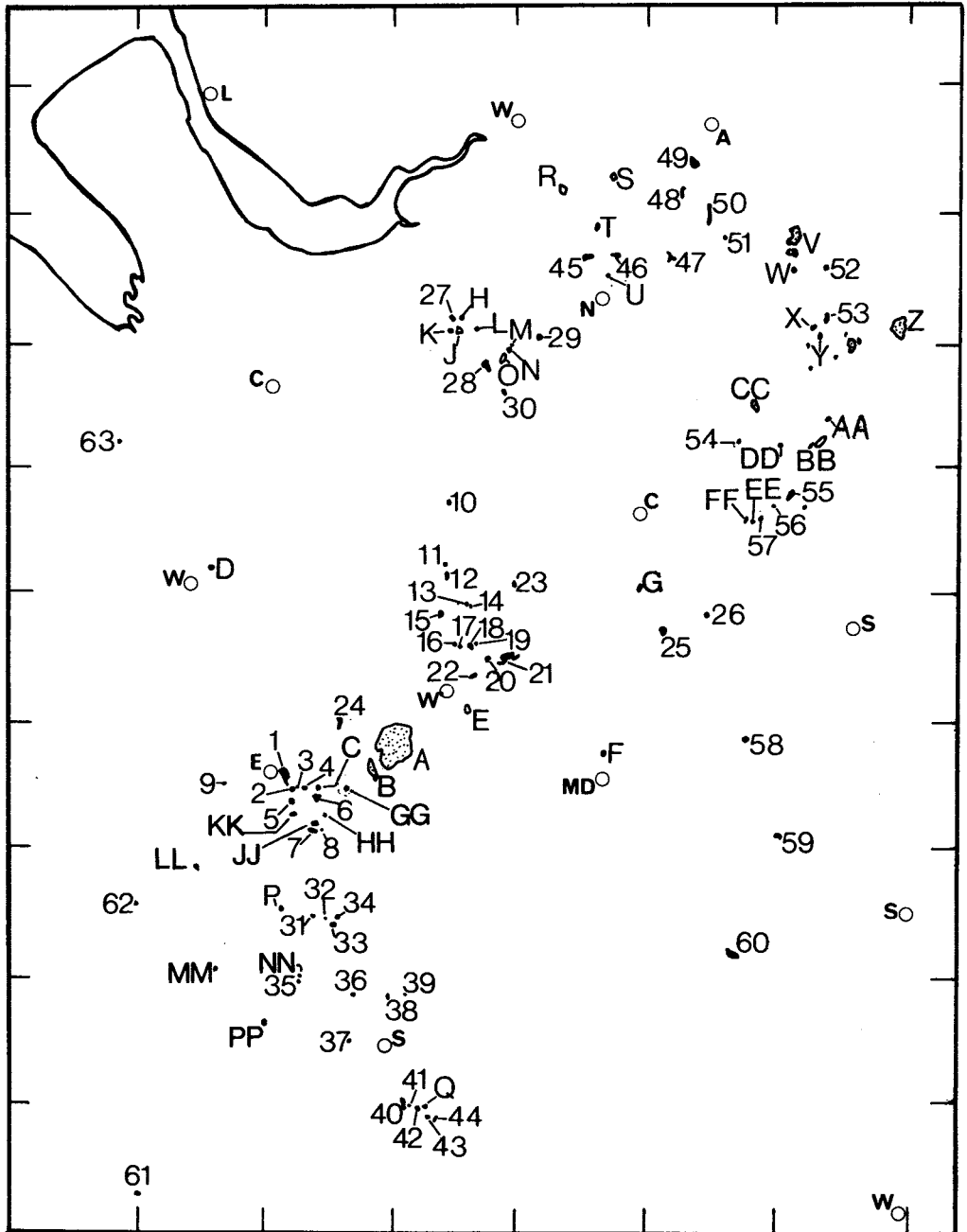
FIG. 4.

Sketch map to show distribution of meres and mosses in the Shropshire-Cheshire Plain. Applying "nearest neighbour analysis" to the distribution of the 63 numbered meres within the total area of 5,400 km², the factor $\emptyset$ (=md^2, where m is the density of meres per km², and d is the mean distance of each mere from its nearest neighbour) has been evaluated at 0·103, representing underdispersed or clumped distribution (random distribution would have yielded a result of $\emptyset$>0.25). For identification of sites, see Tables 1 and 13. Original.

Table 1. *The principal meres of the Shropshire-Cheshire Plain*

Based mainly on the data of Beales (1976), with additional information. Site numbers refer to locations on the map (Fig. 4). *Indicates meres known to stratify in summer. Reproduced from Reynolds (1978a) with permission.

Site No.	Name	Grid Reference (all SJ)	Area (ha)	Max. depth (m)
ELLESMERE GROUP				
1.	Ellesmere Mere*[a]	407350	46.1	18.8
2.	Blake Mere, near Ellesmere*[b]	416334	8.4	13.5
3.	Kettle Mere*[c]	419341	1.7	7.0[d]
4.	Newton Mere*[b]	425342	8.3	16.8
5.	White Mere*[c]	415330	25.5	13.8
6.	Cole Mere*[c]	434333	27.6	11.5[c]
7.	Crose Mere*[f]	430305	15.2	9.3
8.	Sweat Mere[g]	437306	~0.2[h]	<2
9.	Hardwick Pool	371338	3.6	1.5
WHITCHURCH GROUP				
10.	Peckforton Mere[g]	532577	1.0	—
11.	Chapel Mere	541519	6.5	2.4
12.	Deer Park Mere	542508	9.4	3.4
13.	Norbury Big Mere	557492	1.6	0.9
14.	Norbury Little Mere	558494	1.5	1.2
15.	Bar Mere	537479	9.7	5.6
16.	Quoisley Big Mere	546456	4.0	2.4
17.	Quoisley Little Mere	549456	2.2	1.8
18.	Marbury Big Mere	559456	10.5	8.0
19.	Marbury Little Mere[g]	563457	1.3	—
20.	Oss Mere[g]	566438	9.5	—
21.	Comber Mere*[i]	586445	51.5	11.8[j]
22.	Blake Mere, Whitchurch	559426	3.7	4.6
23.	Baddiley Mere[g]	596504	6.7	—
24.	Hanmer Mere[g]	454395	17.7	20.0[k]
WOORE GROUP				
25.	Doddington Pool	705464	19.3	1.3
26.	Betley Mere	749479	9.3[l]	1.8
DELAMERE GROUP				
27.	Hatch Mere	553722	4.7	3.8
28.	Oak Mere	575677	18.3[m]	5.6
29.	Petty Pool*[n]	619701	11.7	3.1
30.	Little Budworth Pool	598657	4.9	1.0
BASCHURCH GROUP				
31.	Berth Pool	430234	2.9	3.8
32.	Birchgrove Pool	436232	1.7	4.7
33.	Fenemere	446229	9.4	2.2
34.	Marton Pool, Baschurch	448234	6.8	2.8
SHREWSBURY GROUP				
35.	Cottage Pool	419182	1.8	1.4
36.	Isle Pool[g]	462170	5.8	5.8[o]
37.	Oxon Pool	454139	1.4	3.0
38.	Alkmond Park Pool	480160	4.4	5.1
39.	Hencott Pool[g]	492160	3.5[l]	—
40.	Bomere Pool	500080	10.3	15.2
41.	Shomere	504079	1.3	4.3
42.	Betton Pool	511079	6.4	10.9
43.	Top Pool	520072	1.8	2.8
44.	Berrington Pool	525072	2.5	12.2

Site		Grid Reference		
No.	Name	(all SJ)	Area (ha)	Max. depth (m)
KNUTSFORD GROUP				
45.	Budworth Mere	657769	39.4	7.2
46.	Pick Mere[g]	684771	17.5	—
47.	Tabley Mere	723767	19.4	4.4
48.	Mere Mere	733817	15.8[p]	8.1
49.	Rostherne Mere[*][q]	742842	48.7	27.5[r]
50.	Tatton Mere[g]	755802	31.7	—
51.	Booth's Mere	768784	6.4[s]	—
MARGINAL GROUP[t]				
52.	Radnor Mere[g]	847758	8.3	—
53.	Redes Mere	849717	17.0	4.5
54.	Taxmere[g, u]	780264	1.2	—
55.	Rode Pool[g]	815575	12.7	—
56.	Lawton Mere[g]	804568	1.3	—
57.	Alsager Mere[g]	793546	3.5	—
ISOLATED MERES				
58.	Maer Pool	789385	5.5	1.7
59.	Cop Mere	802298	16.8	2.7
60.	Aqualate Mere[g]	772204	72.5	—
61.	Marton Pool, near Chirbury[g]	295027	13.7	—
62.	Llynclys Pool	286244	2.8	5.8
63.	Padeswood Pool[g]	278619	~1.0[v]	—

NOTES

[a] *— Mr E. A. Wilson, *personal communication*

[b] *Tait-Bowman (1976)

[c] *— Miss A. E. Clark, *personal communication*

[d] C. M. Tait-Bowman recorded 7.3 m (*personal communication*).

[e] Reynolds (1973b) gave 16.5 m based on local information.

[f] *— Reynolds (1971a, etc).

[g] Not included in Beales' (1976) data.

[h] Open water in 1975, but still shown as 1.6 ha on OS Maps.

[i] *— author, unpublished.

[j] Griffiths (1925) gave 22 m, but this depth is unsubstantiated.

[k] Reynolds (1973b) from local information, but depth unsubstantiated.

[l] Area includes extensive reedswamp.

[m] Most references quote Lind's (1949) figure of 21 ha.

[n] *—Jones & Savage (1969).

[o] Griffiths (1925).

[p] Main mere only: the small north basin separated by concrete retainers and sluice has been excluded.

[q] *— Brinkhurst & Walsh (1967).

[r] Brinkhurst & Walsh (1967), Grimshaw & Hudson (1970), Reynolds and Rogers (1976) all record depths of c. 30 m. However, the bottom is very soft and its limits are determined with difficulty.

[s] Beales (1976) cites an area of 1.5 ha and a max depth of 0.9 m for Booths Park Pool, which he states "may or may not be Booth's Mere". The extent of the mere, approximately as shown on OS maps, has been verified by the author (March, 1977).

[t] The Marginal Group refers to meres within the eastern 'Marginal Belt' of hummocky drift (Evans *et al*, 1968, see also Tallis, 1973).

[u] The mere is not strictly within the Marginal Belt (of Evans *et al*, 1968) but is included here for convenience.

[v] Area in 1971. Pool was then heavily silted and diminishing in area; OS maps show area of water as about 5.5 ha.

around Delamere, Knutsford, Congleton, Ellesmere, Whitchurch and Shrewsbury, in areas dominated by sand and gravel drifts (cf Fig. 2), even though superficial boulder clay covers some 70 per cent of the Plain. Tallis (1973) showed that 66.4 per cent of the north Cheshire basins occur in sands and gravels; a similar percentage

(66.7 per cent) of the 48 meres cited in Fig. 11b lie in predominantly sandy hollows. Many of the basins occur in the hummocky topography associated with the moraine systems or of the eastern "Marginal Belt" (Sinker, 1962; Tallis, 1973). Almost all of them lie within the limits of the most recent ice fronts (cf Fig. 3).

3. Morphometry of mere basins

The major meres are listed in Table 1 together with their approximate areas and maximum known depths. Note that there are two "Blake Meres" (2 and 22) and two "Marton Pools" (34 and 61). Few meres have been systematically sounded; the depth data rely mainly on Beales' (1976) surveys, and should be regarded as being provisional. They are, however, unlikely to be grossly underestimated; where greater depths have been quoted (eg Griffiths, 1925; Reynolds, 1973b) the information was probably not first-hand. The depths of 45 meres are significantly correlated with their areas (Fig. 5); mean values of 6.3 m and 11.6 ha (respectively) have been calculated.
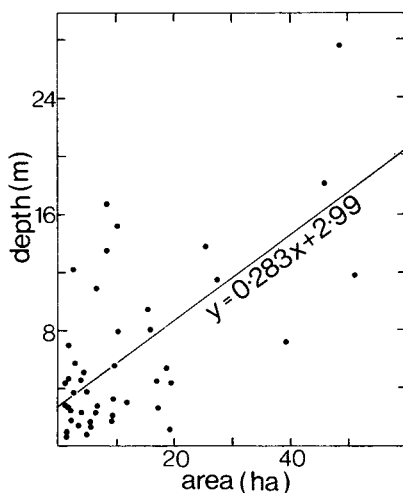

FIG. 5.
The relationship between maximum known depth and the present water surface area of 45 meres, presented in Table 1. Original data of Beales (1976).

Many smaller mere basins are crater-like depressions, roughly circular or slightly elongated in shape, with at least some shores shelving away steeply. Tallis (1973) showed that several small peat basins are markedly asymmetric in profile, while the deepest points of sounded meres are somewhat eccentric. Larger meres may contain more than one basin (this seems to be true for Blake Mere (near Ellesmere), Cole Mere and Doddington Pool) or to include deeper localised troughs (eg Ellesmere Mere; see Fig. 6a). The surfaces of several meres have been artificially lowered by drainage modifications (eg Cole Mere, Crose Mere) or raised by damming (eg Comber Mere, Tabley Mere, Booth's Mere), often resulting in a lake of more irregular shape.

Some of the more extensive raised bog systems occupy one or more relatively shallow saucer-shaped depressions; their present peat deposits rarely exceed 3 m in

depth (eg Danes Moss, Congleton Moss and perhaps Lindow Moss: Tallis, 1973). Aqualate, the largest mere, also seems to be universally shallow over much of its extent (M. M. Pratt, *personal communication*).

4. *Climate*

The factors which contribute to the present climate of the Shropshire-Cheshire Plain are dominated by two principal components: one is the proximity of the Plain to the western seaboard, which ensures temperate, humid sub-oceanic conditions throughout most of the year; the other is its position in relation to the Welsh massif, which effectively provides a rain-shadow from westerly winds and eastward-passing fronts. Climatic data for Ringway (near Manchester) and Shawbury (near Shrewsbury) are compared in Table 2: although the periods covered do not coincide, and are therefore not strictly comparable, the figures are consistent with a weakening oceanic influence further south, with more sun, less rain and greater temperature extremes at Shawbury.

Table 2. *Selected climatic data from Ringway and Shawbury*

Data from Ringway drawn from Pritchard (1961). Shawbury figures prepared from data kindly supplied by the Meteorological Office

Station data		Ringway		Shawbury	
	Grid reference	SJ 818850		SJ 553220	
	Altitude (m)	76		72	
	Period covered	1916-1950		1946-1970	
Precipitation	Mean Annual Total (mm)	802.0		672.9	
	Av. Ann. wet days	193		177	
	Av. No. of days with snow lying	13.0		14.6	
Temperature		min	max	min	max
	Annual mean	5.7	13.1	5.5	13.1
Monthly means	January	1.3	6.1	0.8	5.9
	February	1.9	7.0	0.5	6.3
	March	2.1	9.7	1.7	9.3
	April	3.8	12.3	3.6	12.5
	May	6.4	15.9	6.4	15.9
	June	9.4	19.1	9.3	19.1
	July	11.6	20.5	11.1	20.0
	August	11.3	20.2	10.8	19.8
	September	9.4	17.5	9.2	17.7
	October	6.3	13.3	6.6	14.0
	November	3.4	9.1	3.6	9.2
	December	1.9	6.4	1.6	6.6
	Av. Ann. days with ground frost	88.0		110.0	
Sunshine	Av. Ann. hours	1201.5		1378.4	
	Av. Ann. days with gales	3.0		3.2	

5. *Current state of the meres*

The major land-use of the Shropshire-Cheshire Plain is agriculture, industrial and urban development being largely confined to the seaboards and coalfields at the periphery of the region. Traditionally, the district is renowned for dairy farming, with clay-derived soils given over to permanent pasture. The meres have contributed to this economy in providing watering for stock. There has been some expansion in arable farming over the last three to four decades, especially on the

well-drained sands and gravels (Howell, 1941; Slack, 1945). In both cases, farm-land extends to the edges of the meres. Inevitably, the increased use of inorganic fertilisers influences the chemical composition of natural drainage waters, but few meres can be described as seriously polluted.

Several meres have been "landscaped" into parklands, with ornamental trees and exotic introductions to the local flora present in their vicinities. Blake Mere (near Ellesmere) and Shomere are encircled by plantations of coniferous and broad-leaved trees.

The catchments of a number of meres have been urbanised by domestic or industrial development. Mere Mere, Alsager Mere and Lawton Mere are flanked by "executive" housing; Ellesmere Mere and Booth's Mere lie close to the town centres of Ellesmere and Knutsford respectively. Inevitably, the appearance of each of these lakes has been altered by reedswamp removal and shoreline strengthening, but chemical effects on these waters, for instance, through sewage disposal, may be negligible; Padeswood Pool, Clwyd, however, receives treated effluent from the town of Buckley.

Many meres are legitimately used for recreational pursuits. The most widespread activity is angling, with fishing rights leased almost everywhere to clubs. Sailing and water skiing are restricted to certain sites. Ellesmere Mere, Pick Mere and, to a lesser extent, Hatch Mere, are popular tourist sites. Shorelines and environs have been deliberately modified to cater for large numbers of casual visitors, or constant trampling and car parking have achieved a similar effect.

Nevertheless, a number of sites retain much of their natural vegetation and wild-life and, collectively, show varying degrees of chemical richness, biological productivity and colonisation by emergent plants which characterise the series as a whole. These examples are worthy of continuing formal protection and scientific research.

III. The Origins of the Mere Basins

The present meres and mosses are an integral feature of the drift landscape which had already been substantially cast 14,000 years ago, in the wake of the retreating ice fronts. Although their initial formation was not necessarily a part of any contemporaneous depositional process, it is now known that several meres have been continuously water-filled since 12,000 BP (Beales and Birks, 1973) or earlier (Beales, 1976; Birks in preparation). Several explanations for the origin of the basins have been advanced, but the range of their morphometric variations render it unlikely that any single explanation is universally applicable. These possibilities are considered below.

(a) *Vestigial meltwater lakes*. The popular view that meres are vestiges of once more extensive meltwater lakes (eg Wilson, quoted by Galliford, 1960) is, in a sense, accurate, although the largest examples were, at best, transient features if they existed at all (see preceding section); neither does it account for the origin of local persistent depressions. Smaller examples progessively drained away, the overspill exploiting pre-existing gaps in the surface topography, which are now followed by "underfit" streams (eg the Perry and Roden gorges at Ruyton and Preston Brockhurst respectively: Peake, 1961). Such lakes became filled by laminated mineral deposits at an early stage (eg Lake Buildwas: Shaw, 1972; Pool Meadow,

Bomere Heath: Reynolds, 1973c), and some became overlain by valley mire systems (eg Baggy Moor, Burlton Moor: Pocock and Wray, 1925; further examples are given in Sinker, 1962).

The shallow basins now occupied by the larger expanses of raised bog may have originated from more persistent proglacial lakes impounded at the ice front by morainic drift. Possible examples include Fenn's Moss (E. G. Poole, in Oswald and Herbert, 1965; see also Peake, 1961); conceivably, Lindow Moss (Birks, 1965a) and Congleton Moss (Raybould, 1970, quoted by Tallis, 1973) also arose in this way, although the oldest peat deposits yet recovered are considerably more recent (Pollen Zones VI-VII, ie less than 9,000 years old). Danes Moss occupies the site of an ice dammed lake ponded up in the head waters of the Bollin catchment (Evans et al, 1968).

(b) *Kettle Holes*. At the stagnant ice fronts, detached ice blocks slumped and became buried by ablation and outwash deposits. As the ice blocks melted out, deep crater-like kettle holes separated by hummocks of drift formed the distinctive topography of the moraine and marginal belts. On geomorphic evidence many present mere and moss sites, especially those of the Delamere Forest, apparently occupy true kettle holes (eg Flaxmere; Tallis, 1973). Many larger basins may include kettle holes whose features are submerged by more extensive areas of water or peat (eg Ellesmere Mere, shown in Fig. 6a; Danes Moss: Evans et al, 1968). Moreover some kettle holes in the Ellesmere area are completely dry (Sinker, 1962; see also section IV). Again, basal biogenic sediments have yet to be shown to be generally of an age compatible with a late-glacial origin of the basins, though these have been recovered at at least two sites (Bagmere: Birks, 1965b; Flaxmere: Tallis, 1973).

(c) *Moraine-dammed hollows*. More linear basins in morainic drift that are not obviously kettle holes may have been enclosed by successive terminal moraine ridges.

Initially, meltwater streams would have exploited the intermediate gaps, but as the ice front receded further and meltwater escaped elsewhere, their erosive power would have been reduced. Eventually, standing water would have remained only in the deepest depressions. Further fluvial erosion generated by their limited catchment areas would have been insignificant, thus enabling the early postglacial topography to have been preserved as well as it has. The "Crose Mere complex" (Sinker, 1962) is a probable example of an erstwhile single moraine-dammed basin, having two roughly parallel hollows (now occupied respectively by Whattal Moss and Crose Mere) uniting at the eastern end of a morainic gravel ridge (where Sweat Mere now stands); finer, evenly bedded sands and gravels which underlie the present peat cover attest a previous extent of the lake (Pocock and Wray, 1925). Other basins, which may or may not include true kettle holes, may have originated in this way.

The series of water- and peat-filled hollows in the Shrewsbury area mostly lies within a belt of gravel ridges having a general NW-SE tendency, which were deposited from and aligned by fast-flowing englacial streams draining towards the Ironbridge Gorge (Shaw, 1972; Pannett and Morey, 1976). As the ice melted away, the intermediate hollows became inundated by braided meltwater streams and backfilled with outwashed sands and gravels; some were eventually isolated as
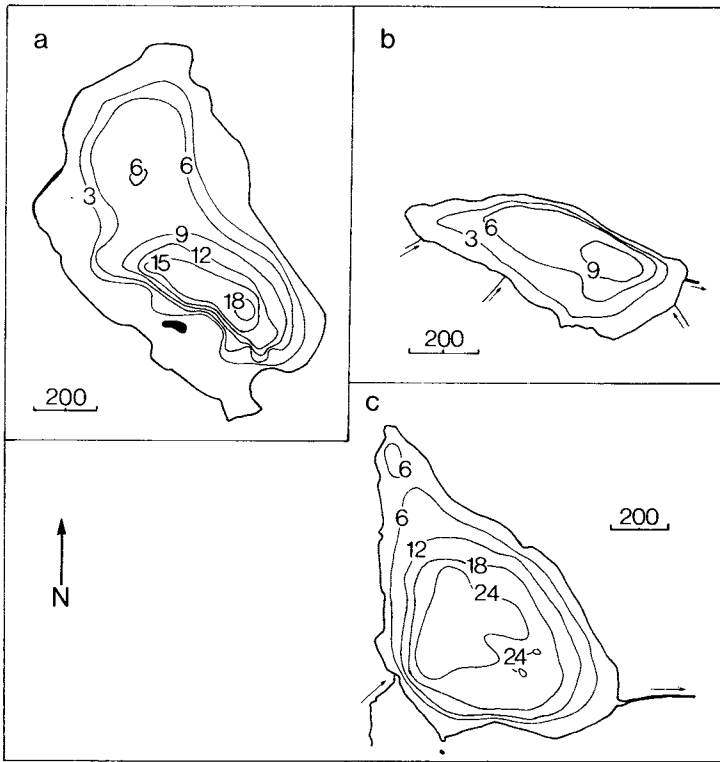
FIG. 6.
Bathymetry of (a) Ellesmere Mere, (b) Crose Mere and (c) Rostherne Mere. Underwater contours and horizontal distances in metres. Fig. 6a is drawn from the depth data in Fig. 4 of Wilson (1966); 6b is re-drawn from Reynolds (1975a) and 6c is re-drawn from Pritchard (1961), which was originally based on the survey of Tattersall and Coward (1914). The contours labelled 6 m, 12 m, etc, are actually 20 ft, 40 ft, etc.

shallow basins, perhaps including kettle holes. Many of the basins are now dry, though several contain water (eg Bomere Pool, Alkmond Park Pool), or are partially (eg Shomere) or wholly infilled (eg Betton Abbots Moss) by peat (see also Pannett and Morey, 1976). Post-glacial diversions in the course of the River Severn which had already carved a deep, meandering channel in the gravel to leave it as a terrace, apparently resulted from its cutting into and exploiting similar basins (Pannett and Morey *loc cit*). These hollows are analogous with those described above, except that the enclosing drifts are alluvial.

(d) *Englacial plunge pools.* Forrest (1941), noting the NW-SE tendency of the Ellesmere, Whitchurch and Shrewsbury group of meres, proposed that their basins were cut out by seasonal falls of meltwater from the still-active ice surface to the drift floor on the lee side of solid rock features. This theory is scarcely supported by the stratigraphy of the adjacent drifts, nor does it match the distribution of glacial land forms across the Shropshire-Cheshire Plain. On present evidence, this explanation can be dismissed.

(e) *Periglacial pingoes.* Oakhanger Moss and White Moss, near Alsager, lie in sharply defined depressions with raised rims. The peat apparently rests on "Middle Sand" deposits suggesting that some localised uplift has taken place, perhaps as a result of frost mound (or pingo) formation (Evans *et al*, 1968). The basins, which are located in the "Marginal Belt", would have developed outside the main glacial margins under "permafrost" conditions, and the progressive accretion and coalescence of ice lenses were sufficient to raise the ground surface into discrete domes. Collapse of the overlying drift would follow the eventual melting of the lens, in a manner analogous to kettle hole formation.

(f) *Post-glacial subsidence hollows.* Saliferous beds belonging to both the Upper and Lower Keuper series underlie large areas of drift in central Cheshire (Fig. 7). Natural subsidence of the drift surface as a result of local "wet-head" solution of buried salt has long been recognised (White, 1860; Calvert, 1915; see also Tallis, 1973). A number of subsidence lakes ("flashes") have developed in recent centuries as a direct consequence of industrial brine pumping in the Northwich and Winsford districts. Green (1965) suggested that natural subsidence could account for the step-like terracing beneath the surface of Wybunbury Moss. Tallis (1973) showed that the number of meres and mosses in North Cheshire either underlain by or lying close to salt-bearing strata was greater than could be expected from a random distribution. Taylor (1965) and Evans (1965, and also in Evans *et al*, 1968) envisaged local salt solution to have been sufficiently widespread and enduring to explain the origin of basin sites occurring in thin (10-20 m) drift deposits overlying saliferous beds and having structural features consistent with subsidence. Several meres in the Knutsford group (eg Budworth Mere, Pick Mere) which coincide with the limit of the up-dip of the Lower Keuper saliferous beds, and some smaller peat-filled hollows (eg Bagmere, Brookhouse Moss, Soss Moss) overlying the base of the Upper Keuper saliferous series apparently satisfy these conditions (Taylor *et al*, 1963; Evans, 1965). Other meres suggested to have originated through natural subsidence
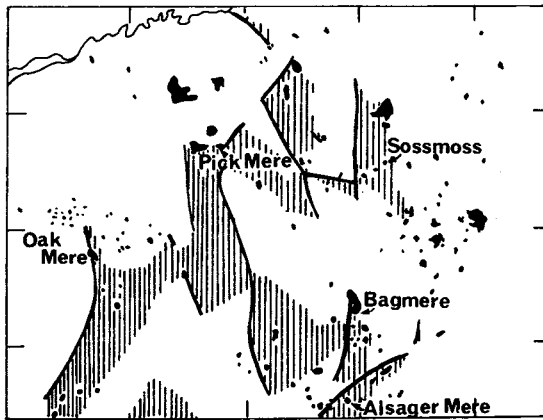

FIG. 7.
Sketch map to show the approximate distribution (shaded area) of the saliferous strata (of both the Lower and Upper Keuper series), and the occurrence of basin sites in the superficial drifts. Named sites have been suggested to have originated through subsidence of the drift following wet-head solution of saliferous rocks. Based on Fig. 3 of Tallis (1973).

include Alsager Mere, Lawton Mere, Redesmere and Taxmere (Evans *et al*, 1968).

Subsidence could also have occurred in existing (possibly glacial) hollows: Pritchard (1961) included a suggestion that Rostherne Mere, whose depth exceeds the estimated thickness of the adjacent drifts, may have been correspondingly enlarged; the bathymetry is inconclusive on this point (Fig. 6c). Secondary subsidence has probably occurred at Wybunbury Moss (Green and Pearson, 1977) while subsidence and inundation of a hollow already filled with peat could have brought about the anomalous structure of the Oak Mere basin (see Lind, 1951).

Coal-mining in Flintshire and Staffordshire has also led to widespread subsidence of the ground surface. Wedd and King (1924) described subsidence hollows near Padeswood, Clwyd, but Peake (1961) regarded the area as one of kettle-drift. Stratigraphical confirmation is required.

Without more detailed information from more sites, it is impossible to conclude which of these modes of origin is more common or typical of the meres generally. However, fortuitously or not, their basins occur everywhere in intimate association with copious deposits formed during deglaciation. In this single character, the meres are distinct from the majority of other British lakes, largely because there are few other regions whose topography received and substantially retained the imported drift. The resultant subdued land forms and isolated shallow water bodies contrast strikingly with the ice-carved troughs and deep linear lake basins of the mountainous districts where the ice sheets were generated.

IV. THE WATER SUPPLY TO THE MERE BASINS

1. *Hydrology*

The almost total lack of natural surface drainage channels is a striking feature of the present-day morainic topography of the Shropshire-Cheshire Plain. The majority of meres have been isolated from streams throughout most of their history so they have been neither naturally drained nor alluviated. Such surface drainage as exists is largely through artificial ditches and culverts constructed during the last two centuries. Precipitation in their catchments passes directly underground, readily percolating through coarser sands and gravels. Rainwater is intercepted by the heavier and largely impervious boulder clays of the underlying lodgement till, and accumulates in the ground above the till, completely filling the spaces between the mineral particles in a zone of saturation, whose upper limit is the water table. Ground water can be expected to fill any closed depression with permeable walls whose floor lies below the local water table; thus, meres have often been regarded as surface manifestations of the water table (Sinker, 1962; Reynolds, 1971a). Water tables are rarely horizontal: elevations and depressions tend to follow corresponding surface features, though they may be modified by local irregularities in the texture and distribution of drift. The differences in altitude of the surfaces of neighbouring meres can sometimes be significant (see Table 3); artificial alterations in the levels may have contributed to these differences, although a 1974 survey of the Ellesmere group of meres showed the levels to be almost unchanged since they were originally levelled (unpublished data provided by the Severn-Trent RWA). Variations in the water table permit gravitational flow through drift, in accordance with Darcy's Law (Land, 1965), and a progressive seepage away from the moraine belts into the surface catchments of the Mersey-Weaver, Dee and Severn systems. The

altitude of the ambient water table is thus in an equilibrium maintained between the climatically determined rate of accretion, and the rate of lateral flow.

Table 3. *Altitudes of Four Ellesmere Group Meres*

Mere	Altitude (m) above OD	Surveyed
Ellesmere Mere	87.8	1901
White Mere	93.0	1901
Cole Mere	83.1	1874
Crose Mere	85.7	1874

Meres are potentially or actually in continuity with ground water; each is likely to have its own characteristics of recharge and discharge (cf Meyboom, 1963). In the short term, however, mere levels generally tend to be remarkably stable. Seasonal variations are also slight; the range in extremes in the level of Crose Mere, for instance, did not exceed 200 mm in any twelve month period between January 1966 and July 1975, and were generally less than 120 mm (Reynolds 1973a and later unpublished data). Over longer periods, however, the ground water supply to a mere is influenced by climatically induced fluctuations in the water table. Evidence for substantial Flandrian changes of water level has been found at Wybunbury Moss (Poore and Walker, 1959) and in Ellesmere district soils (Mackney, 1965), and Tallis (1973) has also commented upon the role of water-table movements in the development of Flaxmere (see also section VII).

Although hydrological investigations of meres or mosses have been few and limited in scope, it is probable that many basins may be partially or wholly sealed by a lining of secondary deposits, including solifluxion and inwashed clays from the surrounding drifts (Johnson, Franks and Pollard, 1970) and organic sediments, including peat material originating in the lake itself (Tallis, 1973). These basins have consequently developed their own "perched" water tables, as at Oakmere, Flaxmere and others in the Delamere area (Tallis, 1973). Ground water can enter the basin only by "inspilling" (cf Reynolds, 1975a) over the lip of the seal. The potential rate of ground water influx into the basin may be affected little when the water table is high, but a fall in water level below the seal would divert ground water around the basin, leaving it hydrologically isolated. Basins thus sealed may be better equipped to have survived the lowered water tables of drier climatic phases (see Fig. 8).

I have attempted to quantify the hydrological input into Crose Mere from indirect observations (Reynolds, 1971a, 1975a). Its catchment area is a broadly semicircular depression in heavy till, mostly overlain by coarse sands and gravels of variable thickness (Pocock and Wray, 1925); its northern perimeter is bounded by a low gravel ridge which separates the mere from Whattal Moss. The altitude of the catchment drops from a maximum of 128 m OD, about 1 km to the south-west of the lake, to the present mere level (86 m). Below the 91 m contour, the drifts give way to finer, more evenly bedded sands, overlain by peat. The clearly defined marginal strip, up to 150 m in width, attests to an earlier extent of the mere surface, standing some 3 m higher than at present. Hardy (1939) implied that the drainage operations in 1864, which lowered the level of the mere, allegedly by 2-3 m, accounted for the full fall. This must be doubted, for an 89 m lake would have flooded the low-lying land between Crose Mere and Sweat Mere and backed up to Whattal, yet these
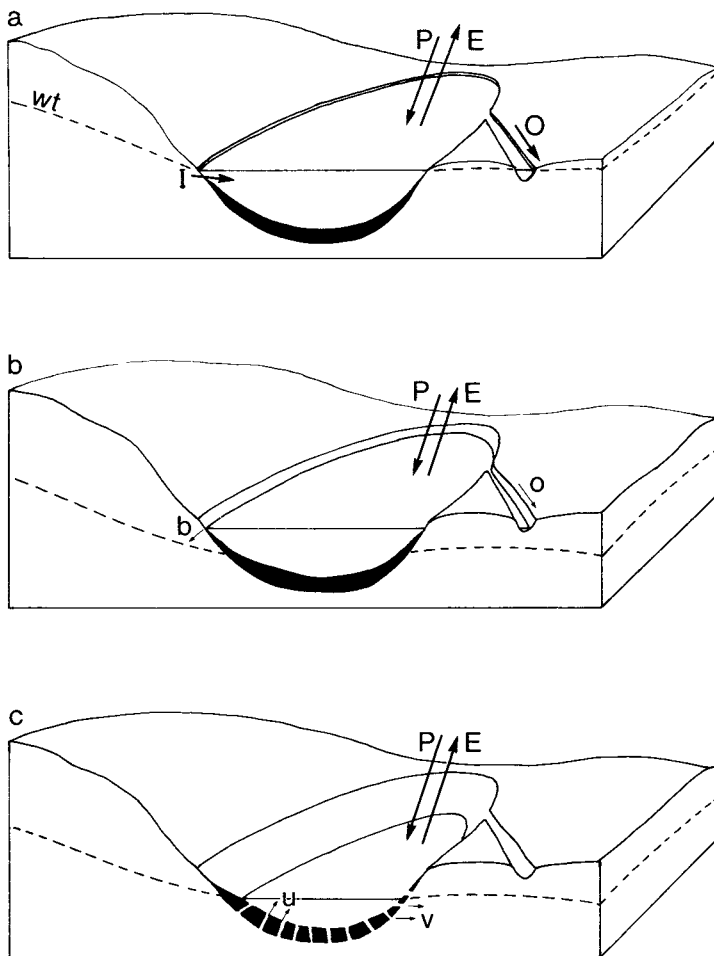
FIG. 8.

Block diagrams to show possible relationships between surface water level in a mere and the adjacent water table. (8a): water inspills (I) over an impervious seal, and the outflow (O) carries away the excess after exchanges involving precipitation (P) and evaporation (E). If the water table (8b) falls, the lake level becomes "perched"; inspill ceases and may be temporarily replaced by outspill (b), in the opposite direction; excess precipitation over evaporation will continue to be regulated to the limit of the outflow. In (8c), the same drop in water table is seen in relation to a permeable basin in which incoming (u) and outgoing (v) percolation prevent "perching" of the lake level which drops proportionately. Original.

basins have been separate for many centuries at least (Eyton, 1854, quoted by Sinker, 1962). The height of the peat platform is about 750 mm above lake level, and the roots of mature alder trees on the northern shore (conceivably a century or more in age: Sinker, 1962) fan out at about the same altitude above the mere. Even allowing for shrinkage of the peat, it is improbable that the 1864 operations reduced the lake level by more than 1 m.

There are no surface inflow streams into Crose Mere. Three small field drains enter the lake on its southern shore; none exceeds 200 m in length, and they often stagnate or dry up completely in summer. Clearly, the catchment area (2.15 km²) is drained largely by underground seepage. With an average annual precipitation for the district (730 mm; Slater, 1972)

less an annual evapotransportation loss equivalent to 518 mm (also from Slater, 1972), the catchment might shed some 456,000 m³ of excess water. From weekly measurements of the outflow in Reynolds (1971a) I estimated an annual cumulative discharge of the same order of magnitude (380,000 m³: see also Reynolds, 1975a), and concluded that the actual ground water catchment probably corresponded closely to the surface topography.

Measurements of lake level and outflow discharge (Reynolds, 1975a) showed seasonal variations: from January to June or July, the depth of the lake fluctuated between 9.16 and 9.21 m, but then dropped relatively rapidly to a minimum of 9.08-9.10 m between August and October: the level was restored during autumn. The corresponding outflow measurements averaged 1,000-1,700 m³ day⁻¹, falling to 100 m³ day or less. Crude monthly influx volumes (I) for 1974, presented in Fig. 9, have been estimated from:

$$I = O + E - P \pm D$$

(where O=outflow discharge, E=potential evaporation from and P=direct precipitation onto the lake surface, and D=observed changes in storage volume) show similar seasonal fluctuations. I have argued (Reynolds, 1975a) that the "sudden" fall in level, supposedly due to an ultimate imbalance between increasing evaporation and replenishment from underground reserves, was inconsistent with the notion that the lake water is in complete continuity with ground water, but rather that it was isolated by an impervious seal, over which ground water "inspills" into the mere.

Some qualification of this conclusion is necessary, since it takes little account of seasonal falls in the local water table, and hence, declining flow attributable to a reduced gradient and head. Unverified, but independent, statements from owners of disused wells in the neighbourhood indicate that the depth of water in their bores showed annual fluctuations of 0.6-0.9 m (ie rather more than the level of the mere); thus some outspilling from a permeable mere could be envisaged (Fig. 8). However, the two possibilities are not mutually exclusive, and in either case it is still required that the inflowing ground water spills into the mere, rather than penetrating uniformly at all depths. Other evidence supports the hypothesised presence of a waterproof seal. Changes in the chemical and faunal characteristics of dated sediments reported by Beales (1976) suggest that the mere may well have been isolated from ground water influx during Boreal times, although no interruption in the presence of open water is indicated. Moreover, it has been suggested (Reynolds, 1975a) that the thermal and chemical properties of deep water layers in summer may represent intact masses of cold, chemically rich ground water, which, if the inspilling model is correct, would depend upon a discrete source of supply to avoid entrainment in the normal epilimnetic circulation of the lake. The only point at which Crose Mere abuts coarse drift is along its north shore; when the mere surface has frozen for more than 24 h, the last place to have become iced over, if at all, was along the north shore (author's unpublished observations); inflowing ground water, now considerably warmer than that of the lake, might explain this effect.

Though evidently complex, the hydrology of Crose Mere and, perhaps, of many others with stable water levels is consistent with their maintenance primarily by ground water. Low rainfall and limited catchment areas combine to give characteristically long retention times. At the annual rate of ground water influx shown in Fig. 9, it would take an average 27 months to displace the volume of Crose Mere (735,000 m³); instantaneous retention times range from 16 (winter) to 85 months (summer).

2. Hydrochemistry

During its slow percolation and lateral seepage through the mineral drift, ground water becomes considerably modified by dissolved substances. The hydrological conditions, and the composition and distribution of drifts are unique to each catch-
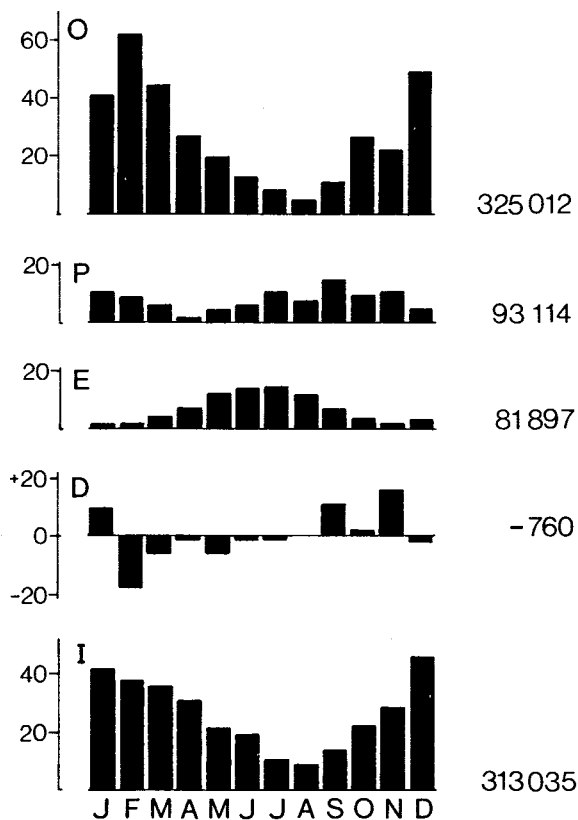
FIG. 9.

Histograms showing the monthly water budget for Crose Mere in 1974 (vertical scale is in thousands of cubic metres). *O* is the outflow discharge (author's measurements). *P*, precipitation at Shawbury (data from Meteorological Office, multiplied by the lake area). *E* is potential evaporation, also measured at Shawbury (by Severn-Trent Water Authority), also corrected to lake area. *D* is the change in storage (from author's lake level records). *I* is the inflow computed from $O+E-P\pm D$. Annual totals for each row are given on the right.

ment; thus the extent of chemical enrichment of inflowing ground waters will vary from mere to mere. As yet, there is little published information on the chemistry of local ground waters, though some data are presumably in the possession of the Regional Water Authorities. Reynolds (1971*a*, 1975*a*, and unpublished) has analysed several spring waters in north Shropshire—for certain elements only. At present, the only guide to their richness lies in the chemistry of the meres themselves; once in the lake, however, the dissolved solute load may be diluted by surface run-off, or be modified by chemical and biological processes within the lakes themselves.

The surface waters of a number of meres were analysed in some detail by Gorham (1957*a,b*). Seasonal variations in lake water composition have also been investigated at a number of sites. [References: Reynolds and Allen (1968), Grimshaw and Hudson (1970), Reynolds (1971*a*). Additional data, in support of other (mainly biological) studies have been given by Pearsall (1923), Reynoldson and Bellamy (1970), Reynolds (1973*b*), Young and Harris (1973), Savage and Pratt (1976), and Tait-Bowman (1976), Rother and Fay (1977).]

The available information is sketchy, and a new comprehensive chemical survey is needed; nevertheless, it does characterise the mere series as having a wide range of chemical composition which is, nonetheless, generally much richer than lakes in mountainous districts of Britain.

(a) *Major Ions*

The extent of available information is summarised in Table 4. The lakes are arranged in ascending order of their specific conductivities as determined by Beales (1976); the alkalinity data are also based upon Beales' survey. The chemical analyses are taken from Gorham (1975a,b) except where later data are available, as noted. Additional measurements of conductivity (Reynolds, 1973b and unpublished; Savage and Pratt, 1976) and calcium concentration (Reynoldson and Bellamy, 1970; Young and Harris, 1973) are included for sites otherwise uncovered.

Calcium and bicarbonate tend to be the most abundant ions, but their concentrations vary conspicuously from mere to mere (>13-fold); alkalinity, which is largely dependent upon the bicarbonate ion concentration, varies by a factor of nearly 200. Sodium and chloride are also common, and relatively constant throughout the series (variation <4-fold); sulphate is remarkably high in Budworth Mere and Pick Mere. Specific conductivities vary within an order of magnitude. Where other data are lacking, the conductivity may thus provide a guide to the bicarbonate and, by implication, calcium content of the mere in question: though they are independent variables, a strong positive correlation (r=0.861) exists between conductivity and alkalinity in 44 meres for which information is available (see Fig. 10).

Gorham (1957a) attributed the variations in composition to differences in the chemical nature of the drifts, and in the extent and duration of contact of inflowing water therewith. He showed that in Newton Mere, one of the most dilute examples, the concentrations of sodium and chloride were increased by a factor of 4–5 with respect to Lake District rain-
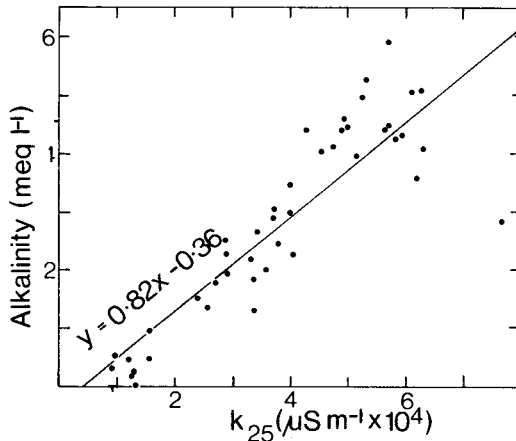

FIG. 10.

The relationship between alkalinity and specific conductivity at 25° (K_{25}) in 44 meres for which data are available (see Table 5).

Table 4. *Chemical Characteristics of some Mere Surface Waters*

Constructed from existing information, 1976, with sites ranked in order of increasing conductivity. Conductivity and alkalinity data are drawn from Beales' (1976) data, with later modifications (P. W. Beales, personal communication). Ionic concentrations are from Gorham's (1975a, b) surveys (1954–1955), except where later analyses are available. Nutrient concentrations cited are the highest obtained in all determinations variously made between 1966 and 1971 (Reynolds 1971a, 1973b). pH ranges embrace published and author's unpublished determinations. Table reproduced from Reynolds (1978a), by permission.

Mere	pH_{20}	Conductivity $\mu S\ m^{-1} \times 10^4$ @25°	Alkalinity (m equiv l^{-1})	Ca^{2+}	Mg^{2+}	Na$^+$	K$^+$	(HCO$_3$)$^-$	Cl$^-$	(SO$_4$)$^{2-}$	SiO$_2$	DRP	NO$_3$
						Major ions (meq l^{-1})						Nutrients $\mu g\ l^{-1}$	
40 Bomere Pool	7.9[a]	0.94	0.35	—	—	—	—	—	—	—	2860[a]	74[a]	930[a]
2 Blake Mere	7.1–8.2	1.21	0.48	0.52	0.12	0.33	0.19	0.54	0.40	0.23	1080	128	581
4 Newton Mere	6.8–9.9	1.27	0.21	0.37	0.11	0.37	0.20	0.30	0.42	0.30	970	362	432
41 Shomere	6.7[a]	1.29[b]	0.27	—	—	—	—	—	—	—	4170[a]	69[a]	1220[a]
28 Oak Mere	4.4[c]–4.7	1.32	0.03	0.38[c]	0.21	0.39	0.06	0.00[c]	0.50	0.54	1400	240[d]	400[d]
51 Booths Mere	6.6–8.8	1.44[c]	0.75[c]	—	—	—	—	—	—	—	952	1700[f]	647
3 Kettle Mere	7.1–8.2	1.58	0.52	0.58	0.12	0.33	0.22	0.57	0.39	0.28	2830	1650[f]	938
5 White Mere	7.5–8.2	2.39	1.54	1.50	0.12	0.36	0.13	1.12	0.44	0.59	2620	1100	940
42 Betton Pool	8.0[a]	2.56	1.36	—	—	—	—	—	—	—	—	—	—
1 Ellesmere Mere	7.5–9.5	2.72	1.82	1.52	0.22	0.49	0.25	1.48	0.53	0.46	2620	1100	940
24 Hanmer Mere	—	2.74[g]	—	—	—	—	—	—	—	—	2600[a]	392[a]	290[a]
6 Cole Mere	7.6–8.3	2.89	2.54	2.34	0.21	0.44	0.13	1.94	0.52	0.62	4770	370	982
35 Cottage Pool	7.5–8.6	2.90	2.30	2.06[h]	0.32[h]	0.50[h]	0.22[h]	1.34[h]	0.94[h]	0.96[h]	4210	370	796
44 Berrington Pool	8.1[a]	2.92	1.93	—	—	—	—	—	—	—	—	—	—
36 Isle Pool	—	3.21[c]	—	—	—	—	—	—	—	—	1650[a]	23[a]	240[a]
61 Marton Pool	—	3.27[i]	—	—	—	—	—	—	—	—	1650[a]	20[a]	1860[a]
37 Oxon Pool	7.2–8.7	3.32	2.23	—	—	—	—	—	—	—	2810	235	688
29 Petty Pool	8.3[a]	3.37	1.86	—	—	—	—	—	—	—	—	—	—
48 Mere Mere	8.5[a]	3.39	1.34	—	—	—	—	—	—	—	—	—	—
12 Deer Park Mere	9.4[a]	3.47	2.70	—	—	—	—	—	—	—	—	—	—
30 Little Budworth Pool	7.3–7.5	3.59	2.03	1.94	1.04	0.53	0.10	1.59	0.68	1.20	8200[d]	40[d]	2450[d]
43 Top Pool	7.1[a]	3.71	2.91	—	—	—	—	—	—	—	—	—	—
7 Crose Mere	7.6–9.1	3.73	3.09	3.66[h]	0.77[h]	0.52[h]	0.12[h]	3.28[h]	0.59[h]	1.24[h]	5930	196	2300
49 Rostherne Mere	7.3–9.6	3.82	2.52	2.46[l]	0.82[l]	0.67[l]	0.11[l]	2.00[l]	0.68[l]	1.24[l]	7280[l]	330[l]	1380[l]
21 Comber Mere	9.2[a]	4.00	3.49	2.44[m]	—	—	—	—	—	—	2840[a]	93[a]	482[a]
38 Alkmond Pk Pool	8.4[a]	4.01	3.02	—	—	—	—	—	—	—	—	—	—
27 Hatch Mere	7.8–8.6	4.06	2.29	1.67	0.97	0.48	0.10	1.65	0.62	0.94	3200[a,d]	—	170[a,d]
18 Marbury Big Mere	9.2[a]	4.28	4.42	—	—	—	—	—	—	—	—	—	—
59 Cop Mere	7.6[a]	4.55	4.04	—	—	—	—	—	—	—	—	—	—
53 Redes Mere	7.7[a]	4.75	4.12	—	—	—	—	—	—	—	—	—	—
25 Doddington Pool	8.1[a]	4.90	4.42	—	—	—	—	—	—	—	—	—	—
13 Norbury Big Mere	8.1[a]	4.95	4.66	—	—	—	—	—	—	—	—	—	—
50 Tatton Mere	7.8[a,d]	4.96[n]	—	2.34	1.15	0.88	0.12	2.39	0.87	1.21	—	50[a,d]	20[a,d]
14 Norbury Little Mere	8.3[a]	5.00	4.50	—	—	—	—	—	—	—	—	—	—
22 Blake Mere	8.1[a]	5.14	3.98	—	—	—	—	—	—	—	—	—	—
16 Quoisley Big Mere	7.8[a]	5.22	4.99	—	—	—	—	—	—	—	—	—	—
11 Chapel Mere	8.8[a]	5.59	5.21	—	—	—	—	—	—	—	—	—	—
34 Marton Pool	8.2[a]	5.65	4.40	—	—	—	—	—	—	—	3460[a]	104[a]	1570[a]
33 Fenemere	8.0[a]	5.70	4.48	4.66	—	—	—	—	—	—	3340[a]	93[a]	2500[a]
17 Quoisley Little Mere	7.5[a]	5.71	5.88	—	—	—	—	—	—	—	—	—	—
58 Maer Pool	7.7[a]	5.85	4.27	—	—	—	—	—	—	—	—	—	—
62 Llynclys Pool	8.3[a]	5.85	4.58	—	—	—	—	—	—	—	1940[a]	543[a]	800[a]
15 Bar Mere	8.5[a]	5.94	4.34	—	—	—	—	—	—	—	2120[a]	14[a]	168[a]
26 Betley Mere	8.2[a]	6.09	5.05	—	—	—	—	—	—	—	—	—	—
32 Birchgrove Pool	8.4[a]	6.31	4.11	—	—	—	—	—	—	—	—	—	—
63 Padeswood Pool	—	6.53[c]	—	—	—	—	—	—	—	—	—	12040[a,c]	19540[a,c]
45 Budworth Mere	8.1[a]	6.69	3.59	3.65	1.88	1.30	0.16	3.10	1.30	2.51	2600[a,d]	290[a,d]	570[a,d]
31 Berth Pool	—	6.79	5.06	—	—	—	—	—	—	—	—	—	—
47 Tabley Mere	—	7.69	2.85	—	—	—	—	—	—	—	—	—	—
46 Pick Mere	—	8.70[h]	—	3.35	1.66	0.89	0.12	2.93	0.96	2.09	2600[a,d]	70[a,d]	80[a,d]

NOTES

[a] Determined on a single sample only.

[b] Reynolds (1973b) gave significantly higher values, but are probably overestimated. Beales' (1976) figures are to be preferred.

[c] Following the introduction of calcium-rich borehole water in 1966 some higher values were obtained (see Reynolds and Allen, 1968), but the mere subsequently recovered its former acid, dilute condition.

[d] Analysis of Gorham (1957b).

[e] Unpublished analysis of Reynolds.

[f] Orthophosphate concentration given by Rother and Fay (1977).

[g] Conductivity figure of Reynolds (1973b), corrected to 25° from original data.

[h] Analyses by J. Heron, quoted by Reynolds (1971a).

[i] Conductivity figure of Reynolds (1971a), corrected to 25° from original data.

[k] From Reynolds (1971a).

[l] Analyses of Grimshaw and Hudson (1970).

[m] Data of Young and Harris (1974).

[n] Conductivity figure of Savage and Pratt (1976).

[p] Data of Reynoldson and Bellamy (1970).

water, which is little more than could be expected from the degree of concentration as a result of catchment evaporation; the possible contribution of salt deposits in the drift was so small as to be indistinguishable. The relatively greater increase in calcium (24-fold) balanced the removal of hydrogen ions in rain. In the waters of Crose Mere, sodium and chloride concentrations are six times more concentrated than in rain, but calcium was increased by a factor of 227. Gorham (1957a) suggested that surface run-off from their small, steep-sided catchments makes a relatively larger contribution to the inflow in the more dilute meres than in richer meres more continuously fed by ground waters percolating through less leached subsoils. The ionic composition of Oak Mere is still more extreme in being almost wholly rain-fed (Gorham 1957b). A complicating feature of Oak Mere is the presence of a large submerged peat deposit at the west end of the basin (Lind 1951).

The soluble minerals in the drifts which provide the major source of ions occurring in the richer meres, were imported by advancing glaciers, or were stripped from the underlying marls and evaporites (eg Pocock and Wray, 1925). They are known to include fragments of limestone, dolomite, calcareous sandstones, glauconite, glauberite, aluminosilicates and apatites. These minerals represent possible sources of calcium, magnesium, potassium, sodium, sulphate, carbonate, silicate and phosphate which are present in mere water. The minerals have differing solubility constants, however, and leaching has proceeded at different rates.

Little is known of the distribution of these minerals in the drift. Local variations may be relatively unimportant, since even Pick Mere and Budworth Mere exhibit ionic proportions which are similar to those of other meres; neither these or any other of the meres considered show any sign of brine infiltration, despite their proximity to the Northwich salt deposits (Gorham 1957b). However, ionic strength varies with geographical groupings (Fig. 11a), and to a limited extent, with four categories of dominant drift type (Fig. 11b: based on information from relevant OS 1 in drift maps): the Baschurch group meres are relatively richer than those of the Shrewsbury group, for example; and meres in boulder clay basins are on average more dilute than those which abut superficial sands and gravels.

Basin morphometry is a further factor in the hydrochemical characterisation of the meres. Beales (1976) subjected his basic data to principal components analysis. The major component distinguished between sites of low alkalinity (usually small meres) from larger and/or richer meres. A second component separated deeper lakes of low to moderate ionic strength and small pools of high conductivity and alkalinity. Together, these components accounted for 71 per cent of the total variance. When Beales plotted out the components against each other, district groupings were observed, and these are listed in Table 5. The classification cuts across geographical groups, though some are preferentially represented: Class A.I comprises many of the Whitchurch and all of the Baschurch meres; many of the Ellesmere meres fall within class D. Three sites (Crose Mere, Oak Mere and Budworth Mere) were not obviously allied with any other.

(b) *Minor Constituents*

Maximum known concentrations of silicon (expressed as silica), dissolved reactive phosphate phosphorus and nitrate nitrogen in surface waters of a selection of meres are included in Table 4. They are expressed in μg per litre, in accord with common practice. Some values are based on single determinations. In more complete series, the highest concentrations were encountered in winter. At other times, concentrations fluctuate in response to the rate of supply and to biological demand (mainly by phytoplankton) and, as in most natural waters, may sometimes limit the rate of organic production.

Recorded maxima of silica are in the range of 1-8 mg l^{-1}. As Gorham (1957b) remarked, these levels are unexceptional, and fall short of the supposed world
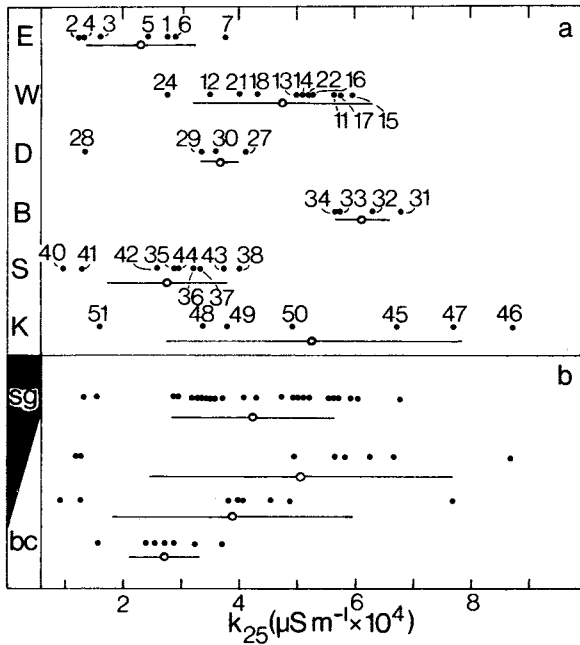
FIG. 11.

(a) The range of specific conductivities of meres in the various groups used in Table 1 (E=Ellesmere Group, W=Whitchurch, D=Delamere, B=Baschurch, S=Shrewsbury and K=Knutsford). Sites identified in Table 1. (b) The same basins grouped according to adjacent drift types; four groupings are used: sand and gravel (sg), sand and gravel with <50 per cent boulder clay, boulder clay with <50 per cent sand and gravel, and boulder clay (bc). Drift dominance assessed from relevant Drift Series maps of the Geological Surveys. Horizontal bars denote the standard error of the mean of each category. Original.

average for fresh water (17 mg l^{-1}: Conway, 1942). Gorham's explanation for this relative poverty was that leaching of the drifts probably had not yet progressed to an advanced stage, only the more mobile elements having been removed in quantity.

The soluble silica concentration in ground water entering Crose Mere (perhaps 8-10 mg l^{-1}) seems correspondingly low (Reynolds 1975a; see also Table 6). Given the longer retention times of the meres, potential deficiencies in the availability of silica may at times inhibit the growth of planktonic diatoms. Concentrations in several Shropshire meres have been observed (see Reynolds 1971a) to fall below 500 µg l^{-1} which under certain conditions, has been shown to be critical to the growth of diatoms (Lund 1949, 1950).

Dissolved reactive phosphate, however, seems typically more abundant than in most natural lake waters. In the richer meres at least, the available phosphorus seems adequate to support the levels of plankton production encountered (see Section V). Though lake concentrations may become substantially depleted during spring and summer, instances when phosphate has fallen to undetectable levels are probably relatively rare (Reynolds, 1973b). Moreover, present concentrations have not increased markedly compared with those determined by Gorham (1957a, b). It is stressed that there is little tangible evidence that phosphate concentration has

Table 5. *Classification of Basin Sites*
Based on Principal Components Analysis (Beales, 1976).

Class	Characteristics	Typical Sites (see Table 1)
A.I	Pools of high alkalinity (>4 meq l^{-1}) and conductivity ($>4 \times 10^4 \mu S\ m^{-1}$)	11, 15, 16, 17, 25, 26, 31, 32, 33, 34, 53, 58, 59.
A.II	Pools of moderate alkalinity (2-4 meq l^{-1})	12, 27, 30, 35, 37, 38, 43.
A.III	Shallow pools of moderate to high alkalinity (>4 meq l^{-1})	13, 14.
B	Small pools, low alkalinity (<2 meq l^{-1}) and conductivity ($<2.50 \times 10^4 \mu S\ m^{-1}$)	3, 41, 51
C	Bog pools of very low alkalinity (<0.2 meq l^{-1})	(Not included in the present treatment)
D	Deeper meres of low to moderate alkalinity (<4 meq l^{-1})	1, 2, 4, 5, 6, 21, 40, 42, 44, 48, 49.

been influenced by artificial enrichment; the relative richness seems natural, and is presumably largely derived from apatite in the drift.

In contrast, maximal concentrations of nitrate nitrogen, even in the richest meres, are scarcely higher than corresponding values in the more fertile Lake District lakes. Rapid leaching of nitrate from soils and drifts may have already left the meres dependent upon rainwater, perhaps modified significantly by microbial fixation and denitrification in terrestrial soil communities, as the main natural nitrogen source. Fixation of atmospheric nitrogen by aquatic micro-organisms may also contribute to lake concentrations. However, in the last few decades, the increased rate of application of nitrogenous fertilisers to agricultural land has inevitably enriched the leachate with nitrogen and augmented the supply to the meres. The impact on nitrogen concentrations in a number of meres is readily detected by comparing Gorham's (1957a, b) 1954 determinations with those obtained between 1966 and 1971. Maximum concentrations in the Ellesmére group of meres are 6-8 times higher than Gorham's winter values.

Enrichment of natural waters with respect to nitrogen causes widespread concern, not least because it can promote the growth of "undesirable" plants, especially algae (see Section V). The meres are not excepted from this view. There is evidence that phytoplankton production has been and, in many cases, may still be limited by nitrogen availability, based upon the relative $N : P$ ratios in healthy algal cells and in lake water, at their maximal concentrations (Reynolds, 1973b; 1976a). Moreover, in summer, inorganic nitrogen often falls to undetectable levels before phosphate (eg Grimshaw and Hudson, 1970; Reynolds, 1971a; 1976a, b). Although the data take little account of the rates of supply or recycling, nor of other available species, the relative abundance of phosphate suggests that at most times plant production in the meres is more likely to be controlled by the availability of nitrogen than phosphorus. In this feature, meres differ significantly from many other British and Continental waters, wherein phosphorus is often critical (Gibson, 1971; Lund *et al*, 1975; Uhlmann, 1975).

Nutrient loading rates on Crose Mere have been provisionally estimated from the data of Reynolds (1975a), which assumed a silica concentration of 9-10 mg l^{-1} in ground water, and
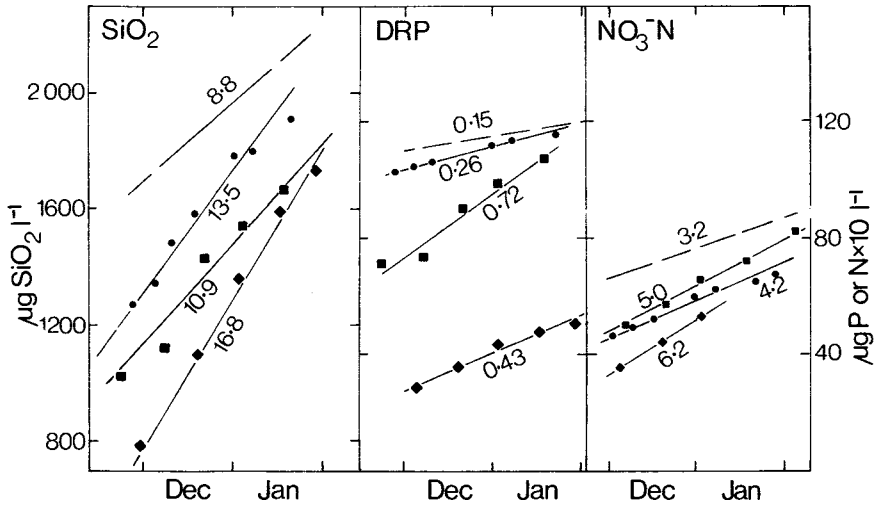
FIG. 12.

Winter increases in concentrations of silica, dissolved reactive phosphate and nitrate nitrogen in Crose Mere in (■) 1971/2, (◆) 1972/3, (○) 1973/4 and (●) 1974/5. Slopes fitted by eye; the units of the gradients are μg. l^{-1}. d^{-1}. Original.

annual influx of 340,000—360,000 m^3. These fall within the ranges 0.49-1.33 g P and 6.04-9.03 g N m^{-2} ann^{-1}. The phosphorous figures may be compared with Oglesby's (1977) estimate of P-loading based on his chlorophyll—phosphorus model equation. To sustain the mean chlorophyll concentrations observed in summer (~50 mg chl a m^{-3}) a loading rate of ~1.1 g P m^{-2} ann^{-1} would be required. Fig. 12 shows that the rates of increase in lake concentrations of silica, phosphorus and nitrogen during the December periods of rapid recovery (and minimum uptake) in each of four successive winters are roughly similar from year to year. Applying the mean daily incremental rate and the deduced rate of inflow (Fig. 9) during December 1974, the concentrations of the corresponding solutes in ground water may be crudely calculated, according to the equation

$$X_A = X_M + \frac{dX_M}{dt} \times \frac{V}{Q_I}$$

where X_A and X_M are the concentrations of the nutrient in ground water and the mere, respectively, dX_M/dt is the mean daily rate of augmentation, V is the volume of the lake (735,000 m^3) and Q_I the mean daily influx volume in December (1,460 m^3). Values of X_A for silica, phosphate phosphorus and nitrate nitrogen are given in Table 6, which also includes a calculation of potential annual loading with respect to each nutrient, as the product of X_A and the annual ground-water influx (Fig. 9). The derived values are of similar order of magnitude to those presented above. Lakes subject to nutrient loadings of >0.4 g P and >5 g N m^{-2} are reckoned to be highly "eutrophic" in the modern usage (cf Moss, 1973a, and see later), and are likely to support intense algal blooms (Vollenweider, 1968). This description probably applies to many of the richer meres shown in Table 5.

3. Thermal stratification and its consequences

All of the meres exceeding 5–8 m in depth which have been investigated have been shown to become thermally stratified in spring (Table 1) and to remain so until

Table 6. *Groundwater Nutrient Concentrations and Annual Specific Loading Rates on Crose Mere in 1974*

(Calculated from data in Figs. 9, 12)

	SiO_2	DRP	NO_3N
Mean daily rate of augmentation $\left(\frac{dX_M}{dt}\right)$, in μg^{-1} d^{-1}	13.5	0.26	4.2
Volume/daily inflow rate $\left(\frac{V}{Q}\right)$, d^{-1}	503	503	503
Initial concentration in lake (X_M), in μg l^{-1}	1314	104	458
Calculated concentration in inflow (X_A), in μg l^{-1}	8105	234	2571
Annual specific loading rate, in g m^{-2}	16.69	0.48	5.45

late summer—late autumn, depending upon their depth and exposure to wind. Stratification results in the separation of the waters into an upper warm layer (epilimnion) and a lower cold hypolimnion, separated by a more or less narrow layer, the metalimnion or thermocline. Very little is known of the shallower pools, which may stratify for short periods. The meres remain isothermally mixed for long periods during winter, but are subject to thin ice covering during still, frosty weather. Long periods of ice cover are exceptional under the moderate, sub-oceanic climate of the north-west Midlands. The deeper meres, at least, may be regarded as warm monomictic lakes, that is, having one period (mid-autumn to mid-spring) of complete mixing per year; the shallower meres may experience several such mixings each year, and would be classed as polymictic waters (cf Hutchinson, 1957). In those lakes for which data extend over more than one season, the hypolimnetic temperatures are similar from year to year: 6-7° in Blake Mere (nr Ellesmere); 7-9° in Rostherne Mere; 10-11° in Newton Mere; and 11-12° in Crose Mere. In earlier work, I suggested that the constant tendency of bottom temperatures in Crose Mere towards ~11.5° may be influenced by ground water influx, and have since identified a distinct increase in the hypolimnetic volume during the early part of summer. No corresponding increase in hypolimnetic volume is evident from the cited data for the other meres. [References: Grimshaw and Hudson (1970), Reynolds (1971*a*, 1975*a*, 1976*a*), Tait-Bowman (1976).]

Falls in the concentration of dissolved oxygen in the hypolimnion of these same meres are detectable within a few days of stratification. The effect is most pronounced near the bottom of the lake, but depletion eventually extends through almost all of the hypolimnetic volume, in many cases to virtual exhaustion (<0.5 mg 0_2 l^{-1}). This condition is diagnostic of eutrophic lakes, according to classical terminology. Its principal cause is the excess of consumption (especially in the microbial decomposition of the abundant organic material produced within the lake) over supply. Probably all the stratifying meres can be described as being eutrophic, regardless of the chemical composition of their waters: the adjective applies equally to Newton Mere, one of the most dilute waters listed in Table 4. [References: Brinkhurst and Walsh (1967), Jones and Savage (1971), Reynolds (1973*b*, 1973*d* and unpublished), Tait Bowman (1976), Rother and Fay (1977), Clark and Walsby (1978*a, b*).]

Hypolimnetic anoxia is complete within 2 months in Newton Mere (Tait-Bowman, 1976) and, typically within 3 weeks in the case of Crose Mere (Reynolds, 1973d; 1976a). The relatively much larger hypolimnetic volume of Rostherne Mere becomes devoid of oxygen in 4-5 months (D. A. Rogers, *personal communication*) where reducing conditions persist in the superficial sediments throughout the year (Brinkhurst and Walsh, 1967). Areal oxygen deficits (see Hutchinson, 1957) calculated from observed rates of oxygen depletion, and values for the hypolimnetic volumes and the area of mud beneath the metalimnion computed from the bathymetric data rank Crose Mere (1.31 g 0_2 m⁻² d⁻¹) and Rostherne Mere (1.16 g 0_2 m⁻² d⁻¹) with other examples of eutrophic lakes (cf Hutchinson, 1957).

Chemical transformations in the anoxic hypolimnetic and sediment environments of the meres have not been adequately studied, though the limited information available permits crude interpretation when considered in relation to researches elsewhere (eg Hutchinson, 1957; Stumm and Morgan, 1970). Following deoxygenation of the hypolimnion of Crose Mere, nitrate rapidly disappears, soluble phosphate increases, and pH stabilises at about 7.2 (see Reynolds, 1976a). The system proceeds quickly to a sulphide system wherein free hydrogen sulphide is released (Reynolds, 1971a; Tait-Bowman, 1976). A low redox potential in the hypolimnion of this lake is indicated (perhaps <-150 mV), ranking with Hutchinson's (1957) Class IV lakes. Free sulphide is also known to be abundant in the hypolimnia of Blake Mere (Tait-Bowman, 1976) and in Rostherne Mere (Brinkhurst and Walsh, 1967); the sediments of the latter are said to be rich in sulphide throughout the year. The data available for Crose Mere (Table 7) suggest that iron interchanges normally between the ferric and ferrous forms in open water, but that hydrogen sulphide removes Fe^{++} by precipitation in the hypolimnion. In comparison with Esthwaite Water, Cumbria, the epilimnetic total iron concentration in Crose Mere is similar (Dr S. I. Heaney, *personal communication*) but it is 4-5 times less concentrated in the bottom mud. This may be due to differences of similar order in hydrological retention time.

Table 7. *Iron Transformations in Crose Mere*

Date:	24 September 1968		15 July 1968		24 August 1975		
Water column stability	Holomixis		Stratified		Stratified		
Concentrations of Fe:	Total Fe	Fe²⁺	Total Fe	Fe²⁺	Total Fe	Fe²⁺	Mn²⁺
at 0 m µg l⁻¹	350	6	354	12	—	—	—
8.5 m	—	—	—	—	528[1]	7[2]	640[2]
9.0 m	377	6	620	90	—	—	—
Sediment Interstitial water µg l⁻¹	—	—	—	—	nil[3]	nil[3]	340[3]
Sediment mg g⁻¹	—	—	—	—	9.6-14.6[3]		1.0-1.2[3]

Analyses, except where appended, by J. Heron and E. Rigg, quoted by Reynolds (1971a). Other analyses by (1) E. Rigg, (2) W. Davison and (3) J. Lishman (*personal communication*).

The surface sediments of the meres are organically rich (Tait-Bowman, 1976) and release of nitrogen (as ammonia), phosphate and silica to the lake water may supplement the supply to the epilimnion. The concentration of N (NH_4^+) may exceed 2 mg and 5 mg N l⁻¹ in the hypolimnia of Rostherne Mere (Grimshaw and Hudson, 1970) and Crose Mere (Reynolds, 1976a) respectively. Resolution of sediment silica has been demonstrated experimentally (Reynolds, 1971a); the supply of released nutrients to the epilimnion has not been investigated, though it may be significant when epilimnetic concentrations are low, and diffusion gradients are steep. Nutrient concentrations are increased in the epilimnion when stratification breaks down in autumn. Under oxygenated, isothermally mixed water columns, thin ($\sim$5 mm) oxidised microzones have been observed at the surfaces of mud sampled from Rostherne Mere and Crose Mere (author, unpublished); its presence may limit chemical exchange between mud and overlying water.

4. Other features of mere water of biological importance

(a) *pH and carbon availability*. The interrelationship between pH and the $CaCO_3$-H_2O-CO_2 (calcium carbonate, water, carbon dioxide) system is important in aquatic ecosystems owing to its influence on the potential rate of primary (photosynthetic) production, and to some extent, the species composition of the plankton (for a full consideration see Talling, 1976). In the majority of mere waters (see Table 4), the high level of bicarbonate alkalinity buffers the medium (generally between pH 7.5 and 9.0) against potential increases in pH resulting from photosynthetic withdrawal of inorganic carbon and, at the same time maintains a utilisable source of the element. In these meres, carbon deficiencies are unlikely to arise frequently, except under conditions favouring intense localisation of photosynthesis and minimal diffusion between layers. Meres of lower alkalinity are subject to greater fluctuations and extremes of pH (see Fig. 13) and carbon limitation is possible at times when large phytoplankton populations are present. The pH of Oak Mere is remarkably low at all times (though the introduction of base-rich ground water from a trial bore led to a temporary increase in pH in 1966: see Reynolds and Allen, 1968), and may be maintained by the presence of a submerged peat deposit (Lind, 1951).

The bicarbonate in the richer meres is undoubtedly supplied by ground water (Gorham, 1957*a*). Leaching of calcium carbonate from drift can be highly significant; at a CO_2 concentration of 1×10^{-4} atmosphere, ground water may become super-saturated with calcium carbonate ($>1.5\times10^{-1}$ M, or about 6 mg l^{-1}). The high levels of calcium carbonate in the recent sediments of Crose Mere (Beales, 1976), and perhaps other richer meres, is presumably due to precipitation (marl formation) in the open water environment. Direct deposition of carbonate into traps placed in Rostherne Mere has been observed by D. Livingstone (*personal communication*).
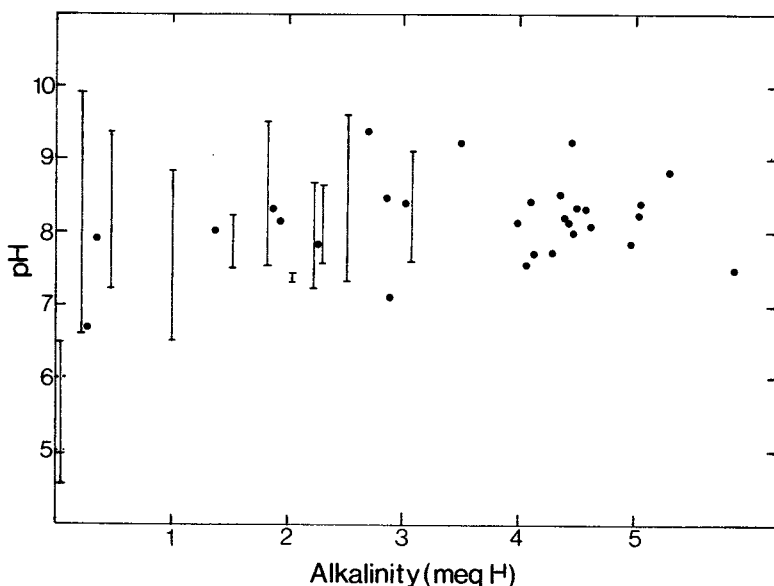

FIG. 13.

Ranges (vertical bars) and spot measurements of pH in various meres plotted against alkalinity. Data from Table 4. Original.

(b) *Transparency*. The underwater attenuation of light is one of the principal components determining the underwater light climate which, together with the intensity and duration of the radiation input and the extent of vertical mixing, may influence the rate of growth of planktonic organisms and the distribution of sub-merged macrophytes (Talling, 1971). Measurements of light penetration, estimated with a Secchi disc, have been made occasionally on a number of meres, and more routinely at Crose Mere and Rostherne Mere. The values determined (Reynolds, 1971a, 1973e and unpublished; D. A. Rogers, unpublished) have rarely exceeded 4.0 m. According to recent treatments in the literature (eg Vollenweider, 1974; Stewart, 1976), this depth suggests maximum euphotic depths (defined as the vertical penetration of 1 per cent of the irradiance present immediately below the water surface) in the range 7-12 m. Generally, however, the water in most meres and at most times is considerably more turbid. Moreover, seasonal variations in Secchi disc readings are superficially correlated with the phytoplankton standing crop (as indicated by chlorophyll *a* concentration): light penetration is apparently highest in mid-spring and least in late summer (Reynolds, 1971a, 1973e).

Regular photometric measurements have been made only at Crose Mere. Some of these are summarised in Fig. 14, wherein coefficients of vertical light extinction in the spectral block of minimum absorbance (or ε_{min}, generally 485-565 nm) are plotted against chlorophyll *a* concentration in the upper mixed layer. Data for stratified and unstratified conditions are shown separately. A high positive correlation under mixed conditions is
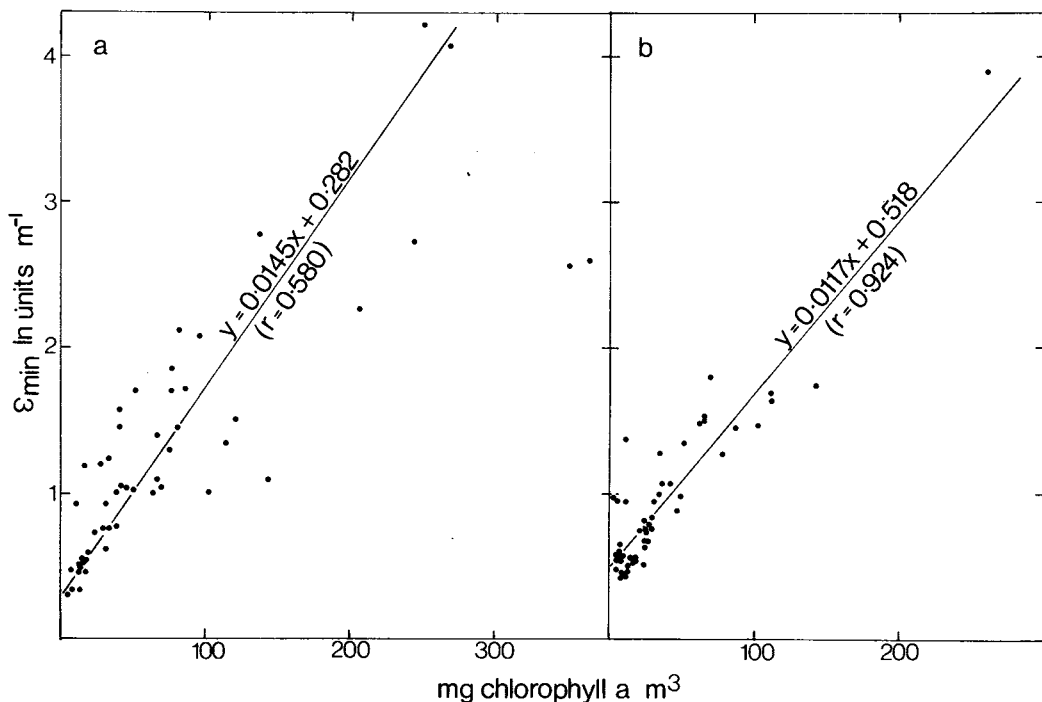

FIG. 14.

Plot of ε_{min}, vertical light extinction coefficients in the spectral block of minimal absorption (almost always 485-565 nm), against chlorophyll content of the upper water layers in (a) stratified and (b) unstratified water columns in Crose Mere. From author's unpublished data. Original.

indicated; the correlation does not fit as well when the lake is stratified, which is partly due to vertical discontinuities in phytoplankton distribution, and partly to variations in the size of dominant planktonic chlorophyll-containing organisms (cf Talling, 1971). The regressions also predict that there is a higher "background" component of absorbance during isothermal mixing, perhaps due to a greater proportion of tripton (non-living suspended matter). The mean increments in light extinction per unit of chlorophyll [ε_s, 0.0117-0.0145 1n units (mg chl$a$)$^{-1}$ m^{-2}] are lower than those given by Talling (1960) for populations of the diatom *Asterionella* in Windermere (0.02) which have sometimes been considered to be representative of phytoplankton generally.

Secchi disc readings (in the range of 0.9-4.2 m) are negatively correlated (r=−0.975) with corresponding ε_{min} determinations (Fig. 15). From the means (2.13 m, 0.985 1n units m^{-1}, respectively) it can be deduced that the average product of Secchi depth and ε_{min} is 2.10 (95 per cent confidence limits 1.46-2.25) and that, on average the Secchi disc reading corresponds to the depth of penetration of 13 per cent (10-22 per cent) of the subsurface irradiance in the spectral block of minimum absorbance. Moreover, the depth of the euphotic zone has been normally found to occur at a point to which 2-3 per cent of the irradiance in that spectral block penetrates; the mean euphotic depth (the depth to which 1 per cent of all visible wavelengths penetrates is thus between 3.6 and 4.0 m or 1.7-1.9 times the Secchi depth. It also follows (i) that the average vertical extinction coefficient of all visible wavelengths is 1.2-1.3× ε_{min} and (ii) that the product of the euphotic depth and ε_{min} is 3.5-3.9. The latter agrees closely with the 3.7 found to be applicable to a wide range of temperate and tropical lakes (see Talling, 1971; Talling *et al*, 1973).

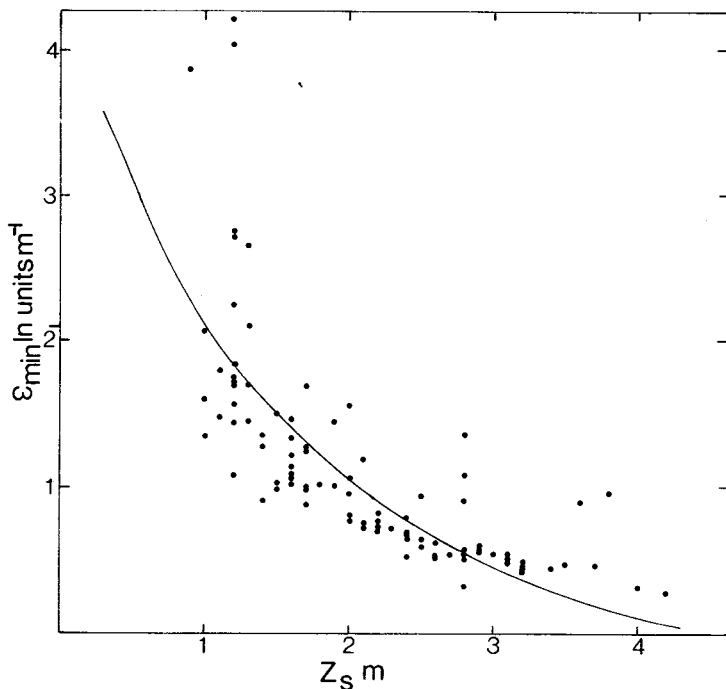Applying the regression equation from Fig. 14 to a well-mixed phytoplankton population

FIG. 15.

The relationship between ε_{min} (the coefficient of vertical light extinction in the spectral block of minimal absorption), and Z_s, (the depth of disappearance of a 300 mm Secchi disc lowered into the water) for Crose Mere. The equation of the regression is y=5.58-3.46 log x. Original.

equivalent to a notional 100 mg chl$a$ m^{-3}, the average minimal extinction coefficients would be 1.69 (in winter) and 1.73 1n units m^{-1} (in summer), the euphotic depth (3.7/1.7)m and euphotic contents (3.7×100/1.7) mg chl$a$ m^{-2} may be derived. These values, presented in Table 8, may be compared directly with data for other eutrophic lakes cited in the literature (eg Talling, 1971; Bindloss *et al*, 1973; Ganf, 1974), and summarised by Jewson (1977).

Table 8. *Euphotic Depths and Euphotic Contents of Mixed Water Columns in Eutrophic Lakes*

Assuming a notional phytoplankton population equivalent to 100 mg chlorophyll a m^{-3}

	Euphotic depth (m)	Euphotic content mg chl a m^{-2}
Esthwaite Water, Cumbria[1]	2.5	250
Loch Leven, Kinross[2]	2.4	240
Crose Mere, Shropshire	2.2	220
Lough Neagh, N.I.[3]	1.7	170
Lake George, Uganda[4]	0.9	90

References (1) Talling (1971), (2) Bindloss *et al* (1973), (3) Jewson (1977), (4) Ganf (1974)

V. THE BIOTIC COMMUNITIES OF THE MERES

1. *Planktonic Communities*

(a) *Phytoplankton*. The phytoplankton of the meres has been studied sporadically for over a century. Descriptive accounts of the algal assemblages collected from various sites in Cheshire, Shropshire and Staffordshire have been given by Phillips (1884), Wardle (1897), Griffiths (1925), Lind (1944) and Reynolds (1973b). Samples collected from Rostherne Mere by Tattersall and Coward (1914) were analysed by Pearsall (1923); later information from the same mere (Griffiths, 1925; Lind, 1944; Pritchard, 1961; Belcher and Storey, 1968; Reynolds, 1976d, 1978b; Reynolds and Rogers, 1976) collectively provides a long-term record of changing phytoplankton dominance, which is possibly unsurpassed for any natural British lake outside the English Lake District. Smaller algae, however, have largely been omitted from the early studies. A provisional list of species known to occur in the meres has been prepared (Reynolds, 1978a).

Among those meres which have been studied in some detail, variations in the composition of the phytoplankton have been shown to occur, both from season to season, and from mere to mere. Some of the underlying factors which influence these differences have been recently reviewed (Reynolds, 1978a). Nevertheless, the presence of large populations of algae (often exceeding 20 g dry weight m^{-2}) of relatively few species (<14 have accounted for more than 50 per cent of the biomass of Crose Mere) seems characteristic (eg Pearsall, 1923; Swale, 1968; Reynolds, 1973b). Moreover, many of the dominant species (eg *Melosira granulata, Stephanodiscus astraea, Microcystis aeruginosa, Aphanizomenon flos-aquae, Eudorina elegans*) are reckoned to be typical of eutrophic waters generally (Rawson, 1956); species groups said to be more characteristic of oligotrophic waters (eg Chrysophyceae, Desmids) are relatively rare in the meres (Reynolds, 1973b). The greater availability of plant nutrients, which can support larger algal crops, especially of those species having faster rates of growth, may account for the species-assemblages encountered (cf Moss, 1973b). High concentrations of major ions, particularly calcium and bicarbonate may also be of selective importance through their relation with pH

buffering of the system, and in maintaining a supply of inorganic carbon (see Moss, 1972; 1973c; Talling, 1976).

Several well-defined seasonal cycles of algal abundance have been identified in the meres (Reynolds, 1973b; 1978a). In some larger, moderately deep meres occupying basins in sandy drift (eg Crose Mere, Cole Mere, Hatch Mere, White Mere), a vernal diatom maximum (variously dominated by *Asterionella formosa, Fragilaria crotonensis, Stephanodiscus* sp) is succeeded by moderate or large growths of green algae (eg *Volvox, Eudorina, Pediastrum*) in late spring, by blue-green algae (*Aphanizomenon, Anabaena, Microcystis*) in summer, and by a late summer maximum of *Ceratium*. Diatoms were often briefly abundant in mid summer; Cryptomonads occasionally dominated during spring. I have argued (Reynolds, 1973e; 1976a, b, c, d) that both the sequence and the sizes of the algal maxima are influenced primarily by factors which control the physical stability of the water column, and the effects of limiting nutrient stress therein. Commonly, however, the upper limit on population size may be determined by the photic conditions imposed by self-shading of the population, and rarely by an ultimate lack of one or other of the inorganic nutrients (eg Reynolds, 1976a; 1978a).

I have dubbed this sequence the "regional type" of succession (Reynolds, 1973f) against which the phytoplankton succession in other meres could be compared. In fact, it is generally similar to the succession of a large number of moderately eutrophic lakes and reservoirs throughout the temperate regions of the world (see Hutchinson, 1967 for examples). Detail
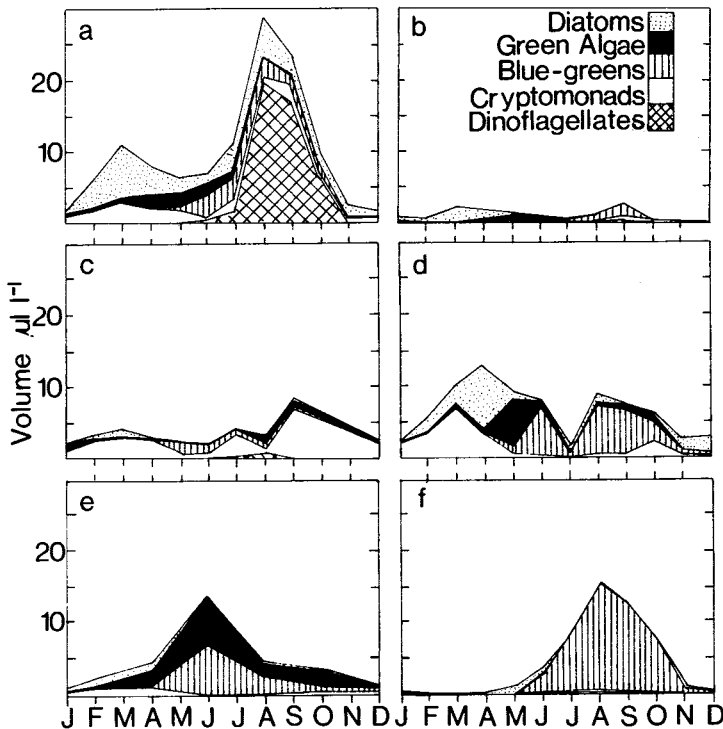

FIG. 16.

Algal periodicity in (a) Crose Mere, (b) Newton Mere, (c) Blake Mere (Ellesmere Group), (d) Cottage Pool, (e) Birchgrove Pool, (f) Rostherne Mere. (a) and (f) are algal cell volumes in μl l⁻¹ of vertical column samples, re-drawn from Reynolds (1976d); (b)-(e) are stylised diagrams, based on surface collections and re-drawn from data presented in Reynolds (1973b).

differences were the earlier commencement of vernal diatom maxima in the (largely ice-free) meres, the paucity of Chrysophyceae, and the summer diatom maxima.

Departures from the "regional type" of succession in the other meres have been loosely classified (Reynolds, 1978a). The variations are more commonly ones of relative abundance of the same species groups than of species composition, except in the case of Oak Mere. Examples of these groupings are stylised in Figs 16a-f, which are based upon information for the representative lakes, variously given in Lind (1944), Belcher and Storey (1968), Swale (1968), Reynolds (1973b, 1978a). The presentation follows the form of Fig. 2 of Reynolds (1976d) from which Figs 16a, 16f are re-drawn directly.

The cycle deduced from occasional collections from Newton Mere is qualitatively similar to the regional type, but the standing populations were, on average, rather smaller and several of the more "eutrophic" species (*Melosira granulata, Stephanodiscus astraea, Microcystis aeruginosa*) apparently grew less well in the period of study, and the most abundant blue-green algae were the heterocystous (ie nitrogen-fixing) genera *Anabaena* and *Aphanizomenon*. *Ceratium hirundinella* however, was more abundant during summer, 1974 (author's unpublished data) than in earlier years, represented in Fig. 16b. Reynolds (1978a) suggested that lower base status and nutrient concentration (especially of nitrogen, among those analysed) may account for some of these differences. Newton Mere is the only known representative of this "mildly eutrophic" category.

In the third type, exemplified by Blake Mere (Ellesmere) (Fig. 16c), Cryptomonads largely replace the diatoms in the vernal maxima, and filamentous blue-green algae are dominant in summer, though *Microcystis* spp. have been abundant in some years (eg Rother and Fay, 1977). A similar cycle has been observed in Kettle Mere (Reynolds, 1973b). The specific loading rates of silica and nitrogen from their small catchments are probably low, but the direct input of leaves from the adjacent deciduous woodland may be significant (Reynolds, 1978a).

The plankton encountered in the smaller meres and pools, which many observers would regard as being ponds rather than lakes, probably does not represent a distinct assemblage of organisms. The morphometric properties of the basins, including relatively high perimeter/area and perimeter/volume ratios, favouring high specific nutrient loading rates are probably significant (cf Findenegg, 1966). The plankton of Cottage Pool, however, shows considerable affinities with the regional type of succession (Fig. 16d) but large dinoflagellates and heavier non-motile diatoms are apparently excluded. Green algae, belonging to the order Chlorococcales (especially *Ankistrodesmus, Scenedesmus* spp) feature prominently in some of the richer small meres (eg Birchgrove Pool, Mere Mere), where higher specific loading rates are augmented, to a greater or lesser extent, by agricultural or domestic effluents. Extreme dominance by these same algae often occurs in sewage lagoons, and has been observed in "hypertrophic" farm ponds in the district (eg Folly Pool, near Shrawardine: Reynolds, 1971a; 1973b), and it is possible that organic input affects the succession observed (Fig. 16e); the information available does not resolve this point. Nevertheless, blue-green algae are often abundant, and *Ceratium* was abundant in a sample taken from Birchgrove Pool in August 1974. Occasional summer samples from Budworth Mere in recent years have also shown co-dominance between blue-green genera including *Microcystis,* and Chlorococcales (including the largest species *Pediastrum boryanum* and *Dictyosphaerium pulchellum*: author, unpublished).

If significant, this apparent extension of the spring plankton assemblage into later seasons may be related to a continuing availability of essential nutrients, and a consequent alleviation of stress conditions which develop in Crose Mere (Reynolds, 1976a). On the basis of Lind's (1944) description of the plankton, I originally grouped Budworth Mere with the "regional type" (Reynolds, 1973b) but have since suggested (Reynolds, 1978a) that it should be reclassified in view of the implied advance in its trophic status.

The dominant algae in the plankton of Rostherne (Fig. 16f) and Ellesmere Meres, among the largest and deepest of the meres, are qualitatively similar to those in Crose Mere, but

their relative abundances are strikingly different. In many recent years, *Microcystis aeruginosa* has been overwhelmingly dominant over all other algae from June-November (Belcher and Storey, 1968; Reynolds, 1973*b*; 1976*d*; 1978*b*; Reynolds and Rogers, 1976); apart from a brief spring phase when *Anabaena* spp or *Aphanizomenon* have been abundant, the biomass of other algae has usually been relatively meagre. In some recent years, however, *Asterionella* or *Stephanodiscus* have been abundant in spring, and substantial populations of *Ceratium* are sometimes observed in summer (Reynolds, 1978*b*). Reynolds (1978*b*) suggested that the greater mean depth of the turbid waters in both meres, coupled with high nutrient concentrations (see Table 2 of Reynolds, 1978*a*) were the principal factors contributing to dominance by *Microcystis*. The ability of vegetative colonies to descend to and overwinter on the bottom muds (Reynolds and Rogers, 1976) is presumably advantageous to the re-establishment of the planktonic population the following year. Renewed growth is apparently correlated with the onset of thermal stratification and the rapid deoxygenation of the lower hypolimnion (Reynolds, 1973*d*, Reynolds and Walsby, 1975), though the mechanisms are, as yet, unclear. In the summers when *Ceratium* became dominant, the maximum biomass was as large as, if not larger than, the *Microcystis* crops in other years. Apparently *Microcystis* failed to become established in these years (Reynolds, 1978*b*).

Dominance of the phytoplankton of Rostherne Mere by *Microcystis aeruginosa* has arisen only within the last 2-3 decades. The analyses of Pearsall (1923, of samples taken in 1912-1913) and Lind (1944) on net collected material indicate an *Asterionella/Coscinodiscus lacustris*—Ceratium—Aphanizomenon* succession; *Microcystis* was present but always in relatively small proportions. The change to a *Microcystis* plankton was evidently well established when Belcher and Storey (1968) made their observations. A recent examination of the algal stratigraphy in the bottom sediments suggests that the change occurred as recently as 1960 (Livingstone and Cambray, 1978).

This change in phytoplankton dominance, which is analogous to experiences in many of lakes throughout the developed world, is presumably attributable to advancing eutrophication. Rostherne Mere has also become richer, especially in nitrogen and phosphorus, as indeed have many other meres (see Section III) mainly through changing land-use practices and the widespread use of agricultural fertilizers. Brinkhurst and Walsh (1967) have considered that the direct deposition of faeces by the large populations of wildfowl ("guanotrophy"), particularly roosting gulls (especially *Larus ridibundus*), has significantly increased the nutrient status of the mere this century. Interestingly enough, Ellesmere Mere also supports a substantial bird population; blue-green algae have been abundant in this lake for at least a century (see records of Phillips, 1884).

Studies on the phytoplankton of Oak Mere (Lind, 1944; 1951; Lind and Galliford, 1952; Swale, 1965; 1968) have repeatedly shown it to be of quite different character from that of any other mere. Almost every sample examined by Lind, between 1941 and 1952, was dominated by the green algae *Botryococcus braunii*; few other species were present, and none was ever abundant (although her net collections would have selected against nannoplanktonic forms). She attributed the differences to the peculiar features of the mere, emphasising the roles of extreme acidity (pH 4.0-4.7), poverty of nutrients (particularly of nitrates), absence of fringing reedswamp and the presence of a large submerged peat deposit. When Swale (1968) commenced her work on the lake in summer 1963, *Botryococcus* was virtually absent from the plankton. Instead, she observed a series of virtually uni-algal populations of *Rhodomonas, Chlamydomonas, Ankistrodesmus, Chlorella, Lagerheimia* and *Closterium*. But in June 1965, *Botrycoccus* reappeared in the lake, and produced a large, dominant population which persisted until August 1966. During the winter of 1965/6, the alga became buoyant, and orange in colour, presumably as a result of lipoid storage and excessive carotenoid content (a feature well-known in cultured populations: Belcher 1968): yellowish scums were frequently observed on the mere at this time. Swale (1968) suggested

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*Coscinodiscus lacustris may be synonymous with *Stephanodiscus astraea*

that the success of *Botryococcus* in competing against small, potentially fast-growing algae may have been influenced by selective grazing of the unicellular species by rotifers (*Keratella* spp) and cladocerans (chiefly *Bosmina obtusirostris*).

That the exclusion of other algal species common in more typical meres is due largely to acidity was clearly demonstrated in 1967, following the pumping of base-rich water from a nearby trial borehole into Triassic aquifers by the (then) Mid-Cheshire Water Board. This operation resulted in the doubling of the calcium concentration to 0.6 meq l^{-1} and the raising of the ambient pH to >6.5. Reynolds and Allen (1968) observed successive dominant populations of *Asterionella* (January-March 1967), *Coelastrum, Pediastrum* and *Scenedesmus* (April-June) and blue-green algae (*Anabaena flos-aquae* and *Microcystis aeruginosa*: June-November). All these species had been previously recorded in Oak Mere, but only *Scenedesmus* had been noted in >10 per cent of Swale's (1968) collections. The lake subsequently "recovered" its former acidic condition: by summer 1968, the pH had fallen to 5.5, and *Closterium* spp were dominant (Reynolds, 1978a).

With the exception of the pattern in Oak Mere, these various seasonal cycles are consistent with the (generally) high base-status and nutrient loadings of the meres. In many cases, the succession seems well-established, suggesting that ecological stability is developed (Reynolds, 1973b). Nevertheless, recent changes in Rostherne Mere, and (perhaps) Budworth Mere, are indicative that further enrichment is still taking place. It is clear that though the biomass of light-limited populations may not alter significantly, changes in species composition seem likely to occur in other meres. The existing data do not resolve the particular factors which contribute to relative increases in (say) green algae as opposed to blue-green algae, although lake morphometry is probably important. Further information would be extremely useful, in predicting the consequences of continued artificial eutrophication, not only in the meres, but in temperate lakes elsewhere.

There are also insufficient data on phytoplankton primary productivity in the meres. I have estimated photosynthetic oxygen production of various phytoplankton populations in Crose Mere: the rate of photosynthesis varies seasonally, and with the dominant species, with maximal values of about 14 mg O_2 (mg chl $a)^{-1}.h^{-1}$ for populations dominated by diatoms, dinoflagellates and *Anabaena circinalis*. Gross photosynthetic oxygen production (expressed areally) has exceeded 1.2 g O_2 m^{-2} h^{-1} in summer, but may be offset by respirational losses over the whole water column in large, light limited populations (Reynolds, 1971a; 1975b; 1978a).

Attempts have been made to determine the net rates of population increase (eg Reynolds, 1976a) in selected algal populations, and under favourable conditions of nutrient availability, temperature and insolation, high productivity is often indicated. Minimum doubling times of ~2 days have been observed for populations of *Asterionella, Fragilaria, Melosira, Eudorina, Volvox, Anabaena circinalis* and *Aphanizomenon*; mean growth rates of *Microcystis* (>4.0 days) and *Ceratium* (>5.0 days) are usually slower.

From the mean weights of individual species, Reynolds (1976a) calculated the dry weight (exclusive of diatom silica) of the algal populations produced in the upper 5 m of Crose Mere, between June and September 1973, to have been equivalent to 17.4 g m^{-3} (or about 63 g m^{-2}, taking the mean depth of the layer to be 3.6 m). I have estimated that typical vernal diatom maxima might account for a further 12-23 g (silica-free) dry weight m^{-2}, to give an annual total of 75-90 g m^{-2}. The gross annual phytoplankton production for the lake (152,000 m^2), allowing for losses due to

direct grazing, sedimentation and decomposition, might be in the range 11-30 tonnes. No comparable data are available for the production of reedswamp, but it is likely to be rather less than that of the plankton: I suggested a provisional figure of about 4 tonnes ann⁻¹ (Reynolds, 1978a). The statement may also be true for other, larger meres, but until more data are obtained, the conclusion must be a tentative one.

The "Breaking of the Meres"

One of the most dramatic and renowned features of the meres is the sudden (often overnight) appearance of thick, greenish floating scums which sometimes cover the entire surface. Both the rapidity with which the waters are transformed to the "colour and turbidity of pea soup" (Sinker, 1962) and the irregularity of their formation have earned the "breaking" of the meres a place in local folk lore. The term supposedly originated from the local brewing industry: when the yeast becomes sufficiently buoyed up by fermentation bubbles, it is said to "break" to the surface. In Staffordshire and east Cheshire, scum formation has been likened to the curdling ("cruddling") of milk (Wardle, 1897). The organisms responsible for the "breaking" are the planktonic blue-green algae *Anabaena, Aphanizomenon, Coelosphaerium (Gomphosphaeria), Microcystis* and *Gloeotrichia* (Phillips, 1884; Griffiths, 1925; Reynolds, 1967). Thus, "breaking" is completely synonymous with "water-bloom" formation (Whipple, 1899; Griffiths, 1939; Hutchinson, 1967), which occurs in many lakes throughout the world, especially those subject to accelerated eutrophication. The water blooms of the Shropshire and Cheshire meres, however, have a long history: the earliest reference is probably that of Leland (1744, quoted by Carter, 1960) who briefly mentioned an "interesting natural phenomenon" at "Hanmere, Ellesmere, Roston [Rostherne Mere?] and Blake Mere". G. C. Davies (1873, quoted by Jackson, 1879) described a break on Ellesmere Mere so well, that it is clear that it was dominated by *Aphanizomenon*. A further passage in Jackson (1879, p. 520) quotes Leighton's account of a *Rivularia* (= *Gloeotrichia*) bloom on the same lake, in 1878.

The causes of the "breaking" have been investigated by Phillips (1884), Wardle (1897), Wilson (eg 1966 and unpublished data) and more recently by Reynolds (1967, 1969, 1971b, 1972, 1973d). Bloom formation occurs in quiet weather mainly in summer and autumn, once the blue-green algae have commenced their annual cycle of growth. The algae owe their buoyancy to the presence of intracellular gas-vacuoles, which normally function to *regulate* the buoyancy of the alga (eg Reynolds, 1973d; 1979; for details of the structure and mechanisms involved, see Walsby, 1972; 1977). In bloom formation, however, there are too many gas vacuoles in existence, and the algae are rendered "overbuoyant". Reynolds and Walsby (1975) concluded that three conditions require to be satisfied before a bloom can develop: that (1) a substantial population of blue-green algae is already present in the lake; that (2) the algae are sufficiently overbuoyant, through failure in the buoyancy control mechanisms; and that (3) water turbulence is too weak to overcome the tendency of these algae to float. Thus, the bloom is the result of rapid upward migration (up to 3-4 m day⁻¹) of existing populations, hitherto distributed over several metres depth. There is no evidence of any explosive increase in the growth of the alga prior to bloom formation (Reynolds, 1971b). Blooms tend to give an exaggerated impression of algal abundance, especially when they accumulate along lee shores. Because the preconditions are not met simultaneously in all the meres, "breaking" is not necessarily synchronous. Other factors, including differences in the specific composition of the blue-green algal populations, nutrient stress, the availability of

carbon dioxide, and the relative sheltering of the basins, also contribute to variations in bloom formation, both from mere to mere, and from "break" to "break" (Reynolds, 1978a).

Prolonged exposure to summer sunshine often results in massive algal mortality (Reynolds, 1967). It may seem paradoxical that the algae should die in this way, though it should be recalled that the main phase of growth is often complete by this stage. Nevertheless, Rother and Fay (1977) have shown that the formation of akinetes (spores), which is most prolific during bloom activity, and their rapid descent to the sediments, provide a survival mechanism for the filamentous species concerned (*Anabaena, Aphanizomenon*).

Although water-blooms are generally considered to be objectionable, mainly on aesthetic grounds, the "breaking" of the meres arouses little public concern locally. Decaying blooms have a distinctive foul odour, which can be damaging to recreational interests; surface scums are also said to interfere with angling (Wilson, 1966; see also Taylor, 1978). However, there is no certain instance of mass fish mortality in any mere, nor of poisoning of livestock in adjacent pastures, which can be attributed to the occurrence of blue-green algal blooms.

(b) *Zooplankton.* The taxonomy and distribution of planktonic rotifers and crustacea in the meres has been investigated by Galliford (eg 1947, 1949, 1954, 1960). A few other records are available (eg Cohen and Lund, 1936; Wilson, 1966 and unpublished; Brinkhurst and Walsh, 1967). These have been summarised (Appendix B of Reynolds 1978a). The most ubiquitous and relatively abundant species include *Keratella cochlearis, K. quadrata, Asplanchna priodonta, Polyarthra dolichoptera, Daphnia hyalina, Bosmina longirostris, Diaptomus gracilis* and *Cyclops strenuus*. The assemblage seems typical for mildly alkaline, productive lakes (cf Ruttner-Kolisko, 1972). *Chaoborus* spp are probably also widespread. The zooplankton of Oak Mere includes *Bosmina obtusirostris* and *Keratella serrulata,* which are said to be more typical of acid or oligotrophic mountain lakes, while many species present in the other meres have not been observed (Lind and Galliford, 1952). *Bosmina corregoni (sensu stricto)* occurred frequently in Blake Mere, Crose Mere and Ellesmere, though it is generally regarded as being rare in British waters (Galliford, 1960).
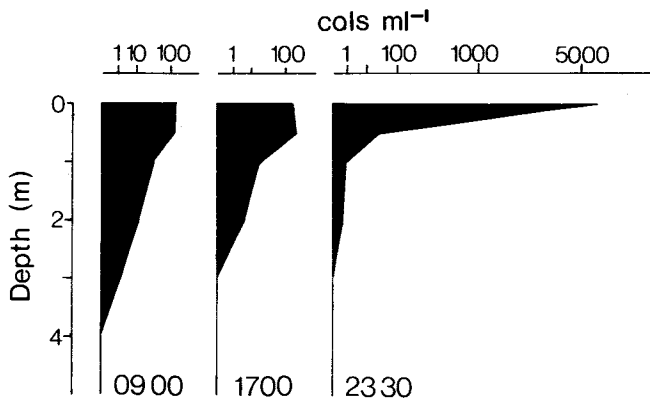

FIG. 17.

The vertical distribution of *Microcystis* colonies with depth in Crose Mere at three different times on 28 July 1971. A bloom had formed before midnight. The concentrations are plotted as "cylindrical curves". Original drawing based on data included in Fig. 8 of Reynolds (1973d).

The seasonality of several common animals in the plankton of Crose Mere has been presented in Reynolds (1978*a*). *Keratella cochlearis, Kellicottia longispina, Asplanchna priodonta, Polyarthra dolichoptera* were usually abundant in two annual peaks, one between March and May, the other in August-September. *Trichocerca similis* occurred mainly in summer. The maximum of *Daphnia hyalina* occurred in mid- or late-spring. The abundance of both *Diaptomus* and *Cyclops* fluctuated throughout the year, but tended to be less numerous in spring. All the data were based on recoveries in a 5 m tube, however: species occurring partly or mainly in deeper water may be under-recorded.

The factor determining periodicity in the meres have not been investigated, but temperature, breeding rate, food availability and predation by other organisms are likely to have important interactions. At times, *Daphnia* have been observed to have fed on algae, including *Asterionella* (1- or 2-celled colonies) and *Eudorina* colonies. Filter-feeding rotifers may feed on smaller ($< 10\,\mu$m) planktonic algae, when they are abundant, and some specific preferences are evident. Grazing may thus be an important factor influencing algal dominance (Reynolds, 1978*a*; cf Nauwerck, 1963). At other times, bacteria and organic detritus probably provide the main potential food source for the filter-feeders. The main foods of the raptorial (ie grasping) feeders (eg *Cyclops*) in this mere have not been determined. Planktonic ciliates (eg *Ophryoglena*) have been observed to feed on filamentous blue-green algae (Reynolds, 1975*b*). Recent re-examination of material collected from Crose Mere during July 1966 has shown that the population maximum attributed to *Pelomyxa* sp (Reynolds, 1971*b*) was, in fact, dominated by another ciliate, *Nassula* sp (Dr H. M. Canter, *personal communication*).

Crude estimates of zooplankton biomass in Crose Mere suggest that through much of the year, the standing crop stands between 3-10 g dry weight m^{-2}, and may rise to up to 25 g m^{-2} in spring (see Reynolds, 1978*a*), perhaps exceeding the standing crop of phytoplankton. However, the generation time of the phytoplankton is generally shorter than that of the zooplankton, so a trophic imbalance is not necessarily indicated. The productivity of the zooplankton, and especially its inter-relationships with the phytoplankton, in the meres as well as in other lakes, requires considerable further research.

(c) *Gas-vacuolate bacteria.* Planktonic communities of lakes generally include a bacterial fraction. The taxonomy and the ecology of bacteria in aquatic habitats have, until recently, received little attention. This is equally true for the meres, but Clark and Walsby (1978*a*) included several meres in their survey of the distributions of gas-vacuolate bacteria in 33 British lakes. They recognised nearly 40 morphologically distinct species, almost all of which occurred in the hypolimnia of thermally stratified lakes; up to 22 species (the most observed in any one lake) occurred in Blake Mere (Ellesmere), Kettle Mere and Crose Mere. This pattern of distribution supports the idea that the gas-vacuoles are important in regulating buoyancy, a function which is relevant only in non-turbulent layers of aquatic systems. Indeed, they were able to demonstrate (Clark and Walsby, 1978*b*) that in Crose Mere various species formed maxima at different depths and times, and that several performed controlled vertical migrations during the summer months.

2. Littoral Communities

The communities of the shallow-watered margins impart, perhaps more than any other, the distinctive appearance of the north-west Midland meres. Their relative accessability has facilitated a number of simple qualitative investigations of their composition but, as yet, there have been few quantitative studies. The structure of littoral communities is influenced by the nature of the substratum, the gradient of the shore line, its exposure to wave action, the fluctuations in water level, and by the

chemical characteristics of the water. Pressures from human activities or from trampling and fouling livestock often significantly modify the effects of these factors. There is thus a range of shore line types represented in the meres and, in many cases, considerable differentiation of the shores of individual lakes (Sinker, 1962).

A survey of the variety of shore line substrata is included in Savage and Pratt (1976, Table I). On open shores the bottom material is frequently dominated by mineral particles derived directly from the adjacent or underlying drifts, and which, to some extent, are sorted by wave action. The finest particles (clay), and organic detritus are removed and deposited elsewhere. The majority of the meres has such shores around at least parts of the margins, where the substratum (be it mud, sand, gravel or stone-dominated) has a low to moderate organic content (<7 per cent, by weight, of core samples: Savage and Pratt, 1976). Mollusc-shell fragments often contribute significantly to the substratum (Kennedy, 1961; Sinker, 1962). Elsewhere shore lines are, to a greater or lesser extent, colonised by aquatic flowering plants, which tend to stabilise the soil around their roots, to accelerate the deposition of finer particles, and to contribute directly to the accumulation of organic debris during the annual cycle of their growth and decomposition. The present organic content of substrata in dense stands of aquatic macrophytes is often very high (up to 85 per cent by weight: Savage and Pratt, 1976).

(a) *Vegetation.* Open shores, by definition, are sparsely vegetated by higher plants. At times, submerged mineral particles support luxuriant algal growths. The species composition, microdistribution and periodicity of these algal carpets have not been systematically investigated, but some of the more prominent forms have been noted by Reynolds (1971a, 1978a). These include diatoms of the *Navicula* and *Acnanthes* groups, *Gomphonema* and *Synedra* spp. In spring, copious growths of green algae (especially of *Enteromorpha, Cladophora, Tetraspora*) sometimes follow closely the initial clearing of the vernal phytoplankton maxima, and apparently show some direct correlation with the level of dissolved nutrients (especially nitrogen) in the water at that time (Reynolds, 1978a).

In the last century, curious objects known locally as "moss-balls" (or "mere-balls") were said to be common in Cole Mere and White Mere (Jackson, 1879). They have not been recorded recently, but the published descriptions bear a close resemblance to the alga *Cladophora sauteri,* a rare plant usually found in clear calcareous lakes. This species still occurs in Malham Tarn, where Sinker says "hundreds of small, dark-green spheres, up to the size of golf balls, can be seen resting on the bottom—though unattached—in sheltered bays, where they roll to and fro with the gentle movement of the water. Each ball consists of a dense mass of branching filaments radiating outward from a central point. As they grow bigger, larch needles and other scraps of fibrous plant debris become entangled among the algal threads, eventually forming large ovoid masses up to 30 cm or more in length. These odd vegetable hedgehogs are washed up on the lee shore by storms, and retain their form long after the alga itself has died" (C. A. Sinker, *personal communication*).

In the more eutrophic meres, there is a scarcity of submerged aquatic vegetation. This condition has been attributed to the combination of steeply shelving sides of the basin, and the generally low seasonal light penetration (Sinker, 1962). *Zannichellia palustris, Potamogeton crispus* (Crose Mere: Sinker, 1962), *P. gramineus,*

Elodea canadensis and *Sparganium minimum* (Hatch Mere: Lind, 1949), however, have been recorded to form (or to have formed) local offshore stands in the lakes named. Griffiths (1925) reported *P. pectinatus* and *E. canadensis* in Tabley Mere, and extensive beds of *Potamogeton* and *Myriophyllum* at the shallow end of Ossmere; *Elatine hexandra* and *Isoetes lacustris* have been observed several times this century at Bomere (Lloyd and Rutter, 1957). *Subularia aquatica,* recorded by Leighton (1841) in Hencott Pool, and *Lobelia dortmanna* (once present in at least four Shropshire meres: Leighton, 1841) now appear to be extinct in the meres.

Shoreline colonisation by aquatic macrophytes ranges from isolated clumps of emergent vegetation (as in the majority of the Ellesmere- and Shrewsbury-group meres), through discontinuous or thinly developed reed beds (eg of the Budworth, Cole, Cop, Crose Meres, Petty Pool and several of the Whitchurch group) to more continuous reedswamp stands (eg Betley Mere, Fenemere, Hatch Mere, Rostherne Mere and the two Quoisley Meres: Savage and Pratt, 1976). Floating swamp has all but closed over the open water at Sweat Mere, while reedswamp and tall fen has more or less completely invaded Hencott Pool (Sinker, 1962).

Well-defined vegetation zones are often strikingly apparent. On the lakeward side water-lily beds, dominated usually by *Nuphar lutea* or, locally, by *Nymphaea alba* rooted in water depths of 1-2 m, form belts of variable width, depending on the gradient and substratum of the sublittoral slope, and on the exposure of the shore line to wave action. The rare *Nuphar pumila,* which has few known habitats in Britain is established in both Cole Mere and Blake Mere (Ellesmere). The reed-swamps which extend from a water depth of about 0.8 m to the water edge are typically dominated either by *Phragmites communis* (as at Budworth Mere, Comber Mere, Cop Mere, Cole Mere, Fenemere and Petty Pool), or by *Typha angustifolia* (eg Hanmer Mere, Sweat Mere) or by mixed *Phragmites/Typha* stands (eg Bar Mere, Betley Mere, Chapel Mere, Hatch Mere, Marbury Big Mere, Pick Mere, the Quoisley meres and Rostherne Mere). At Crose Mere, *Typha* appears to be rapidly displacing *Phragmites* (see Fig. 18). Isle Pool is more or less completely fringed by *T. latifolia.* Where the zonation is best developed, an offshore belt of *Schoenoplectus lacustris** (at two meres; *Schoenoplectus tabernae-montanae* also occurs locally) sometimes precedes the *Phragmites/Typha* zone; and at some sites (eg Alkmond Park Pool, Crose Mere, Hatch Mere) *Cladium mariscus* occurs beyond it. *Glyceria maxima* is locally dominant in the swamp zone at Cole Mere. Common reedswamp associates almost everywhere are *Sparganium erectum* and *Polygonum amphibium.*

At the water's edge there is a sharp transition to a fen community dominated by tussocks of *Carex paniculata* which may lead directly to *Alnus-* (or, more rarely, *Salix-*) dominated carr (eg Sweat Mere, parts of Crose Mere, Hatch Mere and Fenemere), or to fen-meadow, where tree growth has been cleared or prevented from developing by grazing stock (Fenemere has an outstanding example) or to a more acidic ("poor fen") vegetation dominated by a carpet of *Sphagnum recurvum* on which *Eriophorum angustifolium* and *Vaccinium oxycoccus* are typical associates, and where, depending on the relative wetness of the mire surface, either *Molinia caerulea* and (sometimes) *Myrica gale* or *Carex nigra* and *Drosera* spp also occur (eg parts of Hatch Mere, Rostherne Mere and several pools in the Delamere Forest). Further "terrestrialisation" (*sensu* Tallis, 1973) by progressive encroachment of *Sphagnum*-dominated com-

*Nomenclature of water plants follows Haslam, Sinker and Wolseley (1975)
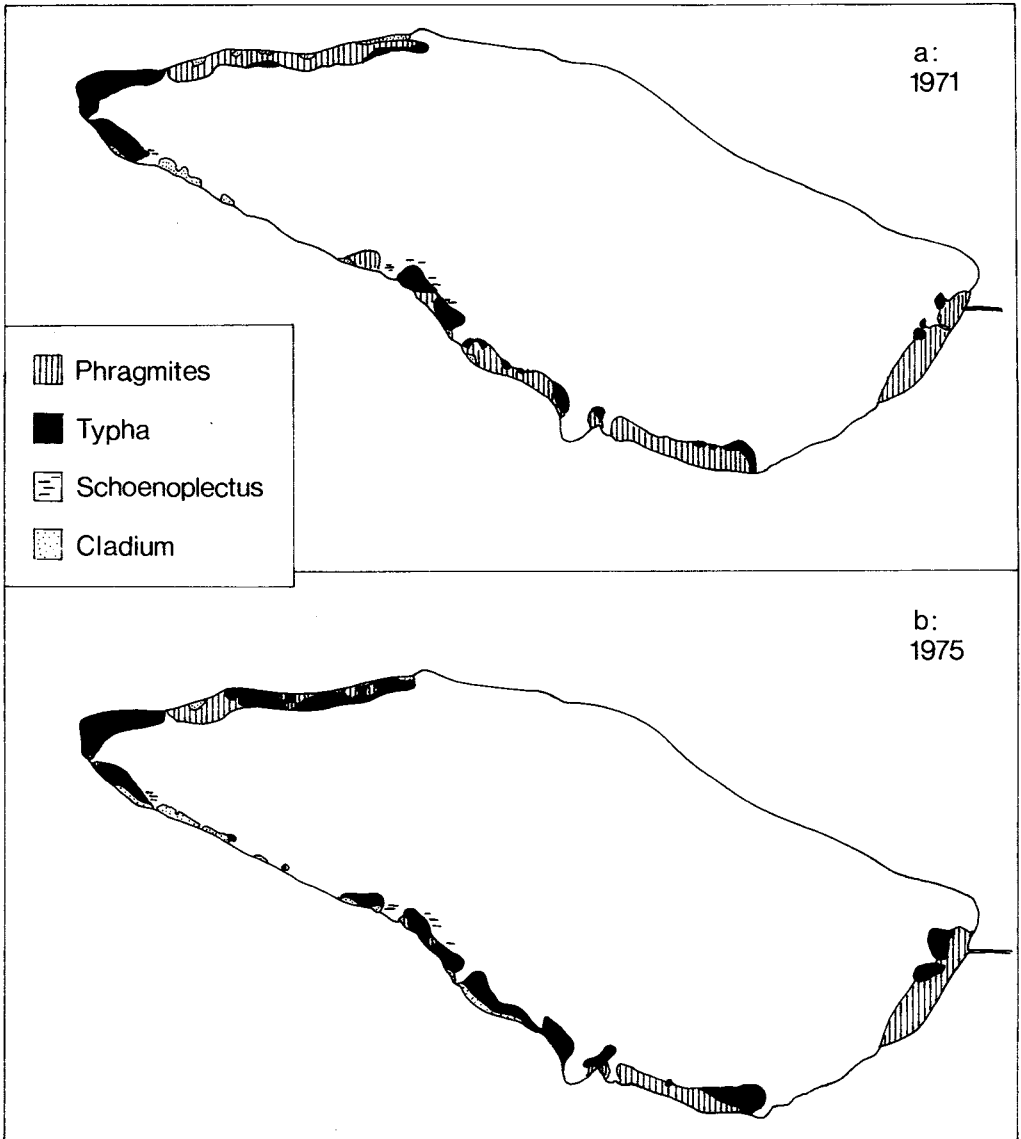
FIG. 18.
The distribution of dominant reedswamp species in Crose Mere in (a) October 1971 and (b) June 1975.
From author's unpublished surveys. Original.

munities and/or by *Betula* scrub is represented at a large number of the mosses (see Section VII).

Although the hydrosere through reedswamp to fen or bog is typical of the fringed meres, it is not universal. In Ellesmere Mere, the principal swamp-forming species are *Polygonum amphibium, Sparganium emersum, Menyanthes trifoliata, Iris pseudacorus, Typha latifolia* and, especially at the southern end, *Phalaris arundinacea* (Wilson, 1966; 1973). *Polygonum amphibium, Sparganium emersum* and *Eleocharis palustries* are (singly or together) the most abundant swamp plants in Mere Mere, Newton Mere and White

Mere. *Sparganium* swamps also occur in bays at Blake Mere (Shropshire). The hydrosere of the lake shore at Oak Mere, where successive zones (proceeding landwards) are dominated by *Eleocharis palustris, Juncus effusus* and *Molinia caerulea* with local *Betula* (see Lind, 1951), is unlike that of any other mere. The extreme acidity of the water and a fluctuating water level are presumably the major selective factors influencing the species composition of the zones.

More complete accounts of the vegetation of several Cheshire and Shropshire meres, together with full lists of associated species, are given in Lind (1949) and Sinker (1962) respectively. The sociological structure and development of *Sphagnum recurvum*-dominated communities is more fully described in Tallis (1973). A detailed description of the flora of Sweat Mere, based on information supplied by Prof A. R. Clapham, is given in Tansley (1939). The species composition of the various vegetation zones represented are presumably determined largely by the local chemical conditions. The zonation itself is presumably controlled by the interaction of specific growth requirements and the relative stability of the water levels, and is a manifestation of a dynamic successional process, whereby the various zones may progressively encroach the mere (Reynolds and Sinker, 1976). However, both the type and rate of successional advance vary between and within the meres, in accord with local conditions of substratum, gradient exposure and adjacent land-use pressures.

(b) *The Fauna.* Until recently the invertebrate fauna of benthic habitats (the littoral terrace, the sublittoral slopes and the profundal) of the meres had only been investigated cursorily. Much of the work has concentrated upon the distribution of individual species or groups of lake-dwelling animals, and has often been restricted to a few selected meres, eg Tricladida (Reynoldson, 1966; Reynoldson and Bellamy, 1970), Microturbellaria (Young, 1970; 1973), Cladocera (Galliford, 1954; 1960), Corixidae (Macan, 1967; Savage and Pratt, 1976) and Chironomidae (Tait-Bowman, 1976). For many other invertebrate groups, the basic task of identifying and naming the animals has still to be completed. Indeed, taxonomic difficulties have largely precluded any detailed surveys of the animal communities in particular lakes. Undoubtedly, the most thorough investigation of this kind has been that of Berg (1938) for Esrum Sø, a moraine lake in northern Denmark. In Britain, almost all the faunal surveys have concentrated on glacially excavated lakes, (eg Windermere, and the larger Cumbrian lakes: see Macan, 1970), while communities in richer, lowland lakes have received relatively little attention (Macan, 1974a; Young and Harris, 1974).

Information about the meres consists mainly of unpublished reports and theses, supported by incomplete species lists, (eg Brinkhurst, 1960; Kennedy, 1961; Pickavance, 1965; Wilson, 1966; Apampa, 1967; Brinkhurst and Walsh, 1967), and supplemented by information on specific groups, as outlined above. Young and Harris (1974) summarised the data then available for the distribution of Tricladida, Gastropoda, Hirudinea, Amphipoda and Isopoda in eight meres. An updated species list for ten meres is given in the appendix which draws additionally on the surveys of Rostherne Mere (by Walsh, 1965; see also Brinkhurst and Walsh, 1967) and Sweat Mere (Kennedy, 1961) and other unpublished sources. It includes over 250 "taxa", but it is still far from being exhaustive. Not all these meres have been investigated to the same extent.

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Of the species identified, less than fifty are known to be common in the ten meres selected, or abundant in any. Pickavance noted 45 "characteristic" species which occurred in most of the samples he collected from each of the four meres he investigated (Blake Mere, White Mere, Cole Mere and Hatch Mere) during a seven-month period (November 1964-May 1965). The list is reproduced here (as Table 9) in a modified form, giving 27 of the "taxa" which Pickavance found regularly in at least two of the four meres, together with a further 7 which were shown to be common or widespread by other workers [References: Kennedy (1961), Young and Harris (1974), Tait-Bowman (1976) and Savage and Pratt (1976)]. Data for selected Cumbrian lakes (from Macan, 1970) and from Esrum Sø (from Berg, 1938) are also

Table 9. *"Characteristic" Species of Littoral Invertebrates in the Meres*

	Blake Mere	White Mere	Hatch Mere	Cole Mere	Butter-mere	Winder-mere	Esthwaite Water	Esrum Sø
Tricladida:	+	+	+	+	+	+	+	+
Mollusca:								
Acroloxus lacustris	+	+	+	+				+
Bithynia tentaculata	+	+	+	+ ·			+	+
Lymnaea peregra	+	+	+	+	+	+	+	+
Planorbis albus	+	+	+	+		+	+	+
Planorbis carinatus	+	+	+	+		+		+
Potamopyrgus jenkinsi	+	+	+	+		+		
Segmentina complanata	+	+	+	+				
Sphaerium spp	+	+	+	+		+		+
Pisidium spp	+	+	+	+		+		+
Annelida:								
Euilyodrilus hammoniensis	+	+	+	+			+	+
Tubifex tubifex	+	+	+	+			+	+
Tubifex ignotus	+	+	+	+				+
Peloscolex ferox		+	+		+			
Limnodrilus hoffmeisteri	+	+	+			+	+	+
Lumbriculus variegatus	+	+	+	+				+
Stylodrilus heringianus	+	+	+	+				
Dero digitata	+	+	+	+		+		
Helobdella stagnalis	+	+	+	+	+	+	+	+
Erpobdella octoculata	+	+	+	+	+	+	+	+
Glossiphonia complanata	+	+	+	+	+	+	+	+
Crustacea:								
Asellus aquaticus	+	+	+	+		+	+	+
Gammarus pulex	+	+	+	+	+	+	+	+
Crangonyx pseudogracilis	+			+		+		
Insecta:								
Cloëon dipterum	+	+						
Caenis horaria	+	+		+		+		
Sigara falleni	+	+	+	+		+	+	+
Sialis lutaria	+	+	+	+		+		+
Polycentropidae	+	+	+	+	+	+	+	+
Limnephilidae	+		+	+				
Molanna sp	+	+	+	+				+
Phryganea sp	+		+	+				+
Leptoceridae	+	+		+		+		+
Chironomidae	+	+	+	+	+	+	+	+
Total "Taxa" (out of 34):	33	31	30	31	9	21	15	25

included for comparison. Although limited in its scope, the comparison shows a high incidence of species which, though common to a selection of productive meres, spanning a wide range of morphometry and water chemistry, and to a lake of similar origin in Denmark, have not been found in the less productive Cumbrian lakes.

Moreover, Pickavance (1965) demonstrated that, at times, littoral invertebrates occur at high densities in the littoral of the meres. His quantitative estimates (summarised in Table 10) were based upon the catches in areal samples taken from selected lengths of open, more or less stony, shore which he considered as being representative of each lake, averaged over seven samplings. However, his results gave no indication of variance attributable to uneven distribution of animals on the shore, or to seasonal changes in abundance due to hatching, cropping by predators or to migration (into deeper water) or to emergence (of insects). Interpretation is therefore statistically limited and inconclusive. Nevertheless, the order of magnitude of these "average" densities (probably 2,000-20,000 individuals m^{-2}) can be compared with Macan's (1974a) findings in Windermere, where the maximum density of animals was about 3,000 m^{-2}, and less than 1,000 m^{-2} at most sampling stations around the lake. Corresponding figures for Esrum Sø (Berg, 1938) were, respectively, >10,000 m^{-2} and >5,000 m^{-2} at nearly all depths.

A second point concerns the relative paucity of insects. In contrast with the stony shores of the less productive Cumbrian Lakes (eg Buttermere, Ennerdale Water, Wastwater) where ephemeropteran and plecopteran nymphs and larval trichoptera are among the most common animals to be found (see Macan, 1970), only three species of mayfly (*Ephemera vulgata, Caenis horaria* and *Cloëon dipterum*) occurred in the Blake mere samples; stoneflies were not encountered, though there were more species of caddis present. There were fewer species of mayfly and caddis in samples from the other three meres, present in smaller (perhaps significantly so) numbers. However, the increase in species diversity and relative abundance of non-insect species evident in the more productive Lake District lakes (eg Windermere South Basin, Esthwaite Water: see Macan, 1970) is continued in the mere series: most species of flatworms, leeches, crustaceans and snails also occur on the stony margins of

Table 10. *Areal Densities of Invertebrates in the Littoral of Four Meres*

(From the data of Pickavance, 1965)

	Blake Mere		White Mere		Hatch Mere		Cole Mere	
	Number of Spp.	Individuals m^{-2}	Number of Spp.	Individuals m^{-2}	Number of Spp.	Individuals m^{-2}	Number of Spp.	Individuals m^{-2}
Triclads (flatworms)	3	10	2	5	3	10	4	40
Gastropod Molluscs	7	130	8	165	10	765	10	715
Bivalve Molluscs	2	80	3	3205	2	925	3	730
Oligochaete Worms	14	815	13	3155	10	755	6	70
Leeches	3	95	5	225	5	140	6	70
Isopods	1	1100	1	250	2	1220	1	1100
Amphipods	1	1200	1	10	2	220	1	1000
Mayflies	3	2010	3	10	—	—	—	—
Damselflies	2	<1	—	—	1	<1	2	<1
Corixids	1	<1	1	<1	3	<1	6	50
Caddis flies	>7	455	>4	95	>4	100	>6	80
Alder flies	1	400	1	10	1	35	1	120
Beetles	3	<1	4	195	2	150	1	>1
Chironomids	?	4500	?	1800	?	330	?	1250
Total/m²		10795		9125		4650		5225

the meres, together with some notable additions: *Glossiphonia heteroclita, Helobdella marginata, Theromyzon tessulatum, Bithynia* spp, *Planorbis vortex, Segmentina complanata*. Many species of oligochaetes and chironomids are found, especially where finer deposits are present. Macan's (1965) comparison of his catches from Windermere with data abstracted from Berg (1938) showed that whereas Ephemeroptera, Plecoptera and Trichoptera together accounted for 54 per cent of the animals collected from the littoral of Windermere, the proportion fell to 11 per cent in Esrum Sø. The corresponding values drawn from Pickavance's (1965) less extensive data are 42 per cent for Blake Mere, and 3 per cent for each of the other three meres.

Macan's (1965) hypothesis to explain the dominance of insects in oligotrophic lakes and their relative replacement by non-insect groups in richer lakes invokes the greater dependence of ancestrally-aquatic groups upon water quality (aquatic insects having invaded water secondarily are relatively free of this constraint); more elaborate egg-protecting adaptations (eg gelatinous egg masses, capsules, brood pouches) provide non-insects with a competitive advantage in richer habitats. The provisional data for the meres thus support Macan's model. That the ratio for Blake Mere is greater than for the other three meres, and is intermediate between the Windermere and Esrum Sø values conforms with chemical and biological evidence presented elsewhere that Blake Mere is a relatively less productive mere.

Species distribution among meres. The tabulated summaries of Young and Harris (1974) emphasise differences in the distribution of certain littoral invertebrates among the meres, which they briefly reviewed in relation to published ecological findings. The paucity of *Dugesia* spp (they did not distinguish between *D. polychroa* and *D. lugubris*; cf Reynoldson and Bellamy, 1970) and *Dendrocoelum lacteum* in Newton and Blake Mere, compared with *Polycelis tenuis* is in accord with Reynoldson's (1966) hypothesis that the distribution and abundance of these flatworms is determined primarily by interspecific competition for their preferred prey (oligochaetes, *Asellus*, snails) whose variety and abundance is generally greater in more productive, calcareous lakes. Two other flatworms, *Bdellocephala punctata* and *Planaria torva* occur in a few of the meres examined, but relatively little is known of their ecology. Equally, the numerical dominance of the leeches *Glossiphonia complanata* and *Helobdella stagnalis* over *Erpobdella octoculata* in all the meres except Newton Mere, conforms with the conclusions of Mann (1955) that they are relatively more abundant in productive lakes. *Erpobdella testacea*, a species tolerant of the relatively anaerobic conditions occurring in reed-swamps of rich ponds, has been recorded in vegetation at Ellesmere, Cole and Crose Meres. *Haemopis sanguisuga* has so far been recorded only in Hatch Mere (Pickavance, 1965), but its seasonal migration patterns may have enabled it to escape detection elsewhere. Young and Harris (1974) recorded *Batrachobdella paludosa* only in Comber Mere but it has since been identified and confirmed from collections at Crose Mere (P. S. Croft, *personal communication*). The fish parasites (*Piscicola geometra, Hemiclepsis marginata*) each occur in a variety of meres and are not mutually exclusive (cf Mann, 1955).

The greater variety of gastropod species as found in the richer meres generally conforms with the information on distribution in Britain, given in Boycott (1936) and Macan (1969). In particular, the species which are rarely found in soft waters (Group 3 of Macan, 1969) are largely confined to the more calcareous meres; those of more widespread occurrence belong to Group 4 (see Table 11). Moreover, *Bithynia leachii*, one of the two group 3 molluscs listed under Newton Mere has been recorded only once (Brinkhurst, 1960) and does not figure in Young and Harris' (1974) quantitative data for that lake. On present evidence, *Viviparus viviparus, Planorbis crista* (in Ellesmere Mere and Cole Mere), *Planorbis leucostoma* (Cole Mere), *Valvata cristata* (Crose Mere, Rostherne Mere) and *Lymnaea glabra* (Crose Mere) are restricted in distribution. Young and Harris (1974) recorded *Valvata macrostoma* in Ellesmere Mere and Crose Mere, far from its other known sites in south-eastern England (Macan, 1969), and is conceivably a misidentification of *Valvata piscinalis*. The single record of *Menetus dilatatus* in

Table 11. *The Distribution of Gastropods in Six Ellesmere Group Meres*

Group	Species	Newton Mere	Blake Mere	White Mere	Ellesmere Mere	Cole Mere	Crose Mere
3	Acroloxus lacustris	+	+	+	+	+	+
	Bithynia leachii	+		+		+	+
	Lymnaea auricularia		+	+	+		
	Lymnaea stagnalis		+	+	+	+	
	Bithynia tentaculata		+	+	+	+	+
	Segmentina complanata		+	+	+	+	+
	Planorbis carinatus		+	+	+	+	+
	Planorbis vortex			+	+	+	+
	Planorbarius corneus			+	+	+	+
	Viviparus viviparus			+		+	
	Total (Group 3)	2·	6	10	8	9	7
4	Lymnaea peregra	+	+	+	+	+	+
	Potamopyrgus jenkinsi	+	+	+	+	+	+
	Physa fontinalis	+				+	+
	Planorbis albus	+	+	+	+	+	+
	Planorbis contortus	+	+	+		+	+
	Planorbis laevis		+			+	
	Lymnaea truncatula		+	+			
	Lymnaea palustris		+	+	+	+	+
	Valvata piscinalis		+	+		+	+
	Ancylus fluviatilis		+		+	+	+
	Planorbis crista				+	+	
	Planorbis leucostoma					+	
	Valvata cristata						+
	Lymnaea glabra						+
	Total (Group 4)	5	9	7	6	11	10
	Total (Groups 3 and 4)	7	15	17	14	20	17

Blake Mere (H. M. Twigg, in 1963) also needs confirmation, although this North American species, which was first discovered in Britain in 1869, has been "moderately successful" (Macan, 1974b) in spreading from its original locality (see also Dance, 1970).

The isopod, *Asellus meridianus* has been recorded in only three meres in recent years (Comber Mere, Crose Mere and Hatch Mere). Elsewhere, *Asellus aquaticus* may have displaced, or be presently displacing, *A. meridianus* (cf Williams, 1963), except in Comber Mere, where *A. meridianus* still occurs alone. The amphipod, *Gammarus lacustris,* is similarly restricted in distribution, occurring in Blake Mere, Hatch Mere and Crose Mere and may be in the process of being displaced by *G. pulex* (Kennedy, 1961). It is apparently no longer common in Crose Mere (author's unpublished observations, 1968-1970) but was "still present" in Hatch Mere in 1973 (Holland, 1976). *Crangonyx pseudogracilis,* a recent introduction (Hynes, Macan and Williams, 1960; Macan, 1974b) has been recorded in five meres since 1960.

Although the variety of Ephemeroptera known to occur in meres is limited, *Cloëon dipterum* and *Caenis horaria* are probably widespread. Since its nymphs, living near the surface of the mud, are not confined to shallow water, *C. horaria* may have been missed by littoral collectors. Pickavance (1965) did not find it in Cole Mere, but specimens have been recovered from the stomachs of Perch netted in the mere in 1974 (unpublished data, Preston Montford Field Centre). The inclusion of *Leptophlebia vespertina* in the species list for White Mere is based on the recovery of a single specimen, but Pickavance (1965) stated that the

species was abundant in Oak Mere. *Nemoura cinerea* is the only stonefly to have been recorded from any mere (Crose Mere: Dr T. T. Macan, *personal communication*).

Of the Trichoptera larvae identified to generic or specific level, *Molanna* occurred in all four meres investigated by Pickavance (1965); *Phryganea* was found in three, and *Anabolia nervosa* in two. *Anabolia* was also recorded in Crose Mere by Kennedy (1961), but his identification of the stream-dwelling *Plectrocnemia* from Sweat Mere may be erroneous (Dr T. T. Macan, *personal communication*).

Bugs of the family Corixidae are often abundant in the meres. In a survey of 25 meres and flashes, Savage and Pratt (1976) found a high degree of similarity in the relative proportions of the commoner species present, although the total numbers varied widely. *Sigara falleni* was the most widespread species, and was often the most numerous in any one mere. They distinguished between those meres in which two-thirds or more of the total number of specimens caught were ascribable to *S. falleni* (their Group-B meres), and those in which *Sigara dorsalis, Sigara distincta* and *Callicorixa praeusta* together made up one-third or more of the total number of corixids caught (Group A meres). Some of their data are represented graphically in Fig. 19. This arrangement of meres does not coincide with those based on size, chemical richness or phytoplankton assemblage; Savage and Pratt (1976) suggest a general correlation exists among Group A meres with a slow rate of "terrestrialisation" (*sensu* Tallis, 1973; and see later), and a lower organic content of their mud, but the relationship is not clearly defined. In Sweat Mere, where the hydrosere is well-developed, Macan (1967) demonstrated a zonation of Corixid species corresponding with the vegetation zones: *S.*
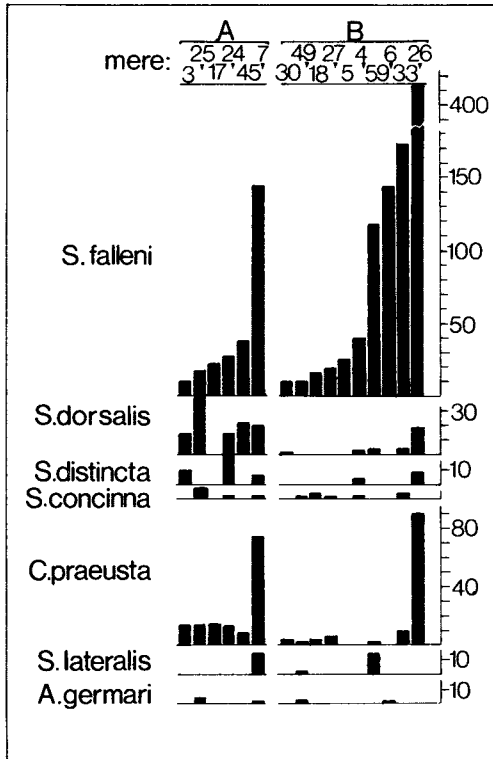

FIG. 19.

The occurrence and total catches of various species of Corixidae in the meres studied by Savage and Pratt (1976). Meres numbered as in Table 1. Drawn from data in Table 1 of Savage and Pratt (1976).

falleni and *S. dorsalis* were most numerous in the open water immediately beyond the *Typha* swamp; *Hesperocorixa sahlbergi, H. linnei* and *Corixa punctata* were the most abundant species in the middle of the swamp; and *H. sahlbergi* was the dominant species in fen pools. Apart from the inclusion of *C. punctata,* a species typical of small ponds (Macan, 1954a), the corixid succession closely resembles the *striata-linnei-sahlbergi* series established for some Danish moraine lake hydroseres, including Esrum Sø (Macan, 1954b). Savage and Pratt (1976) remarked on the absence of *H. sahlbergi* from their collections, even at those meres with reed-bed and carr development. They concluded that the meres they investigated provide largely open water conditions, and still generally lack sufficiently advanced hydroseral vegetation to support populations of the associated Corixids.

Other insect classes are represented in the littoral fauna of the meres and include Megaloptera (*Sialis lutaria*) and Diptera (families Culicidae and Chironomidae, especially *Tanytarus* spp and members of the Orthocladiinae) which are widespread and often abundant; several species of Coleoptera or their larvae have been recorded in various meres, and some may be widespread; adult dragonflies and damselflies (order Odonata) are frequently sighted over the meres in summer, but only *Ishnura elegans* has been recorded in its nymphal stages.

A number of invertebrate species which are well established in Cole Mere (and to a lesser extent in Blake Mere), but which do not occur in other meres, are believed to have reached the lakes from the nearby Shropshire Union Canal. An overflow channel leads directly into Cole Mere, providing a means of entry to several canal-dwelling species. The most striking is the Zebra Mussel, *Dreissena polymorpha* which occurs in small numbers in the canal (Boycott and Oldham, 1936; Croft, 1975), and was already well established in the mere at the time of Brinkhurst's (1960) survey. Presumably, the original colonisers were immigrant veliger larvae which settled and developed in the mere. The Button Ramshorn, *Planorbis leucostoma* and the flatworm, *Dugesia tigrina* are also confined to Cole Mere and, similarly, may have entered directly from the canal. The presence of *D. tigrina* in the Shropshire Union Canal, however, has not been established. In addition, a number of species that are common in the Shropshire Union Canal (Twigg, 1959; Croft, 1975) have a very restricted distribution in the meres: *Ephemera vulgata, Planorbis laevis* (present only in Cole Mere and Blake Mere), *Planorbis crista* and *Viviparus viviparus* (Cole Mere and Ellesmere Mere).

Species distribution within meres. Certain species or groups occur predominantly only within restricted areas of the meres. Their distribution is governed by such factors as substratum type, water depth, the presence of vegetation, aeration, availability of food and vulnerability to predation. It follows that those meres having well-differentiated shores potentially support a more diverse fauna. The data of Young and Harris (1974) are separated according to the method of collection, which was varied to work in vegetation beds, stony shores, and open shores composed of finer particles. The inaccuracies of each method are well-documented (see Young and Harris, 1974 for references) and hinder quantitative comparison, but the treatment permits a qualitative insight into restricted distributions in these broad divisions of the littoral. For instance, *Acroloxus lacustris, Lymnaea auricularia, L. stagnalis, Planorbarius corneus* and *Erpobdella testacea* are all species apparently confined to macrophytic stands; *Ancylus fluviatilis* and *Bdellocephala punctata* were found mainly on stones. Most species, however, were found on two or more shore-types on the meres in which they occurred.

Kennedy's (1961) brief survey of Crose Mere also revealed few obvious associations between particular species and littoral types. His data, too, were necessarily based on several methods of collecting: samples from deeper water (his stations 8-22) were taken with an Ekman Grab. A selection of Kennedy's data are presented as Fig. 20. Subject to methodological limitations some provisional correlations between the fauna and the nature of the substratum are possible. Corixids, *Helobdella stagnalis* and *Potamopyrgus jenkinsi* were
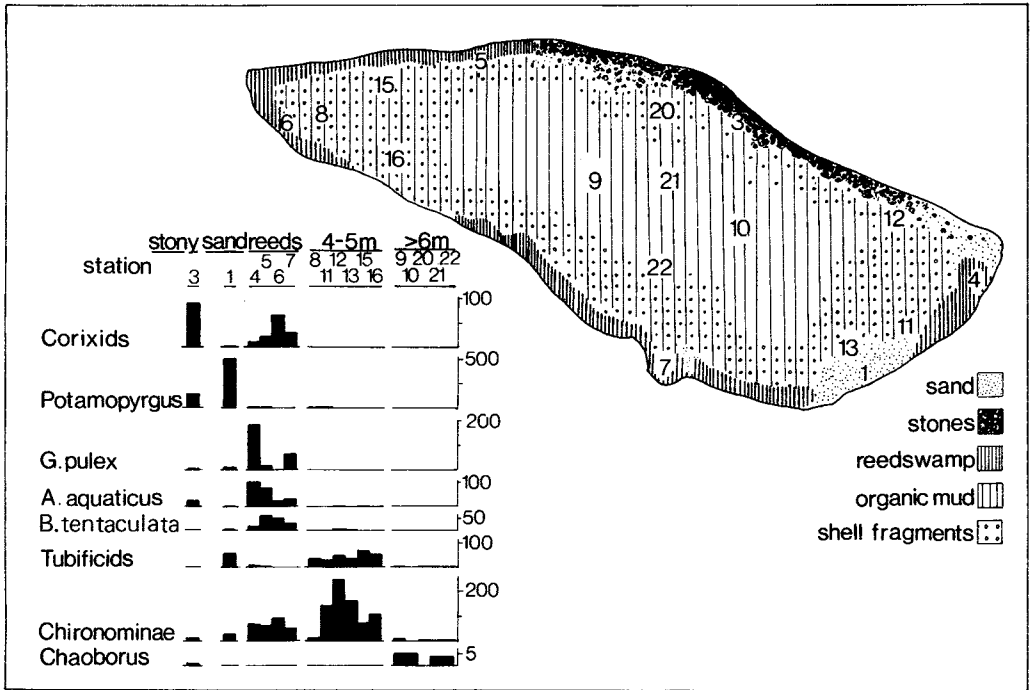
FIG. 20.

The distribution of selected invertebrate groups in Crose Mere in relation to water depth and substratum type. The histograms are based on Kennedy's (1961) tabulated data for animals collected in timed collections (stony, sandy, reedy shores) or in Ekman Grab samples (4-9 m depth) at the stations indicated on the main map. Map re-drawn from Kennedy (1961).

found in larger numbers on open shores (note that *P. jenkinsi* was found by Young and Harris to be most abundant in reedswamp). The Tubificids extended from the open shores into deeper water, though *Limnodrilus hoffmeisteri* and *Lumbriculus variegatus* were essentially littoral. *Caenis horaria* (not shown in Fig. 20) was also more common on open shores. Most littoral species, however, occurred more abundantly amongst reeds.

Brinkhurst and Walsh (1967) compared the distribution of various species at different depths in Rostherne Mere; some of their data are represented in Fig. 21. Most littoral species were reduced in numbers with increasing depth (eg *Caenis horaria*, *Potamopyrgus jenkinsi* and *Valvata piscinalis*) though *Helobdella stagnalis*, *Asellus*, *Limnodrilus hoffmeisteri* (cf Kennedy's observations) and *Euilyodrilus hammoniensis* continued to be numerous well into the sublittoral, to a depth of >15 m.

3. *Profundal Communities*

The bottom deposits of the meres and their associated fauna have yet to be investigated systematically. It is likely that in most instances the primary sediments reflect the more mobile components of the adjacent local drifts—sands, silts and clays which, to a greater or lesser extent, have been sorted and bedded under (initially) flowing or standing conditions. Meres in the Knutsford group may be based on alluvial deposits. These primary deposits may have been laid down on unsorted drift surfaces, or possibly onto bedrock; in Crose Mere, the primary deposits apparently overlie boulder clay (Reynolds, 1975a; Beales, 1976).
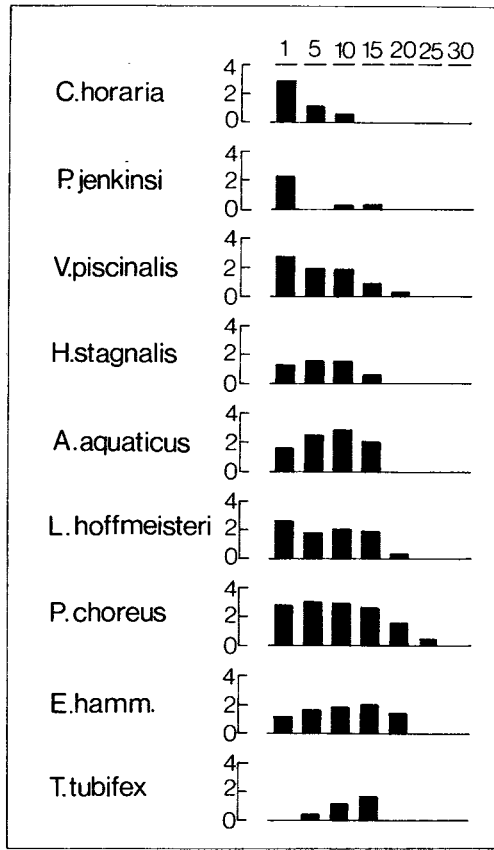
FIG. 21.

The distribution with depth of selected invertebrate species in Rostherne Mere (E. hamm=*Euilyodrilus hammonensis*). The scale of the vertical axes is in $\log_{10}$ number of individuals per m^2. Re-drawn from data presented in Fig. 3 of Brinkhurst and Walsh (1967).

Above the basal sediments, the bottom deposits of most meres comprise finer particles which generally include biogenic material of lake origin to an increasing extent. The organic component is usually measurable and its specific origin identifiable: potentially, these sediments can be used to determine certain environmental characteristics of the lake at the time they were laid down. The organic content of the uppermost sediments in the profundal zone probably varies significantly from mere to mere, but few comparative data are available. The data of Savage and Pratt (1976) include an attempt to classify bottom deposits by their organic content, but they apply strictly to the littoral. Tait-Bowman (1976) determined the calorific value of surface sediment in three Shropshire meres, *viz*, Crose Mere (1.86 kcal gm⁻¹), Newton Mere (2.76) and Blake Mere (4.05). The higher content of the latter presumably reflects the annual input of leaf litter from the wooded catchment; equally, there may be an unidentified factor restricting mineralisation of organic matter. Cranwell's (1978) analysis of organic derivatives (especially the alkanols) in a 1 m core from Crose Mere confirms that, in recent times, the organic matter reaching the sediments originates substantially from

production within the lake, and especially from phytoplankton (cf Reynolds, 1978a, and above).

Existing information on the profundal fauna is based on studies at Blake Mere, Crose Mere, Newton Mere and Rostherne Mere. Kennedy's (1961) investigation of Crose Mere (carried out in July 1961, when the mere was stably stratified: Sinker, 1962), revealed that the bottom fauna of sediments greater than 4.5 m depth below the surface were restricted to tubificid worms and chironomid larvae, and that these too, were much reduced in numbers in the profundal zone (Fig. 20). Brinkhurst and Walsh (1967) showed that chironomids and oligochaetes were the only taxa significantly extending their ranges into water exceeding 15 m in depth, but not below 25 m where only a few dormant cyclopoids were recovered. Moreover, this pattern was substantially maintained throughout the winter: in spite of complete mixing and aeration of the water column, the muds remained anaerobic.

Brinkhurst and Walsh (1967) compared the faunal distribution with published accounts for other eutrophic lakes in Europe (including Esrum Sø) and North America, and with Brinkhurst's unpublished observations made at several Shropshire meres. In each of these, the bottom fauna extended to the maximum depth of the lake during at least some part of the year. They concluded that Rostherne Mere may be unique in this feature, and they proposed that this was in part due to the direct contribution of faeces from the large gull (principally *Larus ridibundus*) roost and wildfowl populations which overwinter there ("guanotrophy").

Tait-Bowman's (1976) recent study of the distribution and abundance of chironomid larvae in the Shropshire meres demonstrates the influence of summer stagnation and concomitant deoxygenation of the hypolimnion in the biology of the profundal zone. She collected from several stations at selected depths in each of the lakes, over a period of two years. Of the total number of individuals collected, 51 per cent were recovered from Newton Mere, 40 per cent from Crose Mere and only 9 per cent from Blake Mere. In all three meres, the most abundant species were *Chironomus anthracinus* and *Procladius choreus*. Both species contain haemoglobin, and show some morphological reduction in their thoracic tracheal patterns, especially in *C. anthracinus*; *P. choreus* is semi-sedentary in habit. Tait-Bowman showed that tracheal anatomy and behavioural adaptations were of considerable importance in the ecology of chironomid larvae found in the meres. *Chironomus anthracinus* larvae were widely abundant at all stations in Newton Mere throughout the year (the numbers being highest after hatching of the first instars, and lowest after emergence), with a maximum of over 7,000 individuals m^{-2}. On average, the numbers of larvae were significantly correlated with increasing depth, an observation which agrees with Berg's (1938) findings for *Chironomus (sensu stricto)* spp in Esrum Sø. *C. anthracinus* larvae were locally abundant in Crose Mere, occasionally exceeding 3,000 m^{-2} at a depth of 3.0 to 4.5 m, but the population became severely reduced below 6.0 m depth in the summer of each year. In Blake Mere, *C. anthracinus* larvae were relatively much less abundant (<1500 m^{-2}), and were virtually absent at the deepest station (13 m) throughout the year. The maximum densities of *Procladius choreus* occurred in a depth of 3-4 m in all three meres, but it was also found in the profundal zone during isothermal conditions.

Tait-Bowman (1976) attributed the reduced population sizes of *C. anthracinus* in Crose Mere to unsuitability of the sediments, which often have a relatively high sand content, and to the production of hydrogen sulphide in the summer epilimnion, and in Blake Mere to the early onset of stagnation, where low temperatures, together with low oxygen levels preclude the development of a profundal population. *P. choreus* is tolerant of a wide variety of environmental conditions, except low oxygen levels. Elsewhere, the success of this carnivorous species is influenced by the distribution and availability of its (mainly) oligochaete prey.

The work of Dr Tait-Bowman demonstrates the overriding effects of summer stagnation, either directly or indirectly, in influencing the distribution of the profundal fauna. It is possible to speculate that in the majority of the deeper eutrophic meres, similar conditions occur. This might be especially true for Rostherne Mere, which may thus represent an extreme case of the evident tendency observed in the Ellesmere group meres. Whilst the contribution of the bird population to the eutrophic condition of Rostherne Mere should not be ignored, it is not clear that "guantrophy" necessarily accounts for the absence of a well-developed profundal fauna in this lake.

4. *Fish populations in the meres*

The fish populations of a lake represent one of the apices of energy flow through the ecosystem, and their relative productivity generally depends upon the abundance and productivity of their foods at lower trophic levels. In view of the high rates of production evident in the planktonic and littoral communities of the meres, it might be expected that fish production would be correspondingly high, and that this would have stimulated a series of scientific studies. The majority of the meres in fact support active coarse fishing, with the angling rights almost exclusively let to registered clubs and societies. However, the reputed quality of the fishing seems to vary from mere to mere, though this may be related to their suitability for angling and to stocking practices as much as to the productivity of the fish. Judging from the experiences of the anglers, it would appear that perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), pike (*Esox lucius*) and eel (*Anquilla anquilla*) are more or less ubiquitous in the meres. Bream (*Abramis* spp), tench (*Tinca tinca*), dace (*Leuciscus leuciscus*), carp (*Cyprinus* spp) and trout (*Salmo trutta*), which occur in some meres, are more restricted in distribution. Ruffe (*Gymnocephalus cernua*) is present in Ellesmere (O. O. Okorie, quoted by Goldspink, 1978) and Cole Mere (P. S. Croft, *personal communication*). Smelt (*Osmerus eperlanus*) which used to ocur in Rostherne Mere, has not been definitely recorded since 1922 (Ellison and Chubb, 1968).

In spite of an evident general interest in the fish production of the meres, only five waters have been subjected to detailed biological investigation; in certain cases these are still in progress. To date, only the findings at Rostherne Mere and Tatton Mere (Banks, 1970; Goldspink, 1978) are available; the results of studies undertaken at Comber Mere (R. J. Pritchard) and Ellesmere Mere (O. O. Okorie) are still unpublished.

Banks' (1970) study of Rostherne Mere (where there is no angling) was carried out between October 1962 and April 1965, and was mainly concerned with the biology of the three principal species in the lake: roach, perch and pike. To varying extents each showed considerable differentiation of the age-class composition of the population. The total catch of roach contained 14 year classes, but with an overwhelming representation ($\sim$75%) of the 1955 year class, and a further 13% 1959 class. Goldspink (1978) observed that the population was still strongly differentiated in 1976. The age-distribution of these fish cannot be attributed to the selectivity of netting. Banks suggested that the most likely cause of this instability was poor survival of eggs and fry, since few young roach were found in the stomachs of predators. There was no obvious sign of restricted fecundity, and poor survival at later stages in growth seemed not to apply. Goldspink was able to also exclude the possible influence of parasitic infestations. Food shortages could not be invoked either, since the stomachs were often well-filled with molluscs, macrophytes, algae,

Asellus, Gammarus and chironomids. Indeed, the growth rate of the roach is surpassed only by that observed in Tatton Mere (Goldspink, 1978).

Fast growth rates and year-class instability also applied to the perch. Although the Rostherne perch were shown to prey heavily on their own fry, especially in the summer months, Banks did not consider that predation had materially altered the population structure. Dipteran larvae (April-June), *Sialis, Asellus* and *Gammarus* (winter) formed a major part of the diet of larger fish (>60 mm) at other times. Goldspink (*ex ore*) quoting Okorie's unpublished findings has stated that *Chaoborus* larvae, as well as fish fry, were relatively important in the diet of the Ellesmere perch.

In contrast, the pike of Rostherne exhibited a relatively slow rate of growth when compared with (say) the Windermere population. Although their food, as elsewhere, included perch, Banks remarked that no size group of pike had less than a 20 per cent occurrence of invertebrate food, and that even the stomachs of larger pike contained relatively large numbers of small fish. Thus, the correlation between pike length and the length of prey which was demonstrated for Windermere (Frost, 1954) did not hold for Rostherne. Banks suggested that this difference may have been related to the greater turbidity of Rostherne Mere, which would significantly impair the ability of the pike (which feeds mainly by sight) to hunt for suitable prey. That the pike of Rostherne may still depend on larger prey for the bulk of their nutrition (see Banks' discussion) perhaps explains their relatively slow growth rate.

Tatton Mere is also effectively dominated by perch, roach and pike, although the lake has been stocked with several other species since it was opened to anglers in 1962 (Goldspink, 1978). As in Rostherne Mere, the roach population was characterised by year-class instability and high growth rates. The concurrence of two strong year-classes (1969, 1973) in both lakes suggested that climate was an important factor conditioning population structure, though it did not account for it conclusively. Goldspink also commented on the perch population, which though smaller than that in Rostherne Mere, also exhibited differential year-class strength.

The provisional conclusions to be drawn from the existing data indicate that the fish population of the meres may be characterised by a low species diversity, high year-class instability and relatively rapid rates of growth in some species. Nevertheless, Banks' (1970) remark that the fish populations of Rostherne Mere were in approximate equilibrium, which few natural events would be likely to disturb, may be general for many of the less disturbed meres, where a high degree of ecological stability exists in the other communities.

VI. THE PALAEOLIMNOLOGY OF MERE BASINS

The reconstruction of the development of a particular lake basin to its present condition depends largely upon the stratigraphical study of its bottom sediments which accumulate more or less continuously as a result of natural processes occurring within the lake and its catchment. The structure and chemistry of the sediments and the fossilised remains of organisms entrapped therein provide the stratigraphic record of past environmental conditions. Analysis of the relative abundance of pollen grains, even though these may have originated far from the lake itself, often provides a reliable indication of climatic variations. Autochthonous remains (eg of fringing aquatic plants, diatoms, rhizopods, crustacea, molluscs and

insects which lived *within* the lake system) may yield fragmentary evidence of the former hydrobiological conditions obtaining. Moreover, all organic remains are potentially datable by their residual radioactive (usually C-14) content.

Palaeolimnological investigations are in progress or have been completed, at Crose Mere (Beales, 1976) and Hatch Mere (H. J. B. Birks, in preparation); diatom remains in sediment cores extracted from Rostherne Mere and Cole Mere are presently being investigated by Dr G. H. Evans *(personal communication)*. Information from several Cheshire moss sites is also available (for a summary of these see Tallis, 1973).

The initial isolation of the first meres cannot yet be reliably dated. Hatch Mere and Crose Mere both contain basal sediments which are clearly Late-Devensian in age; those of Hatch Mere have yielded a radio-carbon date of about 12,200 years BP (H. J. B. Birks, *personal communication*). They are predominantly minerogenic in origin, with a high carbonate content, but they are low in organic matter. Beales (1976) found distinctive pollen assemblages at the bottom of his Crose Mere core (CMC3) which correlated with the well-established Late Devensian Pollen Zones I, II and III (eg Pennington, 1975) brought about by the cold-warm-cold late-glacial climatic fluctuations. Beales showed that the Younger *Dryas* climatic deterioration (Zone III) was not as clearly indicated as in English Lake District or European cores. However, he was able to correlate this lowermost assemblage at Crose Mere with the Ba/Bb zones (cf Pennington and Bonny, 1970) in Blelham Bog, Cumbria, and suggested that the basal Crose Mere sediment was also likely to be more than 12,000 years in age. Biogenic sediments of Late Devensian age have also been recovered from Bagmere (Birks, 1965a) and Flaxmere (Tallis, 1973). However, the oldest deposits so far recovered from several moss sites in Cheshire are more recent (in some cases considerably so), and the Devensian age of the basins has not been demonstrated to be universal.

Allowing for the length of the sediment core (6.1 m), the present depth of water (9.2 m) and a recent fall in the level of perhaps 2-3 m (Hardy, 1939), the original Crose Mere may have been 15-18 m deep, and considerably more extensive in area, coalescing with the adjacent hollows now occupied by Sweat Mere and Whattal Moss. However, there is no precise evidence of the altitude of the late-glacial water surface. Remains of water plants recovered from the late-glacial deposits in Crose Mere include *Typha latifolia* and *Myriophyllum spicatum,* which suggest that the water then had a high ionic content, formed by rapid leaching from the adjacent catchment soils. Beales also showed that the Cladocera were well represented by northern cold-tolerant species including *Alonella nana* and *Acroperus harpae,* with southerly forms (eg *Alona quadrangularis, Pleuroxus uncinatus*) becoming relatively more abundant during the warmer (Allerød) climatic phase, corresponding to Pollen Zone II. The lake was, however, largely unproductive throughout the late glacial period.

An abrupt increase in the rates of pollen deposition and sediment accumulation occurs at the end of Zone III in both lake profiles. This transition has been dated to 10,000-10,300 radio-carbon years BP, which is the accepted chronostratigraphic boundary between the Devensian and Flandrian (post-glacial) periods, and the opening of Pollen Zone IV (Mitchell *et al,* 1973; Shotton, 1977). The organic content of the sediments begins to increase at this point, but the mineral and carbonate contents fall. *Juniperus, Betula,* and then *Corylus, Quercus* and *Ulmus* are increasingly represented in the pollen record, as local forest cover increased in response to climatic amelioration. Basal deposits of Zone IV age are also evident at Abbots Moss, Cranberry Moss, Black Lake (see Tallis, 1973), Wybunbury Moss (Poore and Walker, 1959), Whattal Moss (Hardy, 1939) and Wem Moss (Slater, 1972).

Cladoceran species associated with clear water of relatively low alkalinity are well-represented in the faunal remains at the corresponding stage in Crose Mere (Beales, 1976). These changes suggest a progressive reduction in the leachate from the catchment soils

reaching the lake. They continue well into Pollen Zone IV (about 8,000 years BP), with a notable rise to dominance of *Alonella excisa,* and an increase in littoral species, (eg *Sida crystallina, Graptoleberis* sp) concomitant with the *Quercus-Pinus* vegetational stage. Beales attributed the evident low alkalinity of Crose Mere to drier, Boreal climatic conditions, and to a possible fall in water level, when the mere may have been isolated from the ground water supply.

The start of Zone VII, marked by the decline of *Pinus* and the spread of *Alnus* at the onset of the Flandrian climatic optimum (about 7,400 years BP), is accompanied in the Crose Mere record by an increase in carbonate content, and an expansion in *Alona rectangula* and *Chydorus sphaericus.* Increased discharges and an average rise in water level are indicated. Tallis (1973) also shows active leaching of calcium from the contemporary peat surface at Flaxmere.

In the remainder of the Crose Mere core, the pollen record shows evidence of the increasing influence of human settlement: forest clearance (and the decline of *Ulmus* towards the top of Zone VIIa in particular), erosion of soils, and primitive agriculture. Bronze-Age archaeological finds, including numerous trackways (Chitty, 1956; Rowley, 1972) and a fine looped palstave, discovered in the peat of Fenn's Moss (Chitty, 1933), indicate that the district had become settled by about 3,000 years ago. Two Iron-Age settlements, at the Berth and on the low-ridge separating Crose Mere and Whattal Moss, are closely associated with meres. An oak dug-out canoe, also believed to be of Iron-age construction, has been recovered from peat at Whattal (Chitty, 1927). Settlement increased during Roman and Saxon times, and a large number of present day villages existed at the time of Domesday. Considerable expansion of farmland, at the expense of woodland, took place after the Norman Conquest, although dense forest persisted on the heavier soils until the sixteenth century (Lawson, 1965).

In the upper sediments of Crose Mere, the pollen load became increasingly dominated by herbs, including many agricultural weeds. The major effects of forest clearance on the meres were to alter their water balance and to increase leaching and nutrient loading on the water. Increases in *Chydorus sphaericus, Bosmina longirostris,* and the ratio of planktonic to periphytic diatoms suggest that autochthonous planktonic production had become dominant. The present eutrophic condition of Crose Mere, and perhaps of other meres, probably evolved at this time in response to changes in the catchment (cf Likens *et al,* 1970).

The most profound man-made changes have occurred within the last two centuries, as advancing technology permitted extensive and systematic drainage schemes for the reclamation of former peatlands and marshy areas for agriculture. Drainage of Tetchill Moor was commenced in 1602 (Lawson, 1965), and large tracts of valley peatlands were similarly recovered before 1900. The surface levels of a number of meres (see Sinker, 1962) and around some mosses (Green and Pearson, 1968) are known to have been lowered since 1860. Many small basins have disappeared altogether: in one small study area, just west of Shrewsbury, over half the water bodies that existed in 1800 have been obliterated since the enclosure of Bicton Heath (D. J. Pannett, *personal communication*).

The Organic Chemistry of recent sediments. The presence and diagenesis of various organic derivatives have been investigated in the recent sediments of Rostherne Mere (Gaskell and Eglinton, 1973; 1976) and Crose Mere (Cranwell, 1977; 1978). The distribution of carbon-chain lengths in n-alkanes, n-alkanoic acids and sterols recovered from Crose Mere differed significantly from those of Cam Loch, Sutherland, where the sediments are largely allochthonous (ie derived outside the lake) in origin. Moreover, the organic compounds in Crose Mere were derived mainly from algal diagenesis, while products from higher plants were relatively scarce. This is equally true for Rostherne Mere (Gaskell and Eglinton, 1976) where, in recent years, the phytoplankton succession has often been overwhelmingly dominated by *Microcystis.* In late autumn, populations descend to the lake bottom to form a copious algal layer (Reynolds and Rogers, 1976) which may be (initially) >20 mm in thickness in the deepest water. Moreover, *Microcystis* has only become dominant during the last

two or three decades (see Section V.1). Gaskell and Eglinton (1976) found a sharp change in the structure and chemistry of the sediment about 70mm below the mud surface. Livingstone and Cambray (1978) examined algal remains in a further three cores from the deepest part of the mere. The stratigraphy faithfully reflected alteration in phytoplankton dominance, especially between *Ceratium* and *Microcystis* (see Section V). Moreover, dating based on the decay of the fall-out isotope Cs-137 (which reached a peak in 1963, before atmospheric nuclear tests were suspended) agrees closely over the upper part of the profile. From these data a contemporary mean rate of sediment accretion of 10-12 mm yr^{-1} can be deduced. This is about double the estimate of Gaskell and Eglinton (1976).

VII. The Hydrosere in Basin Sites

One of the undoubted attractions of the wetland sites in the north-west Midlands is their ecological diversity. In addition to the meres which support a variety of fringing swamp and fen habitats, there are many more or less closed peat-filled hollows in the drift surface, the mosses. Several of the mosses have been investigated in some detail, and comprehensive descriptions of these sites are available in the literature (eg Hardy, 1939; Poore and Walker, 1959; Sinker, 1962; Birks, 1965a; Green and Pearson, 1968; Slater, 1972; Tallis, 1973). Typically, they have acidic surfaces (pH <4) dominated by, or derived from ombrogenous *Sphagnum*-based communities, whose growth is dependent upon water held in the peat, above the mineral ground water table (raised bog, or *"Hochmoor"*), or which float on water (quaking bog, or *"Schwingmoor"*). Examples of peat-filled sites in the region are listed in Table 12.

Almost all the mosses have suffered considerably through human interference. There is a long history of turbary, and peat is extracted commercially (mainly for horticultural use) at a number of sites, particularly at Fenn's Moss. The almost complete removal of peat from the gently shelving Brown Moss basin may have given rise to the present heathland area, interrupted by a number of shallow pools (Sinker, 1962). Even at the best-preserved sites (eg Wem Moss, Flaxmere, Abbots Moss), the surfaces have been modified by the exercise of turbary. Several mosses have been planted with conifers (eg Whattal, Pikesend, Oakhanger Mosses), reducing the floristic interest. Other raised bog structures have been drained and reclaimed for agriculture, in much the same way as the valley mires (see Section VI). Elsewhere, improved drainage of adjacent farmland has led to the drying out and humification of bog surfaces. Subsequent neglect of former drainage channels may lead to a slight rise in the local water-table: Green and Pearson (1968) have traced recent fluctuations at Wybunbury Moss, and they attributed expansion of *Phragmites* swamp and renewed growth of a *Sphagnum recurvum* carpet to a net rise in water level since 1911. Tallis (1973) considered that the re-introduction of ground-water onto the shrunken surfaces has probably favoured the recent accumulation of *S. recurvum* peat at Flaxmere and many other Cheshire sites. Borras Bog is another derelict Hochmoor structure: its periphery has been flooded by a rise in the local water table, and its raised central dome stands as an island in a small, shallow pool which has become somewhat enriched by farm effluent (author's unpublished observations).

The history of the mosses and their development is of considerable interest. Many mosses occupy basins which occur in close association with, and which, so far as it is possible to judge, are apparently similar to, those occupied by the meres. Indeed,

stratigraphical investigations on the mosses have indicated that peat-infilling has been preceded by relatively long phases of accumulation of limnogenic muds. Detrital muds, of varying thicknesses, have been shown to occur at the bases of Fenn's Moss, Whattal Moss (Hardy, 1939), Congleton Moss, Lindow Moss, and Flaxmere (see Tallis, 1973), and have been recently demonstrated at the deep centre of Wem Moss (Slater, 1972) although they do not underlie the entire peat surface (Hardy, 1939). In the more uniformly shallow basins, a relatively rapid invasion of reedswamp vegetation (chiefly *Phragmites*) is indicated. Modern equivalents are found in the mere fens (see Table 12). There is thus little doubt that the mosses have evolved directly through the accumulation of peat in basins which were previously occupied by meres, a process which Tallis (1973) has called "terrestrialisation".

The early stages in terrestrialisation of lake basins are sufficiently represented among the present day meres to suppose that similar processes have operated in the past: gently shelving shores of the larger basins have been successively and centripetally invaded by reedswamp, fen and *Alnus,* and (sometimes) by *Betula* and *Pinus,* at many sites (see Section V above); reedswamp; sedge- and wood-peats are represented in the sequence of deposits at Congleton Moss and Lindow Moss (Tallis, 1973) and are also recognisable in parts of Fenn's Moss and Wem Moss (see Hardy, 1939; Slater, 1972). The transition to ombrogenous *Sphagnum-Eriophorum* peat formation in each of these sites is typically abrupt. Similar sequences in the building of *S. recurvum*-dominated communities can be recognised in the recent floristic changes recorded at Hatch Mere (Lind, 1949).

The stratigraphy of many smaller, steep-sided basins, (eg Abbots Moss, Blake Lake, Scouts Wood Pool, Wybunbury Moss), however, reveals a different sequence, where most of the sediment is composed of a rather fluid peat derived (predominantly) from *S. cuspidatum,* directly overlying lake muds (Tallis, 1973). Tallis suggested that the terrestrialisation of these basins has occurred principally by the gradual settling down of successive *Sphagnum* rafts, analogous to the present day Schwingmoor structures.

However, the rapid rates of recent development of swamp-carr (evident at Sweat Mere) and floating *Sphagnum* lawn (eg Lin Can Coppice Pool: Sinker, 1962; Scouts Wood Pool: Tallis, 1973) that have led to the partial or complete overgrowth of open water in rather less than a century, suggest that the transition between major successional stages can occur over relatively short periods of time. Indeed, this is

Table 12. *Principal Basin Mires*

Letters refer to locations in Fig. 4 (?) denotes confirmation required

Raised Bogs (Hochmoor)					
A	Fenn's Moss	EE	White Moss	K	Black Lake	26	Cracow Moss,
B	Wem Moss	FF	Oakhanger Moss	M	Scouts Wood Pool		Betley Mere
F	Betton Moss (?)	GG	Lyneal Moss	N	Shemmy Moss	39	Hencott Pool
L	Breech Moss	HH	Pikesend Moss	O	Abbots Moss		
P	Boreatton Moss	KK	Smithy Moor	AA	Cranberry Moss (?)	*Miscellaneous or*	
U	Holford Moss	LL	Rednal Moss	DD	Brookhouse Moss	*degraded sites*	
V	Lindow Moss			JJ	Whattal Moss	D	Borras Bog
W	Sossmoss (?)	*Quaking Bogs*		MM	LinCan Coppice	E	Brown Moss
Y	Siddington Moss	*(Schwingmoor)*				Q	Betton Abbots Moss
Z	Danes Moss	C	Clarepool Moss	*Mere Fens*		R	Stretton Moss
BB	Congleton Moss	G	Wybunbury Moss	CC	Bag Mere	S	Sink Moss
		H	Flaxmere	NN	New Pool	T	Arley Moss
		J	Blakemere	PP	Shrawardine Pool	X	Massey's Moss

confirmed by the sharp boundaries in the stratigraphic sequence, not only from stage to stage, but also within stages (eg from "white" *Sphagnum* peat to more humified ("black") peat with *Calluna* and *Erica* remains. Chemical analysis of the deposits, where available, shows that the transitions from stage to stage are coupled with considerable shifts in ionic composition and pH. Alternating phases of more vigorous *Sphagnum* peat development and humification of the surface under drier conditions are often evident (see Hardy, 1939). Moreover, significant reversals of the hydrosere, with reedswamp and fen overlying ombrogenous peat deposits have been shown to occur (eg at Sweat Mere: Sinker, 1962; Wybunbury Moss: Poore and Walker, 1959; Green and Pearson, 1968). These various changes illustrate the importance of the hydrological relationship between the mire surface and the adjacent water-table, and its impact upon the supply of ions reaching the basin.

In critically discussing the stratigraphy of Wybunbury Moss, Green and Pearson (1977) concluded that subsidence must have played some part in the formation of the hollows. They considered that an initial mid-Flandrian subsidence could explain the lack of pre-Zone VI deposits. A more recent subsidence of a basin, by then perhaps enclosing a raised bog, might account for the present Schwingmoor structure and the dominance of *Sphagnum cuspidatum* peat in the solid profiles. If significant subsidence of basin sites might either offset or exaggerate changes in the level of the mire surface relative to the water tables.

The chronology of active *Sphagnum* peat-building can be approximated from pollen profiles. Hardy (1939) showed that *Sphagnum* peat began to accumulate initially in Whattal Moss in Pollen Zone VIIa, and this, or an earlier date apparently applies to the smaller basins in north Cheshire (Tallis, 1973). At Wem Moss, the earliest base of the *Sphagnum* apparently occurs in late Zone IV. A second major phase of peat-formation commenced·near the VIIb-VIII boundary (about 3,000 years BP), when Fenn's Moss, Congleton Moss, Lindow Moss and perhaps Danes Moss, apparently became infilled for the first time, and when the main accumulation occurred in Whattal Moss, which eventually led to the eradication of open water by raft formation (but presumably post-dating the dugout canoe: see Section VI). Comparing the peat stratigraphy of Sweat Mere with that of Whattal Moss, it seems likely that *Sphagnum*-dominated communities became established there at about the same time.

These periods can be related to the onset of more oceanic (wetter) climatic conditions of (respectively) the Atlantic and Sub-Atlantic periods. Both followed somewhat drier climatic phases, in which local water tables probably stood at lower levels. As Beales' (1976) palaeolimnological investigations of the Crose Mere sediments indicate, the meres may have been relatively less alkaline and oligotrophic, owing to their possible isolation from inspilling ground water (see also Reynolds, 1975a). The centripetal invasion of swamp and fen communities may also have been favoured by falling water levels.

Tallis' (1973) investigation of Flaxmere showed an absence of limnogenic deposits above a depth of −4.0 m relative to the peat surface, suggesting that in late-glacial and early Flandrian times, the (open) water probably stood some 3-4 m below its present level. Subsequent accumulation of fen peat occurred across the basin, and some drying of the surface layers during Zone VI is indicated. The onset of wetter conditions early in Zone VIIa is clearly defined, and coincides with the rapid development of *Sphagnum*-Cyperaceae dominated communities in shallow water. In

the deeper parts, Tallis found evidence of a second increase in wetness (perhaps raising the water table to approximately its present level) with a sharp transition to unhumified *Sphagnum cuspidatum* deposits, suggesting raft formation.

Chemical analysis of the Flaxmere deposits shows that bases (especially calcium) are high in the fen peat, but decline in association with the change to *Sphagnum* peat; still lower levels of calcium occur in the raft *Sphagnum*. That the chemical composition of the water and the vegetation has been so sensitive to climatic change emphasises the likely isolation of the basin from the adjacent water table. Nevertheless, the initial accumulation of *Sphagnum* in poor-fen deposits does not depend on the reduction of calcium, but is rather a product of its development (Tallis, 1973). The building of peat in response to rising water level probably reduces the lateral spread of base-rich water from the margins of the basin, either by physically impeding flow, or through the removal of bases in the peripheral zone. This effect is clearly shown in the transition from fen "lagg" to acid bog surface evident at Wem Moss and in the narrow artificial lagg that has developed along the edge of the Shropshire Union Canal where it crosses the Fenn's Moss basin.

Burial of fen and wood-peat under 2-3 m of *Sphagnum* peat at Whattal Moss, Fenn's Moss (see Hardy, 1939), Sweat Mere (Sinker, 1962) and Wybunbury Moss (Green and Pearson, 1977) also point to a considerably lower water surface under Boreal or Sub-Boreal climatic conditions. As in Flaxmere, development of *Sphagnum*-dominated communities may have been dependent upon the initial establishment of shallow water conditions, coupled with a depletion of the supply of ions reaching the basin (Tallis, 1973).

In this way, the "conversion" of meres to mosses may have depended upon the existence of shallow-watered margins which were open to colonisation by poor-fen peats when reduced water levels were prevalent, and the subsequent overgrowth of peat by *Sphagnum* (or over open water in small, deeper basins) under oceanic climatic conditions. Larger, deeper basins, having been less conducive to successional invasion, remained as predominantly open water sites throughout the Flandrian, and persisted as the modern meres. Because the supply of base-rich water, increasingly loaded with plant nutrients, has been maintained, they have developed as eutrophic lakes; the contrast with the ombrotrophic conditions of the mosses, which have developed separately but under the same climatic influences, is remarkable.

The apparent absence of any peat deposits or limnogenic sediments older than Zone VIIb in age from the shallow Fenn's Moss, Congleton Moss and Lindow Moss basins (<4 m depth) may be due, not to a relatively more recent origin of the depressions (see Section II) but to a lower water table thoughout the Flandrian period. From the stratigraphy of deeper sites, it seems possible that these saucer-like depressions could have been dry until the onset of the Sub-Atlantic period, when their shallow waters were evidently invaded by aquatic vegetation in rapid succession. Equally, the spread of *Sphagnum* peat beyond the confines of a small, central basin (>10m) of Wem Moss, in a manner analogous to the spread of blanket-bog over terrestrial communities, may account for the previously reported absence of an aquatic stage in the stratigraphic record (Slater, 1972). Wybunbury Moss possibly represents a further variation, in which the basin formerly colonised mainly during Pollen Zone VII became deepened by subsidence, and has since been overgrown by a *Sphagnum* raft (see Green and Pearson, 1977).

VIII. CONCLUSIONS

Certain characteristics of the north-west Midland meres, established in this account, require special emphasis. Their basins, together with those of the mosses, vary considerably in morphometry, in the probable modes of origin, and in the length of time in which they have contained water. The property which they share in common is that they apparently occur exclusively in glacial drift. The distribution of the depressions still occupied by water or peat suggests that they originated in a series of processes associated with the stagnation and wasting of the Late Devensian ice-sheet, between 18,000 and 14,000 years ago. Basin formation was evidently most prolific in areas where drift ablation was substantially retained, either between ice fronts (eg in the Ellesmere and Whitchurch groups) or between ice fronts and solid outcrops (eg in the eastern Marginal Group, and along the mid-Cheshire Ridge). Delta-formation, fluvio-glacial reworking and, perhaps, periglacial activity have also contributed to the post-glacial landscape which still survives today. Even those hollows which apparently originated through salt-subsidence are in contact only with drift.

Deeper water-filled basins are evidently supplied to a greater or lesser extent by ground water. At the present time, the hydrological regime ensures a supply of bases and nutrients generally favouring a high fertility of the water. In the past there have undoubtedly been conspicuous fluctuations in the elevation of the water table, which have affected the water level and hydrochemistry of the impoundments, and it is possible that some basins currently filled with water or peat could have been "dry" for long periods in the Flandrian (see Section VII). However, more permanent lakes may have effectively sealed their own basins, so that ground water now reaches the lake mainly by "inspilling" from adjacent permeable drifts (Section IV).

Hydrobiological studies on various meres have shown that communities are characterised by the low species diversity but large populations of organisms associated with nutrient richness. Though few quantitative data are available, a high level of biological productivity is indicated; in many instances, a high degree of ecological stability is apparent. Almost all of the meres seem to justify the description of "eutrophic", at least in its modern usage: even Oak Mere can support dense plankton populations, in spite of its extreme acidity. On the limited evidence available, only Bomere seems to be exceptional in this respect.

Palaeolimnological investigations, however, show that the present eutrophic condition of the meres is a relatively recent development, having been related to past climatic and hydrological fluctuations, and to changes in land-use, in particular. The drifts are probably far from being completely leached, and present climatic conditions favour continuing fertility of many meres.

Thus, I would propose the following definition of a mere:

A small, potentially fertile lake occupying a hollow in glacial drift deposits and maintained principally by ground water flow.

This definition is by no means exclusive to the meres of the Shropshire-Cheshire Plain: other British waters which, conceivably, could be similarly characterised occur either at the peripheries of glaciated hill masses in Herefordshire, on either side of the Pennines, in parts of Scotland (eg Dumfries and Galloway), or more remotely (eg the Norfolk Breckland meres). They also represent, on a much smaller scale, examples of the many lakes associated with moraine deposition during

deglaciation in northern Europe (eg the Polish Masurian lakes, the Pomeranian lakes of Germany, the North Sjælland lakes in Denmark), and in North America (Minnesota, Wisconsin, Michigan and Indiana). The biota of our meres show more affinities with these examples than with those of mountain lakes in Britain (Section V).

The proposed definition of a mere does not exclude salt-subsidence hollows. It may be taken also to include the open-water phases of closed moss basins, before they became infilled by peat deposits. Limnogenic deposits, of varying extent and thickness, underlie peat in many of the sites so far investigated (Section VII). *Sphagnum*-dominated communities in these basins initially developed under suitable environmental conditions. These have been determined through the interaction of fluctuating climatic and hydrological conditions with the morphometric characteristics of the original basins. In this way, it is possible to account for the approximately synchronous phases of active peat building and the initial "terrestrialisation" of the moss basins, and the simultaneous persistence of open water conditions in the surviving meres. The critical factor may have been the areal extent of deep water, which is amenable neither to rapid encroachment by fen, nor to overgrowth by floating vegetation rafts. Equally, the maintenance of mineral-rich ground-water supplies to the deeper basins may have been critical. The morphometric characteristics of lake basins are also continuously altered by the accretion of lake sediment, thus modifying the potential reaction to gross changes in the environmental conditions. It may be suggested that, in any future climatic change to first drier, and then wetter conditions, many more of the present meres will become similarly terrestrialised.

At the present time, however, the major threats to the well-being of the meres are posed by the activities of man. Many of the recent changes in the ecology of the meres have been the direct result of manipulations in local drainage, and the intensification of land-use, especially through forest clearance, agriculture and urbanisation. The eutrophication of the meres is closely correlated with these developments. There is evidence that nutrient loadings are still increasing, especially of inorganic nitrogen, which may have been severely limiting in the past (see Section IV). Increased nutrient availability permits the larger average standing crops of phytoplankton to be maintained, even if the maximal populations are scarcely increased. Shifts in phytoplankton dominance in favour of green algae or coccoid blue-green algae seem consistent with these changes, though the mechanisms are generally obscure. Nitrogen-fixing blue-green algae, however, are presumably better adapted to tolerate deficiencies in the external nitrogen supply (cf Schindler, 1977), and it may be significant that species of *Anabaena, Aphanizomenon* and *Gloeotrichia* are more prevalent in the early records from Rostherne Mere (Pearsall, 1923) and the Shropshire meres (Phillips, 1884) than *Microcystis*. The general disappearance of submerged macrophytes may be due directly to nutrient enrichment (cf Mulligan and Baranowski, 1969), or as an indirect effect of the greater planktonic biomass supported and the consequent deterioration in the average underwater light penetration. *Lobelia dortmanna* and *Scheuzeria palustris* have become extinct at the mere sites (and in the latter case, from the mosses as well) where they were known to occur a century ago, whilst there have been reductions in the ranges of *Anagallis tenella* and *Hypericum elodes* (Sinker, 1962). Recent faunal changes (eg in the distributions of molluscs and crustaceans) may be related to more general

invasions, which, on the scanty evidence available, seemingly have little to do with eutrophication.

Nevertheless, the present eutrophic condition of the meres renders them attractive to scientific study, both from the points of view of enhancing understanding of freshwater ecology and biological productivity in calcareous lowland lakes, and to improving the ability to predict the consequences of continued nutrient enrichment in lakes elsewhere. In this context, existing knowledge of the meres and their developmental history is sufficient to refute two popular notions about eutrophication: one is that while sustained inorganic nutrient enrichment of lakes may bring about significant changes in the structure of the plant and animal communities, and lead to the replacement of "desirable" species (eg salmonid fish), it does not necessarily "kill" the lake. For example, Crose Mere is a eu-polytrophic lake on the Vollenweider (1968) scale, receiving "dangerously high" loadings of nitrogen (>2.0 g N m^{-2} ann^{-1}) and phosphorus (>0.13 g P m^{-2} ann^{-1}) probably for some considerable period, but its vitality and its intrinsic beauty are far from being unattractive. It must be admitted, however, that blue-green algal blooms present little attraction to water-based recreation, and that the meres have only a latent potential as commercial fisheries or as a source of potable water supplies. The second feature is that eutrophication cannot be viewed as a natural successional process: the principal tendency is for the lakes to become progressively terrestrialised, following either an "oligotrophic" or a "eutrophic" successional series. Variations in trophic status are established essentially through the changing relationship between the lake and its catchment; moreover, the fossil record suggests that changes in the trophic condition are fully reversible.

In this account, I have attempted to piece together a general picture of the northwest Midland Meres. In doing so, I have tended to stress the similarities rather than the differences between individual sites. More importantly, tentative conclusions have been applied to the series of meres as a whole, on the basis of evidence from a limited number of sites. Much of that evidence is, at best, inadequate and is often circumstantial, if not speculative. There is still a fundamental need for much more basic research in this district. There is scarcely any aspect of the work described here that does not require further amplification; the following topics deserve special attention.

Further information on glacial chronology would sharpen the precision of dating the retreat phase of the Late Devensian ice fronts and the creation of the mere basins. Dating of Irish Sea outwash deposits in the lower Severn valley might clarify the origin of the Ironbridge Gorge. The ages of primary sediments in further mere and moss basins, including those believed to have arisen through salt-subsidence, are needed to gain a more comprehensive view of their development. The hydrological model proposed in Section IV requires verification: the existence and location of point-sources of ground-water within mere basins should be investigated, perhaps applying recently introduced techniques (eg Lee, 1977); these would also permit direct analysis of the incoming ground-water and, hence, improved calculations of nutrient loading. The meres are especially suitable for the study of chemical transformations and fluxes, especially those involving calcium, iron, phosphorus, nitrogen and sulphur; a new seasonal survey of major ion and nutrient concentrations is also needed. Contemporary rates of sediment accumulation require clarification.

Future biological studies might be aimed at the structure and population dynamics of zooplankton, and among littoral invertebrate populations. Further information on the ecology of fish populations is desirable. On the botanical side, the periphyton has been scarcely studied, and little is yet known about the microbial ecology of the meres. Quantification of productivity at each trophic level, and of energy flow through the ecosystem would also be welcomed. I believe that, apart from telling us much more about the meres, the solutions to these problems would have considerable relevance to limnology generally.

Conservation interests would also be well served by a better understanding of the meres and mosses, both in identifying the scientifically more interesting sites, and in the management of existing reserves and designated areas. Several meres and mosses already receive the formal protection of the Nature Conservancy Council (eg Rostherne Mere, Wybunbury Moss), local naturalists' trusts (eg Wem Moss) or the local authorities (eg Cole Mere, Ellesmere Mere, Brown Moss). It is to be hoped that adequate management practices can be maintained at other "classic" sites, including Abbot's Moss, Bagmere, Black Lake, Clarepool Moss, Crose Mere, Fenemere, Flaxmere, Hatch Mere, Oak Mere, and especially Sweat Mere. It is clear that the use of land adjacent to the meres and mosses may often be as important as the uses of the sites in question. There may also be a case for arresting hydroseral development at selected sites to preserve their educational value. Burning, cutting, draining, and possibly minor recent climatic changes have led to drying of the surfaces of many of the mosses (Sinker, 1962). There may be little that can be done to reverse these processes, but further deterioration might be resisted at selected sites. Local regeneration of *Sphagnum* might be encouraged by cutting new pools at carefully selected points on the bog surfaces, especially where these might enhance the survival of disappearing plant and animal species (cf Reynolds, 1974).

IX. SUMMARY

The north-west Midland meres are small, generally fertile lakes occupying hollows in the glacial drift surface which covers much of the Shropshire-Cheshire Plain. Many of the basins originated through kettle hole formation and moraine damming during the stagnation and retreat phases of the Late Devensian ice fronts, less than 18,000 years ago. They are markedly clumped in distribution, occurring in distinct groups. Primary limnogenic deposits exceeding 12,000 years in age have been identified. Some basins may be more recent in origin, through natural subsidence over wet-head solution of underlying saliferous rocks.

The meres are, to a greater or lesser extent, fed and maintained by mineral-rich ground water flow. Long retention times may be typical. Recharge may be effected by "inspilling" of groundwater into sealed basins. Ionic strength of lake waters is conspicuously variable, ranging between 0.1 and 6.9 meq l^{-1}. The dominant ions are usually calcium and bicarbonate; the richer lakes are alkaline and well-buffered. Maximum nutrient concentrations, especially of phosphorus, are naturally high; nitrogen supplies are currently increasing. Specific nutrient loading rates are apparently relatively high. The deeper meres are "eutrophic" in the classical sense; almost all would be so described according to "modern" usage.

The biota of the meres may be typical of base-rich, productive lakes. Communities tend to be dominated by large populations of relatively few species.

Phytoplankton crops are often limited by light attenuation rather than by nutrients. Except in Oak Mere, the zooplankton is generally dominated by species characteristic of temperate eutrophic lakes. The extent of littoral vegetation ranges between sparse fringing reedswamps to the almost complete overgrowth by carr. Well-defined vegetation zones are often apparent. In most meres, there is a scarcity of submerged macrophytes. The littoral invertebrate fauna is dominated by non-insect species, some of which frequently occur at high populations densities. The distribution of invertebrates in the profundal zone is influenced by the effects of summer stagnation and oxygen depletion. The fish populations may be characterized by low species diversity (mainly "coarse" fish), year-class instability and rapid growth of certain species.

Since their formation, the meres have been vulnerable to fluctuations in ground water level and supply brought about by climatic variations, and hence to changes in tropic status. Reductions in water level has apparently favoured hydrological isolation. In some basins, subsequent rises in level, brought about by the onset of oceanic climatic phases, have led to the establishment of ombrogenous conditions and the development of *Sphagnum*-dominated communities. Many erstwhile meres became "terrestrialised" (the mosses) during either the Atlantic or Sub-Atlantic periods. The eutrophic condition of the surviving meres may have evolved following forest clearance, which commenced about 3,000 years ago. More research is required to amplify these generalised conclusions.

Glossary of Units, Symbols and Scientific Terms Used in this Paper

For the benefit of the non-specialist reader, the following notes may be helpful:

1. Units

Wherever practicable, I have presented numerical data in basic SI units or multiples thereof, in accordance with the Royal Society's Symbols Committee (1975) recommendations. Units marked * are not true SI units, but are in common usage elsewhere.

Length:

m	metre
km	kilometre ($=10^3$ metres)
mm	millimetre ($=10^{-3}$ metres)
μm	micrometre ($=10^{-6}$ metres)

Area:

m^2	square metre
ha	hectare ($=10^4$ square metres, or $(100 \text{ m})^2$).
km^2	square kilometre

Volume:

m^3	cubic metre
l	litre ($=10^{-3}$ m^3)

Mass:

kg	kilogram
g	gram ($=10^{-3}$ kg)
mg	milligram ($=10^{-6}$ kg)
μg	microgram ($=10^{-9}$ kg)
t	tonnes ($=10^3$ kg)

Time:

s	second
h	hour*
d	day*
yr, or ann,	year*

Customary Temperature:

°	degrees Celsius

Energy:

kc	kilocalorie*

Supplementary units:

M	molar (of solution; 1 mole, or 1 gramme-molecule of substance dissolved in 1 l of water).
m eq	milliequivalent (of ionic solutions: 1×10^{-3} gram-equivalents of ion in 1 l of water).
mV	millivolts ($=1 \times 10^{-3}$ V)
pH	Negative logarithm of hydrogen ion concentration: acid solutions have a pH of 7 or less; alkaline solutions have a pH exceeding 7; a solution of pH 7.0 is neutral.

S	Siemen, the unit of electrical conductivity. Conductivity, the reciprocal of electric resistance, was formerly measured in reciprocal ohms, or mhos, per unit distance; 1 S m^{-1} is equivalent to 10,000 μmho cm^{-1}.

2. Derived and Combined Units

m^{-1}, cm^{-1}	per metre, per centimetre, etc.
m^{-2}, cm^{-2}	per square metre, per square centimetre, etc.
m^{-3}, cm^{-3}	per cubic metre, per cubic centimetre, etc.
g m^{-2}	grams per square metre.
g m^{-3}	grams per cubic metre.
g O_2 m^{-2} h^{-1}	(of photosynthetic oxygen production) grams of oxygen evolved per square metre of lake surface per hour.
kcal gm^{-1}	(of the potential energetic content of mud) kilocalories per gram.
ln units (mg chl$a)^{-1}$ m^{-2}	(of vertical light attenuation in relation to chlorophyll *a* concentration in the water). The extinction coefficient, expressed as a natural logarithm, per milligram of chlorophyll *a* pigment present per square metre of lake surface.
m^3 d^{-1}	(of discharges) cubic metres per day.
mg l^{-1}	(of solute concentration) milligrams per litre.
mg m^{-2}	(of concentration, expressed areally) milligrams per square metre of lake surface.
mg chl$a$ m^{-2}	(of chlorophyll concentration, expressed areally) milligrams of chlorophyll *a* pigment per square metre) of lake surface).
meq l^{-1}	(of ionic solutions) one milliequivalent per litre.

3. Other Abbreviations and Symbols

BP	(of dates) before present.
chl$a$	Chlorophyll *a* pigment.
d	rate of change of a variable (eg d[X] is the rate of change of concentration of ion in a lake).
D	Change in lake storage volume.
E	Volume of water evaporated from lake surface.
I	Influx volume into a lake.

N   nitrogen

O   Outflow volume from a lake.

OD   (of altitude) above Ordnance Datum (mean sea level at Newlyn, Cornwall).

P   phosphorus

P   Volume of water added to a lake by direct precipitation.

Q   discharge, as in stream flow.

r   the coefficient of correlation between two variables.

t   unit of time (here only used to denote days, as in d$[X]$dt, the rate of change of concentration of X per day).

u   groundwater flow into a mere basin (see Fig. 8).

v   groundwater flow out of a mere basin.

V   lake volume.

$|X|$ concentration of a solute, as in $|X|_A$, (its concentration in ground water), $|X|_M$ (its concentration in the lake).

z   depth of water, below surface.

z_{eu} euphotic depth, or the depth of water to which sufficient light penetrates to allow net photosynthetic production. (Sometimes also called the "*compensation depth*"). It is difficult to establish this point exactly as it may vary continually during the day; however, it is usually evaluated as the depth to which 1% of the immediate subsurface irradiance penetrates.

ε the vertical extinction coefficient of light with depth (expressed in logarithms to base 10 or base *e*).

ε_{min} the vertical extinction coefficient of light of the spectral block of minimum attenuation. The greater the attenuation, then the shallower is the euphotic depth; Talling (eg 1971) related these two qualities as approximately $z_{eu}=3.7/\varepsilon_{min}$ (when ε_{min} expressed as a natural logarithm).

ε_s the component of minimal vertical extinction which is due to the presence of algal chlorophyll pigment in the water.

4. Terms

ablation   (of ice sheet) a gradual thaw whereby more ice melts during the summer than re-freezes in winter.

allochthonous   (eg of biogenic and mineral material) derived from outside the lake.

autochthonous   material produced or derived from inside the lake system.

anoxic   (eg of hypolimnia) devoid of oxygen.

biogenic   (eg of material) resulting exclusively from biological production.

diagenesis   changes in a sediment after deposition through compaction, cementation, etc.

epilimnion   the upper, warm-water layer of a stratified lake.

hypolimnion   the lower, cold-water layer of a stratified lake, separated from the epilimnion by the *metalimnion* or *thermocline,* a layer characterised by rapid temperature change in relation to depth increments.

limnogenic   (eg of sediments) generated entirely within the lake system.

littoral   the shallow-watered margins (shores) of a water body; the term is borrowed from marine biology, where it refers to the shore zone sometimes covered and sometimes uncovered by the sea. No such rigid definition exists in freshwaters. Pickavance's (1965) understanding of the term, "the bit of the lake which can be worked without a boat", serves extremely well.

periphyton   the fauna 'around plants': that is living on and amongst the vegetation.

STRATIGRAPHICAL TABLE

Years B.P.	18000	14000	10500	7000	3500	0
Chronostratigraphic Zone	LATE DEVENSIAN			FLANDRIAN		
Climatic Features	Devensian Ice Maximum ?	Ice front retreats to Wrexham-Bar Hill line	Rapid wastage of ice	Rapid Climatic Amelioration	Warm, wet (Atlantic Period)	Drier (Boreal Period)	Cooler, wetter (Subatlantic Period)
Pollen Zone			I II III	IV V VI	VIIa	VIIb	VIII
Water Tables		Permafrost ?		Falling ?	Rising	Falling	Rising
Basin Histories	Many mere basins come into existence: Deeper basins ⟶			'oligotrophic' mere ⟶	partial ⟶ / complete raft formation ⟶	eutrophic mere ⟶	e.g. CROSEMERE / e.g. WHATTAL MOSS / e.g. FLAXMERE
	Shallow basins ⟶			dry out? - - - - - - ⟶	? flooding ⟶		e.g. SWEAT MERE?
					open water passing rapidly to Hochmoor? - - ⟶		e.g. FENNS MOSS
						subsidence & flooding? ? - - →	e.g. OAK MERE
						schwingmoor formation ⟶	e.g. WYNBUNBURY MOSS
Peat Building					ACTIVE	ACTIVE	

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APPENDIX

List of Benthic Species of Invertebrates Recorded from some Shropshire and Cheshire Meres

KEY
(Meres)
Nt: Newton Mere; Bl: Blake Mere; Wh: White Mere; E: Ellesmere Mere; Ro: Rostherne Mere;
Ha: Hatch Mere; Cm: Combermere; Co: Cole Mere; Cr: Crose Mere; Sw: Sweat Mere.

(Recorders)
B—Brinkhurst (1960); G—Galliford (1960); K—Kennedy (1961); L—Unpublished data of E. A. Wilson; M—Macan (1967); P—Pickavance (1965); R—Reynoldson (1966); S—Reynoldson and Bellamy (1970); T—Tait-Bowman (unpublished); U—Young (1973); V—Savage and Pratt (1976); W—Walsh (1965); X—Unpublished data of Dr T. T. Macan; Y—Young and Harris (1974); Z—Unpublished data of Preston Montford Field Centre (compiled by H. M. Twigg, F. Arnold, M. Redfern, M. R. Litterick, R. J. Pritchard, C. S. Reynolds and P. S. Croft).

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
PHYLUM: PROTOZOA										
CLASS: CILIOPHORA										
Vorticella sp									Z	
PHYLUM: COELENTERATA										
CLASS: HYDROZOA										
Hydra sp		Z							Z	K
PHYLUM: PLATYHELINTHES										
CLASS: TURBELLARIA					–					
ORDER: TRICLADIDA										
Bdellocephala punctata (Pallas)						Y	S		X	
Dendrocoelum lacteum (Müller)	S	P		S		P		P	S	
Dugesia polychroa (Schmidt)	S	S	S	S		Y	S	S	S	
Dugesia tigrina (Gerard)								R		
Dugesia lugubris (Schmidt)			S	S				S		
Planaria torva (Müller)								P	Z	
Polycelis nigra (Müller)	S	P					S		Y	
Polycelis tenuis Ijima	Y	P	P	Y		P	Y	P	Y	
ORDER: CATENULIDA										
Stenostomum leucops (A. Duges)	U	U	U	U				U	U	
Stenostomum unicolor O. Schmidt	U	U	U	U		U		U	U	
ORDER: MACROSTOMIDA										
Microstomum lineare (O. F. Müller)	U	U	U	U		U	U	U	U	
Macrostomum distinguendum (Papi)	U	U	U	U				U	U	
Macrostomum rostratum (Papi)		U	U	U		U	U	U	U	
ORDER: LECITHOEPITHELIA										
Prorhynchus stagnalis (M. Schultze)	U		U							
Geocentrophora baltica (Kennel)	U		U	U						
Geocentrophora spydrocephala De Man	U									
ORDER: PROLECITHOPHORA										
Plagiostomum lemani (Du Plessis)		U						U		
ORDER: SERIATA										
Otomesostoma auditivum (Du Plessis)	U			U				U		
ORDER: NEORHABDOCOELA										
Microdalyellia armigera (O. Schmidt)							U		U	
Microdalyellia brevimana (Beklemischer)			U							
Castrella truncata (Abildgaard)	U		U							
Mesostoma lingua (Abiligaard)	U		U	U			U	U		
Bothreostoma personatum (O. Schmidt)										
Phaenocora typhlops (Vejdovsky)				U					U	

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
Gyratrix hermaphroditus Ehrenberg	U	U		U		U			U	
Opisthocystis goettei (Bresslau)	U	U							U	
PHYLUM: NEMATODA		P	P		W					
PHYLUM: NEMATOMORPHA										K
PHYLUM: ROTIFERA										
Cephalodella spp				G						
Platyias quadricornis (Ehrenberg)				G						
Trichotria pocillum (Müller)								G		
Testudinella patina (Hermann)		G								
PHYLUM: GASTROTRICHA									Z	
PHYLUM: ECTOPROCTA										
Cristatella sp									Z	
Plumatella sp									Z	
PHYLUM: MOLLUSCA										
CLASS: GASTROPODA										
SUB-CLASS: PROSOBRANCHIA										
Potamopyrgus jenkinsi (Smith)	Y	P	P	Y	W	P	Y	P	K	K
Bithynia tentaculata (L.)		P	P	Y	W	P	Y	P	K	
Bithynia leachii (Sheppard)	B		B			P		P	Z	
Valvata cristata Müller					W				XX	
Valvata macrostoma (Steenbuch)				Y					Y	
Valvata piscinalis (Müller)		Z	P		W	P		Y	K	K
Viviparus viviparus L.				Y				Y		
SUB-CLASS: PULMONATA										
Acroloxus lacustris (L.)	Y	P	Y	Y	W	P	Y	P	K	K
Ancylus fluviatilis (Müller)		Y		Y	W			P	Y	
Lymnaea auricularia (L.)		Y	P	Y	W	P				
Lymnaea glabra (Müller)									Z	
Lymnaea palustris (Müller)		Y	Y	Y		Y		P	Z	
Lymnaea peregra (Müller)	Y	P	P	Y	W	P	Y	P	K	K
Lymnaea stagnalis (L.)		Y	P	Y		P	Y	Y		
Lymnaea truncatula (Müller)		Y	Y							
Physa fontinalis (L.)	Y					P		P	Y	
Planorbarius corneus (L.)			Y	Z				Y	Z	
Planorbis contortus (L.)	Y	Y	P		W	P		Y	X	
Planorbis laevis Alder		Z						B		K
Planorbis albus (Müller)	Y	P	P	Y	W	P	Y	P	K	K
Planorbis carinatus (Müller)		P	P	Y	W	P	Y	P	K	
Planorbis crista (L.)				Y				Y		
Planorbis leucostoma Millet								Z		
Planorbis vortex (L.)			Y	Y	W			P	K	
Segmentina complanata (L.)		Y	P	Y	W	Y		P	K	K
Menetus dilatatus (Gould)		Z								
CLASS: LAMELLIBRANCHIA										
Anodonta anatina L.								Z		
Anodonta cygnaea L.		P	P		W			P	K	
Dreissena polymorpha (Pallas)								B		
Pisidium spp		P	P		W	P		P	K	
Sphaerium spp		P	P		W	P		P	K	
PHYLUM: ANNELIDA										
CLASS: OLIGOCHAETA										
Family: Tubificidae										
Tubifex tubifex (Müller)		P	P		B	B		P		
Tubifex ignotus (Stole)		P	P			P		B		

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
Tubifex templetoni (Southern)					W					
Aulodrilus pleuriseta (Piguet)		B	P		W				K	
Euilyodrilus hammoniensis (Michaelsen)		P	P		B	P		B	K	K
Euilyodrilus bavaricus (Oschmann)					W	P			K	
Euilyodrilus moldaviensis (Vejdovsky and Mràzek)					W			B		
Limnodrilus hoffmeisteri (Claparede)		P	P		W	P			K	K
Limnodrilus udekemianus (Claparede)		P	B		W				K	
Limnodrilus claparedeanus (Ratzel)		P	P		W					
Peloscolex ferox (Eisen)			P		W	B				
Psammoryctides barbatus (Grube)						P		B		
Rhyacodrilus coccineus (Vejdovsky)		B	B		W			P		
Family: Lumbriculidae										
Lumbriculus variegatus (Müller)		P	P			P		P		
Stylodrilus heringianus (Claparede)		P	P		W	P		P	K	K
Eclipidrilus lacustris (Verrill)		P								
Family: Naididae										
Dero digitata (Müller)		B	P			P		P	K	
Stylaria lacustris (L.)		P			W	P			K	
Family: Glossoscolecidae										
Sparaganophilus tamesis (Benham)		P								
Family: Enchytraeidae										
Sp indetermined		P	P							
Family: Lumbricidae										
Eiseniella tetraedra (Savigny)				P						
CLASS: HIRUDINEA										
Piscicola geometra (L.)		P		Y				P	Y	
Haemopsis sanguisuga (L.)						P				
Erpobdella octoculata (L.)	Y	P	P	Y		P	Y	P	K	K
Erpobdella testacea (Savigny)				Y				P	Y	
Glossiphonia complanata (L.)	Y	Y	P	Y	W	P	Y	P	Y	
Glossiphonia heteroclita (L.)	Y		P	Y	W	P		Y	K	K
Hemiclepsis marginata (Müller)		P		Y		Y	Y	P		
Helobdella stagnalis (L.)	Y	P	P	Y	W	P	Y	P	K	K
Theromyzon tessulatum (Müller)	Y	Y	P	Y	W	P	Y	P	K	K
Batracobdella paludosa (Carena)							Y		Z	
PHYLUM: CRUSTACEA										
CLASS: BRANCHIOPODA										
ORDER: CLADOCERA										
Sida crystallina (O. F. Müller)					G					
Diaphanosoma brachyurum Lieven		G			G					
Scapholeberis mucronata (O. F. Müller)					G					
Daphnia obtusa Kutz.					G					
Simocephalus vetulus (O. F. Müller)	G				G					
Eurycercus lamellatus (O. F. Müller)	G				G					
Alona affinis (Leydig)	G	G			G			G		
Alona quadrangularis (O. F. Müller)			G							
Alona guttata (Sars)					G					
Rhynchotalona rostrata (Koch)	G									
Graptoleberis testudinaria (Fischer)		G								
Pleuroxus laevis Sars					G					
Pleuroxus aduncus (Jurine)					G					
Chydorus sphaericus	G	G	G		G					
Monospilus dispar Sars	G									
Polyphemus pediculus (L.)		G			G			G		

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
ORDER: BRANCHIURA										
Argulus foliaceus L.		Z							Z	
CLASS: COPEPODA										
ORDER: CYCLOPOIDEA										
Cyclops albidus Jurine				G	W					
Cyclops agilis Koch				G	W					
Cyclops leuckarti Claus				G	W					
Cyclops viridis (Jurine)					W					
CLASS: MALACOSTRACA										
ORDER: ISOPODA										
Asellus aquaticus (L.)	Y	P	P	Y	W	P		P	K	K
Asellus meridianus Racovitza						P	Y		K	
ORDER: AMPHIPODA										
Gammarus pulex Schell	Y	P	P	Y	W	P	Y	P	K	K
Gammarus lacustris Sars		B				P			K	
Crangonyx pseudogracillis Bousfield	Y	Y		Y				Y	Z	
PHYLUM: ARTHROPODA										
CLASS: INSECTA										
ORDER: EPHEMEROPTERA										
Ephemera vulgata (L.)		P						P		
Leptophlebia vespertina (L.)			P							
Cloëon dipterum (L.)		P	P		W				X	K
Caenis horaria (L.)		P	P		W			Z	K	K
ORDER: PLECOPTERA										
Nemoura cinerea (Retzius)									X	
ORDER: ODONATA										
Ishnura elegans (V. der Lind.)		P	P			P		P		
Erythromma najas (Hans.)		P						P		
Coenagrion pulchellum (V. der Lind.)		P	P					P		
Calopteryx splendens (Harris)		P								
ORDER: HEMIPTERA										
Family: Corixidae										
Arctocorisa germari (Fieb.)					V			V	M	
Callicorixa praeusta (Fieb.)					V	P		P	K	M
Corixa dentipes (Thomas)								P	•	
Corixa punctata (Illig.)									M	M
Hesperocorixa linnei (Fieb.)						P				K
Hesperocorixa sahlbergi (Fieb.)										M
Sigara distincta (Fieb.)	V							P	M	K
Sigara dorsalis Leach		P						P	K	M
Sigara concinna (Fieb.)	V				V	V		P	M	
Sigara fossarum Leach)									M	
Sigara falleni (Fieb.)	V	V	P	V	V	P		P	K	M
Sigara lateralis (Leach)									K	
Family: Notonectidae										
Notonecta glauca (L.)								P	K	K
Family: Nepidae										
Nepa cinerea (L.)		Z	P							
ORDER: MEGALOPTERA										
Sialis lutaria (L.)		P	P		W	P		P	K	K
ORDER: TRICHOPTERA										
Family: Phryganeidae										
Phryganea spp.		P			W	P		P		

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
Family: Molannidae										
Molanna sp.		P	P		W	P		P		
Family: Polycentropidae										
Plectrocnemia sp.										K*
Sp. indetermined		P	P			P		P		
Cyrnus flavidus McLachlan					W					
Family: Limnephilidae										
Spp. indetermined		P				P		P	K	K
Anabolia nervosa (Curt.)		P						P	Z	
Family: Leptoceridae		P	P					P		
Mystacides longicornis (L.)					W					
Oecetis sp.					W					
Family: Hydroptilidae			P		W					
Family: Hydropsychidae								P		
Family: Goeridae										
Silo sp.		P	P							
Family: Odontoceridae									K	
Odontocerum sp.									K	
ORDER: COLEOPTERA										
Family: Hydrophilidae										
Anacaena limbata (L.)		Z								
Family: Haliplidae										
Haliplus confinis (Stephens)			P							
Haliplus fulvus (Fabricius)										K
Family: Chrysomelidae										
Donacia spp.			P			P				
Family: Gyrinidae										
Gyrinus marinus (Gy.)					·	P				
Family: Dytiscidae										
Dytiscus sp		P							K	K
Hydroporus spp.		P	P		W					
Hyphydrus ovatus (L.)			P					P		
Ilybius fuliginosus (Fabricius)		Z								
Family: Elmidae										
Limnius troglodytes (Gy.)		P								
ORDER: DIPTERA										
Family: Culicidae										
Chaoborus spp.	T	T		L	W				K	
Culex sp.									Z	
Anopheles claviger (Meigen)									X	
Culicella morsitans (Theobald)									X	
Theobaldia annulata (Schrank)									X	
Family: Chironomidae										
(Sub-family: Tanypodinae)									K	K
Ablabesmyia monilis (L.)	T	T								
Macropelopia nebulosa (Meigen)									T	
Procladius choreus (Meigen)	T	T			W				T	
Procladius crassinervis (Zett.)									T	
Procladius sagittalis (Kieff.)									T	
Psilotanypus flavifrons (Edw.)		T								
Psilotanypus rufovittatus (Wulp)	T	T							T	
(Sub-family: Orthocladiinae)					W				T	
Prodiamesa olivacea (Meigen)									T	
Metriocnemus hygropetricus Kieff.		T								

*See text, p. 140

	Nt	Bl	Wh	E	Ro	Ha	Cm	Co	Cr	Sw
Metriocnemus sp.									T	
Isocladius sylvestris (Fabricius)		T							T	
Isocladius ornatus (Meigen)									T	
Isocladius reversus (Hirvenoja)									T	
Isocladius tricinctus (Meigen)									T	
Isocladius obnixus (Walker)		T								
Isocladius trifasciatus (Panzer)		T							T	
Trichocladius cf. *rufiventris* (Meigen)									T	
Psectrocladius spp.		T							T	
Heterotanytarsus apicalis (Kieff.)		T							T	
(Sub-family: Chironominae)		P	P	L	W	P		P	K	K
Pseudochironomus prasinatus (Staeger)					W					
Chironomus anthracinus Zett.	T	T							T	
Chironomus riparius Meigen	T	T							T	
Chironomus lugubris Zett.	T								T	
Chironomus plumosus (L.)	T	T							T	
Chironomus dorsalis Meigen	T	T							T	
Chironomus annularis (Degeer)									T	
Camptochironomus tentans (Fabricius)									T	
Camptochironomus pallidivittatus (Mall.)		T								
Limnochironomus pulsus (Walker)	T	T							T	
Limnochironomus lobiger (Kieff.)		T								
Limnochironomus notatus (Meigen)		T								
Limnochironomus nervosus (Staeg.)	T	T								
Cryptochironomus sp.										
Parachironomus falcatus (Kieff.)		T								
Cryptocladopelma viridula (L.)	T									
Demicryptochironomus vulneratus (Zett.)	T									
Glyptotendipes glaucus (Meigen)	T	T							T	
Glyptotendipes paripes (Edw.)	T	T								
Glyptotendipes gripekoveni (Kieff.)	T	T							T	
Endochironomus albipennis (Meigen)	T	T							T	
Endochironomus impar (Walker)	T									
Paratendipes albimanus (Meigen)					W					
Microtendipes chloris (Meigen)	T	T							T	
Microtendipes diffinis (Edw.)									T	
Microtendipes pedellus (Degeer)									T	
Stictochironomus pictulus (Meigen)					W					
Polypedilum nubeculosum (Meigen)	T								T	
Pentapedilum tritum (Walker)	T	T							T	
Lauterborniella agrayloides (Kieff.)					W					
Phaenospectra flavipes (Meigen)	T								T	
Phaenospectra sp.					W					
Tanytarsus spp.	T	T							T	
Stempellina bausei (Kieff.)									T	
Family: Ceratopogonidae					W				Z	
Family: Dixidae									Z	
PHYLUM: CHELICERATA										
CLASS: ARACHNIDA			P			P			Z	K
ORDER: HYDRACARINA										
Mideopsis orbicularis (Müller)					W					
Arrhenurus nobis (Neum)					W					
Arrhenurus securiformis (Piers)					W					
Arrhenurus crassicaudatus (Kram.)					W					