FRESHWATER STUDIES IN THE SHROPSHIRE UNION CANAL

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I. Introduction

This paper was written with three considerations in mind—(a) The desirability of recording, however briefly, the present stage in the rapid ecological changes taking place in a canal which has fallen into disuse; (b) The possibility that the author's methods of observation and recording might be of use in the study of canals (and slow rivers) elsewhere in the country; (c) The need for a preliminary survey of canal habitats in Shropshire for the guidance of biològy students at Preston Montford, with whom this is a popular subject.

Like all inland waters, canals present a wide range of plant and animal forms, and have a natural balanced economy with well-marked seasonal fluctuations. But in addition to these common characteristics, canals have certain advantages over other bodies of water as subjects for biological study. A canal may traverse widely differing tracts of country, and yet as an "engineered" waterway all its reaches are physically comparable. It is usually both narrow and shallow enough to be sampled easily from the towpath without elaborate equipment. Its flow maintains aeration and nutrient supply, but its regime is carefully controlled so that neither flooding nor drying out can occur. Canals may be found in urban areas where few other profitable habitats exist; it is seldom difficult to get permission for access. The character of a canal is such that once abandoned, it very rapidly develops a good hydrosere (a hydrosere is a natural succession of plant communities colonizing an aquatic habitat and eventually converting it to "dry land"); the rapidity of this process, enhanced by the falling water level of a canal in disrepair, makes it possible to record quite striking changes over a short period of years.

The field work carried out in 1958 was concentrated on the north-western branches of the Shropshire Union Canal system. These are readily accessible from Preston Montford, and are much used for teaching purposes. Very little ecological work has been done previously on this (or any other) canal. A paper by Boycott and Oldham (1936) deals with the Mollusca; Wilson (1952) has contributed popular but useful articles, chiefly on historical aspects, to the Shropshire Magazine. Work on the river Lark by Butcher, Pentelow, and Woodley (1931) shows many interesting points of comparison with the present study. The flora of the Llanymynech branch between that village and Welshpool has been studied and listed by the Montgomeryshire Field Club and members of the Cambridge University Botany School (unpublished).

II. THE SHROPSHIRE UNION CANAL

The original headquarters of the Shropshire Union Canal is at Beech House, near Ellesmere. From there the canal system extends into five neighbouring counties (more than half of its length lies outside Shropshire), linking up with several other canals and rivers (Fig. 1). Its greater part runs through the Shropshire-Cheshire plain, penetrating country of higher relief only at its western extremities.

The plain is a basin-like syncline of New Red Sandstone (Trias), with a rim of Carboniferous rocks—Coal Measures and limestone—to the west and south (Pocock and Whitehead, 1948). Beyond this rim more ancient rocks rise into

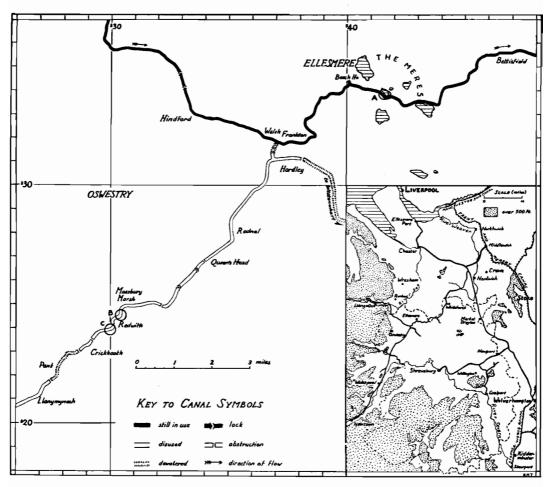


Fig. 1.

Map of canal system in north-west Shropshire, showing the condition of each branch at the present day and the three localities studied in detail (A: Blakemere reach; B: Redwith/Maesbury Marsh reach; C: Redwith/Crickheath Wharf reach), with the width of the canal exaggerated × 10 for emphasis.

Inset: The Shropshire Union Canal network (heavy black line) in relation to major rivers, high ground, and some neighbouring canal systems (ticked black line). The full extent of the original canal is shown both within and beyond the county boundary (broken line), including branches no longer in use.

sharp relief. The surface of the plain is thickly mantled with glacial deposits ranging from heavy boulder clay to loose sands and gravels, which give variety and fertility to the soils. A belt of hilly country with scattered pools and bogs

("meres and mosses") marks the line of the Ellesmere Moraine.

Industries are concentrated on the Carboniferous outcrop, with its resources of coal, iron and lime. Elsewhere the economy is largely rural, with dairy farms on the plain giving place to sheep farms in the Welsh hills. The pattern of the canal network can best be understood in terms of these physical and economic factors. Its original traffic depended on the exchange of mineral and agricultural produce; a barge carrying coal or iron in one direction might return laden with cheese or wool.

The Shropshire Union Canal had its origins in the eighteenth century, when the iron foundries of Coalbrookdale were a focus of the Industrial Revolution (Raistrick, 1953). Telford's Ellesmere Canal from Chester to Llangollen (Telford in Plymley, 1803; Rolt, 1958) was one of the first and greatest steps to meet the need for improved communications in the region. Its later extensions and the absorption of minor independent branches resulted in several hundred

miles of canal operating by the mid-nineteenth century.

Improvement in road and rail transport brought about the decline of the Shropshire Union Canal. At the present day only Telford's original branch is still open and only pleasure traffic plies on it. The Shrewsbury Canal through Newport is abandoned, and its offshoots east of Wellington are buried in industrial wasteland; the Llanymynech branch and its Montgomeryshire extension fell into disuse before the recent war. Some stretches of the latter have been dewatered; at Pant, for instance, the water is piped overground along the old bed, for the benefit of farmers whose stock depend on it; the side branch from Hordley to Weston-wharf is now completely dry. The biological influence of these "degrees of abandonment" forms the main theme of this paper.

Over most of the plain the canal runs through gently undulating land no higher than 300 ft. O.D. There are few locks and its course is little influenced by the form of the ground except in the Ellesmere Moraine belt. Local relief exerts more influence to the west, where the canal comes not only for commerce but also for its water supply. Three large rivers flowing eastwards out of Wales

—the Severn, the Tanat, and the Dee—have been used as feeders.

The canal is cut mostly to the 300 foot level. To maintain its level with a minimum of locks, even in the lowland, the course of the canal shows a sequence of cuttings and embankments. A series of locks (now derelict) brought the Llanymynech branch to the level of the Ellesmere branch at Welsh Frankton. Special constructional features include a number of wharves, double-width "passing places", and overflow weirs to control the water level. Numerous hump-back bridges cross the canal (though several have been levelled in the interests of road traffic); at these points the channel narrows to barge-width, and provision is often made for damming the canal with "stop-planks" and draining limited reaches for maintenance work. On the abandoned Llanymynech branch many of the stop-planks have been left permanently in place, and the water is led through culverts under the demolished bridges (see obstructions marked on Fig. 1). These operations are responsible for the ponding up of short reaches, and for the relative stagnation of their water. Such reaches are thus

largely cut off from the main feeders and must be dependent on local field

drains for their supply.

The average width of the original canal bed was 35 feet, and the maximum depth about 6 feet at the centre. The towpath bank is steep, being banked up or "pitched" with stones. As much of the canal in Shropshire runs through unconsolidated glacial deposits, it was necessary to strengthen the sides with stone and then to line the bed with puddled clay. The stone used for lining or pitching is almost entirely limestone brought from Llanymynech or the Eglwyseg crags near Llangollen. Only in parts of its Denbighshire length was puddling unnecessary, because the bed was here cut into the living rock.

Full maintenance operations are still carried out on the Ellesmere branch. The towpath is kept in repair and mown annually; patches of the bottom and sides are relined with clay where this is essential; water weeds are cut occasion-

ally; dredging is carried out as required over a period of years.

Even in the disused Llanymynech branch, bridges and other essential structures are still kept in repair. Mowing is still carried out in some of the watered reaches, and cattle are permitted—though this can scarcely be called

maintenance—to graze the towpath.

The plant and animal life of the canal is rich and varied. The nature of the vegetation was used in the first place as an obvious visual criterion of differing ecological situations, and was soon found to be closely linked with the state of use or disuse of the waterway. The combined study of plants and animals in a particular environment is not very often undertaken. A glance at the illustrations might give the impression that this is purely a botanical study; but plant ecology is so essential a background to freshwater zoology in this kind of habitat that some bias is inevitable. Insufficient work has been done on micro-organisms and certain other groups to justify their inclusion in this account.

III. METHODS

(1) Selection of localities for investigation

It was not thought possible to investigate the full 29 miles in the area (Fig. 1) intensively. Dewatered stretches were not dealt with, since they have ceased to be aquatic habitats in the full sense. After extensive reconnaissance three short reaches (A, B and C) were chosen for detailed study, each representing a well-marked stage in abandonment and plant colonization. All three are readily accessible from main roads.

(2) Compilation of species lists

Species lists, as complete as possible, were made for the selected localities. The preparation of the lists within a broad ecological framework proved helpful in defining the main plant and animal communities. The final lists (Tables 3 and 4) are a modified presentation of these data. Species in certain invertebrate genera could not safely be identified in the field. Comparisons between numbers of species in the different localities and microhabitats studied are therefore of limited value.

(3) Analysis of habitat factors

The limitations of field and laboratory equipment, not to mention time, made it difficult to obtain all the quantitative data useful to a study of this kind. The field techniques used were simple and conventional and they do not call for description at this stage.

(4) Synecological plant studies

Synecology is the study of plant and animal communities in relation to their environment. The techniques that have been developed for this work in the case of plants are very numerous, but this is no place for a theoretical discussion of their relative merits. Two methods were found to be of practical value for the present work, and they are dealt with below. The first was the preparation of a vegetation map at each locality, the second the surveying of a particular kind of transect. The methods used in surveying and recording for both these tasks are given in some detail below, since the second at least has not been adequately described before in a readily accessible source.

(a) Vegetation maps. A typical 60 foot length was chosen at each of the three localities. These were mapped at a time of year when the vegetation had attained its fullest development (August). A straight base-line was laid out with a tape along the towpath. Rectangular offsets to the opposite bank were then made at 10 foot intervals, by stretching graduated plastic clothes-lines across the canal. Each 10-foot-wide strip was then worked in turn (it was found convenient to

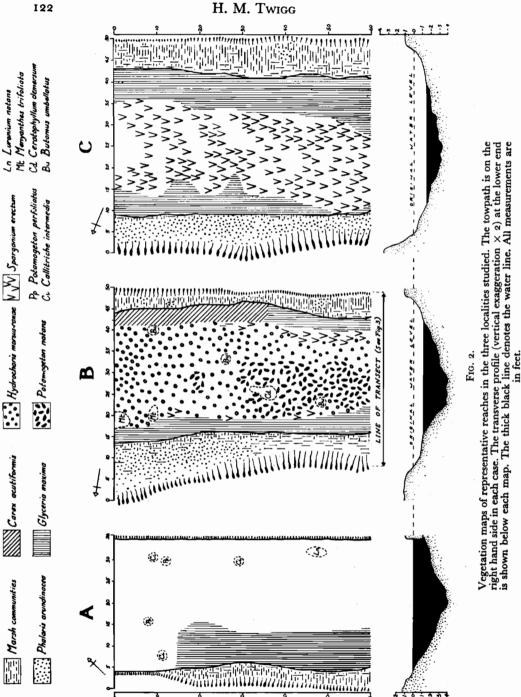
have a pair of recorders, one working from either bank).

The vegetation was mapped in graph paper notebooks at a reduced scale (1:60). The most difficult part of the operation was to decide initially how much to show on the map; whether to represent communities, or individual plants, or a combination of both, is a decision which depends on the size of the area mapped, the size and spacing of individual plants, and the scale of reduction. In this case the boundaries of the main communities, which fell into well-marked zones (aquatic, reedswamp, and marsh), were plotted to an accuracy of \pm 6 in., and the location of clumps of conspicuous individual species (apart from the normal dominants) was recorded. The width and steepness of the banks, and the position of the water's edge, were also noted.

Since it had already become apparent that depth of water and shoreline were two of the principal determining factors for the vegetation pattern, each map was supplemented with a transverse profile. This was taken at one end of a mapped stretch. The bank profiles above the water were measured by means of a spirit level (line level) hung centrally on a taut piece of string between two vertical rules, noting the height discrepancy at one foot intervals; depth

soundings were taken at the same frequency across the channel.

In preparing the final maps (Fig. 2), it had to be decided how to show the recorded features clearly at a further reduction (1:2). In general, the same considerations apply as in the original plotting. Communities are best shown by differential shading, individual plants or clumps by letters (or symbols). The banks are indicated by "wedge hachures". Scale-lines are ruled along both axes. The profiles are drawn in below the end of the mapped stretch where they were measured, with a vertical exaggeration (×2) to emphasize their differences.



(b) Transects. It is often most instructive to study belted plant communities (zonations and successions) along a line at right angles to the belts. These sampling lines or "transects" are of various kinds, some much more informative than others. One of the most useful is what may be called a "ladder transect". This records quantitative as well as qualitative data, and shows the correlation of changes in communities and individual species with habitat variations.

A strip I foot wide was marked out across the canal (at the western end of the mapped stretch B in the illustrated example) by means of tapes. The strip was examined in a continuous series of I foot squares: in each square every species present was recorded, with an indication of its quantity. In practice, relative assessments are very difficult to make for species of different stature and growth form; cover and numerical abundance can give very different results, and perhaps the most satisfactory compromise is provided by Braun-Blanquet's Cover/Abundance Scale or one derived from it (Braun-Blanquet, 1932, p. 34). For the illustrated example (Fig. 3) a more rapid subjective estimate was made in terms of the categories abundant, frequent, occasional, and rare; this gives satisfactory general impression, but tends to make small plants (e.g. Lemna minor) too conspicuous by comparison with larger ones (e.g. Sparganium erectum); this approach takes no account of the vertical layering of most plant communities. The profile was measured as in the previous example and additional notes were made on the nature of the bottom.

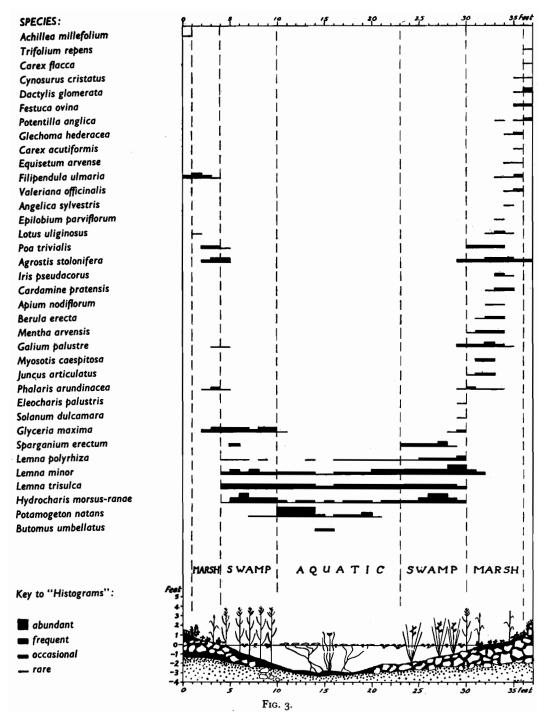
The plotting method is an important feature of this technique. The profile was first drawn in at the bottom of the page (embellished in this case with diagrammatic sketches of a few conspicuous plants). The list of recorded species was then arranged in such an order as to give the clearest picture of the vegetation changes. The frequency variations for each species were plotted by means of a histogram or block diagram along a line across the profile, so that the frequency in a particular square showed directly above the appropriate part of the profile. The boundaries of the main zones were added to the diagram.

This type of figure has the advantage of condensing the maximum amount of information into the minimum space, and at the same time remaining easily readable at a glance. Other variables (e.g. pH, light intensity) can be plotted in graph form at the bottom, but none was thought necessary in this case.

(5) Synecological animal studies

The mobility and inconspicuousness of most freshwater animals call for a different approach to quantitative studies. Many of the latter are based on comparative population counts between different localities or microhabitats, using sampling methods standardized according to volume, area, or time. It is not thought necessary to describe such techniques in detail, nor to compare their merits and disadvantages; it is especially true of freshwater ecology that standard techniques must be suitably modified to fit the problem in hand.

It may be worth giving a brief description of the simple method used to compare the bottom fauna in two types of sediment (silt and organic mud) in the Blakemere reach. A perforated biscuit tin was pushed upside down into the sediment to a depth of about 2 inches. By sliding a spade underneath and righting the tin, it was possible to collect a population sample from a known surface



"Ladder transect" diagram across Redwith/Macsbury Marsh reach (see Fig. 2 for location). Species frequencies are plotted in the form of histograms, and may be correlated with the profile drawn below. The plants drawn on the profile are diagrammatic and represent the dominants of each zone.

area of sediment. The material was washed systematically in small batches through a kitchen sieve. The extracted animals were transferred to a pie dish, sorted into species and counted. The results are shown in Table 2; these are based on two samples only in each microhabitat—ideally a much larger number should be taken. This work was done in October, when some animals were descending to overwinter on the bottom. They are grouped together at the bottom of the table (it is interesting to note that the majority were found in the organic mud only, having come down from the dying reedswamp).

Similar comparisons were made between the animal populations associated with certain water plants. These are discussed in a later section (p. 132). A start was made on a number of long-term projects. Some preliminary data have been gathered on seasonal changes. A comprehensive study of "food chain" relationships, which may be regarded as the climax of an investigation of this kind, has hardly been begun yet. This involves a balanced investigation, usually over a period of several years, of the entire biological economy of a body of water. A good ecological knowledge of the site is a necessary basis, and the complete pattern can only be built up by the examination of the gut contents of every species.

IV. CLASSIFICATION OF HABITAT FACTORS

(1) State of repair

The state of repair exerts a direct or indirect control on almost every other influential factor. Use and maintenance ensure a fairly constant flow and level, and keep the channel clear of weeds. Disuse and neglect lead to stagnation and a fall in water level, and permit the encroachment of vegetation.

(2) Dimensions

The canal bed is 30 to 50 feet wide (average 35 feet). The full width is not occupied where the water level has fallen. There is room for a good plant succession on either side which is further favoured by the gentle gradient of a slumped shoreline. An abrupt drop into deep water makes a poor shoreline biologically. The canal is shallow enough throughout to be inhabited to its full depth (4-5 feet).

(3) *Flow*

The only feeder still operating (at Llantysilio above Llangollen) has an estimated maximum input of $6\cdot 25$ million gallons per day. Without allowing for other variables (friction, water-loss, etc.), this should give a flow of 9 feet per second, which agrees well with the observed midstream rate of 10 feet per second in the Blakemere reach. This constant flow is sufficient to maintain good supplies of both minerals and oxygen, the latter being supplemented by the turbulence induced by passing traffic. At the same time it is probably not enough to detach sessile organisms from their anchorage, or to hinder the movement of the larger free-swimming animals "upstream". The current can transport nothing coarser than clay. Minnikin (1920) associates a mud bottom with a velocity of less than 5 in./sec., and describes the prevailing condition of the habitat as "pond-like". But the local redistribution of coarse materials can be brought about by the action of barge propellers as well as by slumping from the banks.

The disused Llanymynech branch is probably no longer dependent on longrange water supply. Some reaches may well be watered only by drains and rain. At many points the stop-planks are permanently in position, and the water only spills over them in "flood". Stagnation is more or less complete.

(4) Nature of bottom

The bed was originally made of stones with a uniform cover of clay, but this puddling is no longer continuous. Stones, sand, and silt have fallen in from the bank and spread over parts of the bottom, especially in cuttings. This variety of superficial deposits (most marked in the used branch) is important in the

consideration of the bottom fauna.

While the varied deposits of the used branch are largely mineral in origin, those in the disused reaches are almost wholly organic. The reedswamp and other plants contribute an annual quota of rotting litter giving rise to a black organic mud which is highly humified, strongly reducing, and rich in dissolved bases. When bank collapse has accompanied a fall in water level, the fluctuating shoreline exposes a type of mud which is both less exclusively organic and less deficient in oxygen.

(5) pH and mineral content

Boycott and Oldham (1936) found a marked pH gradient from the intake of soft Dee water at Llantysilio down into the Shropshire reaches. All the latter, used and disused, are alkaline at the present day. At Ellesmere this is so in spite of the prevalent acidity of the surrounding soils, and the substantial calcium carbonate content may derive from the limestone used in the canal's construction. It is hardly surprising that the water of the disused branch has an even higher pH, for it passes close under the limestone outcrop of Llanymynech Hill.

Samples were taken in August 1958 at the three stations (A, B and C) described below; Table 1 (see p. 138) shows the results of analysis for important ions. In general, the differences between the stations are not particularly marked, and stations B and C on either side of Redwith bridge have very similar figures. Calcium (with bicarbonate) is lower at Blakemere (A) than at the other two stations, a result which tallies with the pH differences; magnesium is highest at B and lowest at A, but nowhere very abundant. Sodium and chloride are closely linked, and probably represent impurities introduced from domestic effluents—the slightly higher figures at B and C may reflect accumulated pollution in stagnant water; the same is probably true of sulphate. Potassium is low at all three points, but significantly higher at A; this might possibly be connected with the silting of the bottom (see Tansley, 1953, p. 609). Nitrate is also rather low throughout, but again highest at A. No figures are available for phosphate and silica, nor for indicators of pollution other than those mentioned above.

Notwithstanding the discrepancies between rich Ca/Mg. and poor K/NO3 supplies, all these waters should certainly be classed as calcareous and eutrophic (i.e. having an adequate and balanced supply of mineral nutrients). None of them is foul, in that toxic impurities are well below the critical level.

(6) Light intensity

The canal is well exposed to incident sunlight, except where cuttings, bridges, and trees overshadow it. Light can reach the bottom where the water is clear and open; but in the disused branch, a dense summer growth of floating aquatic species cuts down both the intensity and the wavelength range of light penetrating the water, while the reedswamp shades the surface.

(7) Temperature

The water is generally shallow, slow-moving, and well lit, and so tends to warm and cool rapidly. In used parts it is open, and mixed by the current and the passage of barges; the temperature gradient from the surface downwards is therefore slight. In disused parts the gradient varies according to the stage of choking by the vegetation; where there is a good growth of aquatic plants with floating leaves, sunlight warms the surface water but has a restricted penetration to lower layers, and the temperature gradient is steep in summer; where plants of a different habit, such as reeds, predominate, little sunlight reaches the surface of the water and the summer gradient is less steep.

The following figures were recorded on 22nd August, 1958:

	Air Temp (°F.)	Surface Temp. (°F.)	Temp. at 1 ft. depth (°F)
Α	61		65
В	64	65 66	61
\mathbf{C}	65	63	61

Local temperature variations of the kind brought about by cold springs or warm industrial effluents are unlikely to occur in a canal. Superficial freezing takes place in all reaches for short periods; during these spells most organisms are overwintering in the bottom mud.

(8) Biotic factors

In this artificial habitat the human factor is dominant; the interaction of other organisms is more properly considered in the discussion of the ecology of the selected localities below.

V. ECOLOGY OF SELECTED LOCALITIES

This section deals with the three reaches (one still in use and two abandoned) studied in detail; a descriptive summary of each locality is given followed by observations on the flora and fauna.

(1) Blakemere reach (Fig. 4, A)

This lies parallel with the southern shore of Blakemere close to the junction of the main Shrewsbury-Ellesmere road (A528) with the Whitchurch-Ellesmere road (A495); the reach examined was 200 yards long. After 150 years of use its traffic has declined to summer pleasure craft, whose wake still influences the shoreline biology. The bottom has been neither dredged nor repuddled recently, but the towpath bank is mown annually. The water is about 31 feet wide and 4 feet deep in the middle. The towpath bank falls 1 foot vertically to the water



A. Blakemere reach looking E; open water still used by pleasure traffic. B. Redwith/Maesbury Marsh reach looking N; disuse since 1938 and fall in water level have resulted in spread of floating plants and reedswamp. C. Redwith/Crickheath Wharf reach looking S; similar disuse and further loss of water have led to complete reedswamp cover.

surface and nearly as much again to the bottom, while the opposite shore shelves gently down from a marshy field. Redistributed silt and fine sand cover much of the bottom, but there are patches of fallen stones on the towpath side and of black organic mud under rooted reedswamp on the opposite shore. Trees and rising ground give little shade but some shelter from the wind. Certain lengths of the towpath bank are fringed underwater with tree- and grass-roots.

The vascular plants (excluding terrestrial "meadow" species) recorded in the Blakemere reach are listed in Table 3. Comparisons of total species numbers between this reach and the others would be of little value, because of the disparity of the lengths studied, but the relative numbers under each ecological heading are of great interest. No species is abundant in this reach, and the vegetation as a whole is sparse. There are more aquatic species here than in B or C, but the majority are of the submerged type and the water surface is open from bank to bank. Pondweeds (Potamogeton spp.) are well represented, but P. natans is absent. During the "tourist season", more detached than rooted specimens may be seen, and this disturbance is probably a significant dispersal factor. Two rare species, Callitriche hermaphroditica and Luronium natans, deserve mention; the habit of the latter is quite uncharacteristic in that it tends to form a dense submerged sward which rarely produces the normal floating stems and leaves. Free-floating plants (Hydrocharis morsus-ranae, Lemna spp.) are confined to sheltered water in the marginal reedswamp.

Reedswamp forms a narrow interrupted fringe on the shoreline opposite the towpath. Glyceria maxima is the only common species. There is no sharp boundary or bank on this side, and the swamp grades back into marsh-meadow. On the towpath bank (where there is no reedswamp) a few marsh plants are rooted in crevices. Here the wake of passing traffic may be influential: Filipendula ulmaria which grows here is said to depend on a fluctuating water table, and Mimulus guttatus shows adventitious roots 3-4 nodes above the base.

Numerical comparisons of animal species lists are of even less value than those of plants, because of incomplete identification (see note at head of Appendix.) Nevertheless, it is safe to infer from the records a progressive decrease in faunistic variety from A to C, and a proportionate change in the representation of each ecological category. Both "skaters" and "swimmers" require a combination of open (unchoked) water with shelter, and these conditions are best met in the Blakemere reach. The Watermeasurer (Hydrometra stagnorum) and a swimming caddis (Triaenodes), together with several water beetles, are only found in this station. It is interesting to note that one of the latter, Noterus clavicornis, is replaced by the related N. capricornis in B and C.

"Crawlers and clingers" are the best-represented category in all three stations, and they may be further subdivided according to their substrate preferences. The sparseness of the vegetation may be responsible for the low individual frequencies of the various animals which dwell on plants. A microhabitat of particular interest here is the soil-free roots of alder and grasses under the towpath bank; these carry a distinctive population including the beetles Anacaena limata and Hydroporus pictus, and a number of caddis (species of Anabolia, Phryganea, Polycentropus, Limnephilus) most of which use the roots for case-making material as well as for attachment. Spongilla is notably more abundant in A than

in B; it is often found attached to the larger alder roots (the normal green colour due to symbiotic algae disappears on shaded parts), but its long finger-like growths are especially conspicuous on the stone work under bridges.

The "burrowers" (some of which might be better called "bottom crawlers") are a small but rather mixed category. The mayfly Caenis horaria and the beautiful caddis Molanna angustata are only found in A and the peashells Pisidium are commoner there. Silt and organic mud provide distinct microhabitats (see Table 2): the true burrower Ephemera vulgata, unable to live in the latter, is significantly abundant in A but absent from B and C.

It is probable that good oxygenation and the varied nature of the bottom are largely responsible for the distinctive character of the invertebrate fauna in this reach, accounting for the quantity of such organisms as Spongilla, E. vulgata, and

several of the caddis.

Fish are plentiful, and catches by the Ellesmere Angling Club show a high proportion of perch, with a few roach, tench, pike, and bream, apart from the smaller species (minnows and sticklebacks). The parasitic fish-leech *Piscicola geometra* is common here, being favoured by good aeration. Waterfowl nest on the adjacent mere, where there are also large numbers of migrant visitors. Some of them may alight at times on the canal—their leech parasite *Theromyzon tessulatum* is also present.

(2) Redwith/Maesbury Marsh reach (Fig. 4, B)

This lies a short distance to the north of the demolished bridge at Redwith on the Knockin-Llynclys road (B4396) and is 700 yards long. The Llanymynech branch was abandoned in 1938 when a breach occurred near Welsh Frankton. The Redwith bridge was levelled in 1948. There has been no scything or other maintenance for at least two years. The breach caused a fall in the water level, whose middle depth is now about 3 feet, and whose width is about 28 feet except at a former passing place (49 feet wide); the channel has a shelving shoreline in all parts. Flow is negligible except after heavy rain. Slumped soil forms most of the shoreline except where limestone "pitching" is bare, while from the reedswamp to the centre an increasing thickness of organic mud has accumulated. The entire reach is well illuminated (apart from the shading effect of the water plants themselves). There is limited grazing by cattle on the towpath side.

There are proportionately less aquatic and more reedswamp species here than at A. The hydrosere is fully developed and the vegetation cover is continuous. From the middle to either bank three main zones are recognizable, corresponding with the headings in Table 3. Hydrocharis morsus-ranae and Lemna minor are co-dominant over most of the aquatic zone, with L. polyrhiza as a frequent associate; L. trisulca forms a continuous submerged "understorey", and may help to maintain the oxygen supply in this stagnant water. Nuphar lutea is locally dominant (e.g. in the deeper passing place) and smaller patches of Potamogeton natans occur. Ceratophyllum demersum occupies a short stretch to the exclusion of

nearly all other plants.

The reedswamp dominants often grow in pure stands. Butomus umbellatus and Sparganium erectum appear as isolated clumps well out in the channel, and the latter forms a discontinuous fringe along either side of it. Glyceria maxima forms a broad conspicuous belt between the Sparganium and the shore, with Alisma

plantago-aquatica, Equisetum fluviatile, Oenanthe fistulosa, and Rumex hydrolapathum as occasional associates. There is sometimes a third belt of Carex acutiformis, and

it replaces Glyceria in one stretch (see Fig. 2, B).

The marsh zone is introduced by a narrow strip of *Berula erecta* at the water line, but it becomes very mixed floristically as it extends inshore; *Phalaris arundinacea* is a common member of this community. The upper part of the bank is occupied by a dry, calcicolous, grass-dominated "meadow" zone. Clumps of alder and hawthorn have sprung up along the towpath, but occasional scything has kept them in check.

The animal population is high, and there are a number of organisms here which were not found at A. The Water Spider (Argyroneta aquatica) is frequent, being favoured by still water and plants for attachment, and arachnids are also represented by the water-mites Megapus and Hygrobates; the Phantom Midge

(Chaoborus) is found here, preferring stagnation and possibly shade.

Plants in the aquatic zone introduce a new ecological element. The fish-leech Hemiclepsis marginata (replacing P. geometra) lives on the undersides of floating leaves in its free state; certain snails and insect larvae of restricted microhabitats are discussed under Ceratophyllum demersum and Hydrocharis morsus-ranae (pp. 132, 134). There is a considerable overlap in the lists for this and the last station, but it should be noted that individual snails (especially Planorbis vortex and P. carinatus) are far more abundant here, chiefly on Sparganium erectum.

As would be expected from the reduced range of bottom materials, the list of burrowers is shorter than at A and there are no additions. The slumped bank soil in the marsh zone replaces the silt at Blakemere as a habitat for Sialis lutaria and Pisidium; Sphaerium is commoner here, showing a preference for the

black organic mud.

Lower aeration and current, together with the greatly increased density of plants providing food, attachment, shade, and shelter, summarize the factors

responsible for the distinctive invertebrate fauna of this reach.

The same species of fish are to be found here as in the Blakemere reach, but in lower numbers. Moorhens are common, and a pair of swans regularly make their nest on the canal bank at the northern end of this reach. Numerous water-voles burrow into the dry towpath bank and feed on the reedswamp.

(3) Redwith/Crickheath Wharf reach (Fig. 4, C)

This is adjacent to B but just south of the old Redwith bridge, and because of its uniformity only 100 yards were chosen for study. It is generally similar to the preceding reach, apart from the effects of a greater fall in water level. The maximum depth recorded is 1 ft. 9 ins., and the width of water 26 feet or less with a wide and gentle shoreline. The water is stagnant and poorly aerated. Black organic mud fills the channel to a thickness of 2 ft. 3 ins. in the middle; only in the marsh zone is slumped soil exposed. Rising ground and a tall neglected hedge reduce exposure and illumination to a small degree. Neglect is even greater than in B but cattle graze the towpath here as well.

The aquatic zone has disappeared as a separate entity, and its few surviving species occupy gaps in the reedswamp which has spread right across the channel. Sparganium erectum dominates the middle belt, while the belts of Glyceria maxima

extend above the water line on either shore.

The marsh zone is wider than in B, but similar in other respects; *Phalaris arundinacea* is notably abundant on the steep north-west bank and there is an

increase in the grass/herb ratio on the opposite one.

The decrease in variety of microhabitats is reflected in the fauna. Only the mosquito Anopheles is an addition to the total list but it may have been overlooked at the other stations. It is interesting to note the complete disappearance of caddis (Trichoptera) and the reduced representation of other insect orders; this is least marked in the Diptera, whose individual frequencies are in fact higher. Snails are less abundant in spite of the expansion of reedswamp.

From the point of view of the freshwater fauna, this reach is under-aerated

and over-choked.

None of the larger species of fish have been seen. There are no swans, and moorhens are reduced in number, because of the lack of unobstructed water. By contrast with this general pattern of depopulation, watervoles reach their peak here.

VI. AUTECOLOGY OF CERTAIN WATER PLANTS

Autecology is the study of individual plant and animal species in relation to their environment and to their associates. There is some danger in concentrating attention on a single species before a general ecological picture of a habitat has been obtained; but such a study, involving careful observation and attention to detail, can bring to light points which would be missed in a broader survey. Autecology comprehends a complete "biography" of the organism—it can therefore involve many years of intensive work.

Because of the intimate dependence of so many animals upon plants, autecological studies of the latter are perhaps more instructive to the general biologist than those of the former. Four water plants were chosen in the Redwith/Maesbury Marsh reach for brief observations to illustrate this point, with emphasis on the role of the plant as a microhabitat for animals.

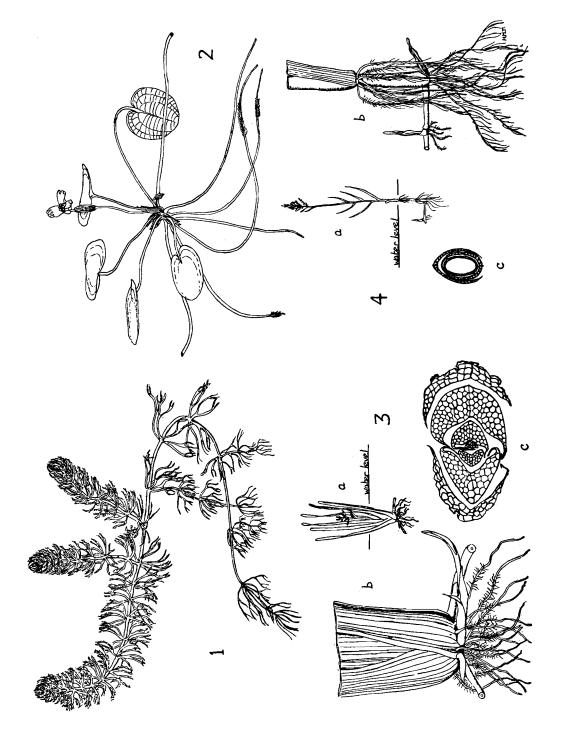
Ceratophyllum demersum. Hornwort (Fig. 5, 1)

This is a submerged aquatic species loosely anchored to the bottom by modified leaves instead of roots. It cannot withstand the drag of a current, and is absent from the Blakemere reach. Hornwort usually grows in thick extensive patches with few associates. Dispersal is mainly by detached portions of the rather brittle shoots; the axillary dioecious flowers are water-pollinated and fruits ripen occasionally, but viable seed may not be set.

Fig. 5.

Drawings of four water plants found in the canal, which are the subjects of autecological studies:

- 1. Ceratophyllum demersum $(\times \frac{1}{4})$.
- 2. Hydrocharis morsus-ranae ($\times \frac{1}{4}$).
- 3. Sparganium erectum (a) whole plant (diagrammatic $\times_{1\overline{0}\overline{0}}$).
 - (b) base of plant $(\times \frac{1}{8})$. (c) T.S. through shoot just above base $(\times \frac{1}{4})$.
- 4. Glyceria maxima (a) whole plant (diagrammatic \times_{100}).
 - (b) base of plant $(\times \frac{1}{8})$. (c) T.S. through shoot just above base $(\times \frac{1}{4})$.



The architecture of the leafy shoot, crowded with stiff spiky leaves, provides a good microhabitat for the freshwater fauna, and the benefits are enhanced by the lack of wax or mucilage. Here is a natural scaffolding around which certain caddis can build their homes—Cyrnus spins a silken tent, and Agraylea attaches the ends of its fine-grained case like a hammock to the leaves; the tiny snail Planorbis crista is only found in this microhabitat. Besides these absolutely restricted species, several other snails, flatworms and leeches are common inhabitants, making the Hornwort a veritable "zoological garden".

This species and the following are discussed at some length by Arber (1920)

in her classic Water Plants.

Hydrocharis morsus-ranae. Frogbit (Fig. 5, 2)

This floating aquatic plant is not rooted to the bottom, but is supported at the surface by its smooth waxy leaves; it is confined to still water, where it may be abundant (as in the Redwith/Maesbury Marsh reach).

During the growing season it spreads rapidly by means of stolons. Winter-buds or turions are formed at the ends of special stolons in autumn. The three-petalled white flowers are produced freely throughout the summer in open stretches, but not among reedswamp; the seeds are said never to be set in England, but in 1958 at Redwith fruits were seen to approach maturity before they were caught by the first frost. At this stage the plants turned brown and died away; the turions, heavy with starch, broke off and sank, to overwinter in the bottom mud (this mechanism is a common one among water plants—Potamogeton spp. share it, while in Lemna small thallus-lobes behave in the same way).

The number of animals living on Frogbit is low. None have been found on the smooth roots, petioles and stolons. The leaves, being small in area but at the same time thick and turgid, carry a sparser population than those of Nuphar lutea and Potamogeton natans. Occasional egg-masses of certain leeches and other unidentified animals are attached to the undersides. The larva of the China mark moth Cataclysta lemnata wraps itself in a "blanket" of Lemna fronds beneath a Frogbit leaf. The related Nymphula nymphaeata (which makes its case by cutting an oval patch from the margin and sticking it down to the leaf surface) is common enough on the water lily, but it has not been seen on Frogbit at Redwith. The most habitable part of this plant is the space within the transparent membranous stipules, which protect the developing leaf buds and persist throughout the season. But these are relatively small and frail, so that animals larger than flatworms are seldom found within them.

Sparganium erectum. Branched Bur-reed (Fig. 5, 3)

The robust shoots of the Bur-reed are firmly rooted to the bottom in relatively deep water (as a rule more than 18 inches). The leaves are all produced from the base, and spring almost erect from below the water surface to a height of about 4 feet above it. For most of their length they are roughly triangular in section, but towards the base they become broader, channelled, and loosely sheathing. The consistency of the leaf tissue is spongy in the lower parts (Fig. 5, 3c), as a result of the air-conducting tissue (aerenchyma) which occupies most

of its volume. The plant grows in moderately open stands, spreading by pithy rhizomes at the surface of the mud. The roots at the base of each shoot are short but apparently contractile, giving a strong but resilient anchorage.

The flowering stems, which do not overtop the leaves, bear separate heads of male flowers on their upper and female flowers on their lower branches. Ripe fruits are produced—they have been seen floating abundantly on the water surface in October—and probably act as the sole agents of dispersal; the shoots are not readily uprooted, but once free are buoyed up by their aeren-

chyma and probably find it difficult to re-anchor themselves.

The major ecological role of this swamp plant (from the point of view of freshwater animals) is the manner in which its emergent shoots give a cellular but freely intercommunicating pattern to the water, further limiting turbulence. But the shelter this affords must be more than offset by increasing stagnation and oxygen deficiency, which may partly account for the progressively lower number of swimmers in B and C. By contrast with this low population in the open water is the high frequency of animals (mostly crawlers) on the plant itself; these are concentrated in the readily accessible shelter among the sheathing bases of the leaves: here a dense population of snails, leeches, and flatworms is found. These cavities may well be food traps for the detrital feeders (Asellus aquaticus) present, but the question of oxygen supply is puzzling in such cramped quarters. Possibly the inhabitants can tap the abundant air within the damaged leaf tissue; it is interesting to note that larvae of Tabanus and Chironomus plumosus have been found living within the broken aerenchyma of old leaves.

Glyceria maxima. Reed sweet-grass. (Fig. 5, 4)

Of the four species here described, this is the only one so far dealt with in the Biological Flora. Lambert (1947) gives a very full autecological account, and

detailed notes need not therefore be given in the present work.

The plant is of rhizomatous habit like *Sparganium erectum*, but more closely spaced and of different shoot morphology. The leaf sheaths enfold the hollow stem very tightly and are united (connate) at the back (Fig. 5, 4c); the blades stand out at intervals above the water surface. Dead leaves rot quickly, providing little shelter at the base of the plant.

This, the commonest of all species in disused reaches, has a wider ecological amplitude than *Sparganium*; it overlaps the range of the latter in depths of water from 18 ins. to 2 ft. and extends into the marsh zone on the other hand, but performance is poor at both extremes. It has been seen to survive (but not to flower) on old dry heaps of mud some years after dredging. This adaptability may account for its presence in the used reach of Blakemere, where (unlike *Sparganium*) it can spread outwards from the shore. Normally it is rooted to the bottom, but at Blakemere the outer fringe of the reedswamp is in fact a floating mat.

Animals find Glyceria far less hospitable than the Bur-reed. Not only is its spacing more dense, but the lack of loosely-sheathing leaf bases reduces both shelter and surface area underwater; the population is the same as that of Sparganium, but in lower numbers. In addition to the truly aquatic snails, Succinea and Zonitoides nitidus (not listed below) are found on the aerial parts.

SUMMARY

The introduction deals first with the reasons for undertaking this study, and previous work on the subject is mentioned. The physical and historical back-

ground of the Shropshire Union Canal is briefly described.

The methods used during the course of the investigation are dealt with in chronological order: three short reaches of the canal (one in use and two disused) were selected in N.W. Shropshire. Species of plants and animals (other than micro-organisms) were identified as far as was practicable from these localities and ecologically classified lists were compiled. The salient habitat factors were recorded, where possible quantitatively. Synecological studies of the plant communities included the preparation of vegetation maps in a short length of each selected reach, and of a "ladder transect" (a quantitative belt transect) across reach B. Studies of animal populations were mainly descriptive in terms of microhabitats but included the comparative sampling of two types of bottom sediment.

A convenient classification is given, with short comments, of the major habitat factors—state of repair, dimensions, flow, nature of bottom, pH and mineral content, light intensity, temperature, and biotic factors.

The three selected localities are compared and contrasted in terms of their physical character and their plant and animal populations. (In all three the content of lime and certain other minerals is high, pollution negligible):

- A. Blakemere reach: still in use and fully maintained, midstream depth 4 ft., slow but constant flow, periodic turbulence and scouring produced by barges, inorganic sediments of various grades; sparse flora of submerged aquatic plants (e.g. Potamogeton spp.), very little reedswamp; long and ecologically varied list of freshwater animals, indicating good aeration.
- B. Redwith/Maesbury Marsh reach: disused and little maintained, depth reduced to 3 ft. by fallen water level exposing gentle slumped-soil shore-lines, normally stagnant, bottom of organic mud; broad central zone of floating aquatic plants (e.g. Hydrocharis morsus-ranae, Lemna spp) fringed with reedswamp (Glyceria maxima) on both sides, zones of marsh plants above water line; moderate aeration results in shorter list of animals, mostly on plants.
- C. Redwith/Crickheath Wharf reach: disused, no maintenance, further fall in water level to less than 2 ft. depth, complete stagnation, organic mud bottom; full reedswamp cover (central zone of Sparganium erectum, marginal zones of G. maxima); over-choking and under-aeration cause lowest animal numbers, nearly all on plants.

Four water plants (Ceratophyllum demersum, Hydrocharis morsus-ranae, Sparganium erectum and Glyceria maxima) are discussed as animal microhabitats.

Four tables are given in the appendix: (1) an analysis of water samples at the three localities. (2) Comparative counts of animals in silt and organic mud. (3) and (4) Lists of vascular plants and invertebrate animals respectively, ecologically classified and annotated. A final note compares the molluscs listed in the present work with those found by Boycott and Oldham in 1936.

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REFERENCES

ARBER, A. (1920). Water Plants. Cambridge.

BOYCOTT, A. E., and Oldham, C. (1936). Mollusca of the western parts of the Shropshire Union

Canal. N.W. Naturalist, 11, 217-227.

Braun-Blanquet, J., Fuller, G. D., and Conard, H. S. (1932). Plant Sociology. New York.

Butcher, R. W., Pentelow, F. T. K., and Woodley, J. W. (1931). A Biological Investigation of the river Lark. Fisheries Investigation Series (Min. of. Ag. and Fish.), 3. LAMBERT, J. M. (1947). Biological flora of the British Isles: Glyceria maxima. J. Ecol., 34, 310-344.

MINNIKIN, R. C. (1920). Practical river and canal engineering. London.

PLYMLEY, J. (1803). General view of the agriculture of Shropshire. London.

POCOCK, R. W., and WHITEHEAD, T. H. (1948). The Welsh Borderland (Handbooks on the Regional Geology of Great Britain. H.M.S.O.). London.

RAISTRICK, A. (1953). A dynasty of ironfounders. London.

ROLT, L. T. C. (1958). Thomas Telford. London.

TANSLEY, A. G. (1953). The British Islands and their vegetation. Cambridge.
WILSON, E. A. (1952). The Shropshire Union Canal. Shropshire Magazine. March-July issues.

APPENDIX

In the lists given below, species have been named wherever possible; but for some records only the genus has been given, either because the animals concerned (e.g. Chironomus) were at a stage in their life history where closer identification was impossible, or because related species could not readily be separated in the field. In such cases—both in the following list and throughout the text—the generic name stands alone: to indicate whether one species (sp.) or more (spp.) is represented would often be a matter of guesswork. Total numbers of species cannot therefore be compared. The total number of records in each locality column gives its minimum species number, to which could be added n-1 representatives of each of the individual genera.

Names are given without authorities throughout the list and text. They are based on the

following sources:

Plants—CLAPHAM, A. R., TUTIN, T. G., and WARBURG, E. F. (1959). Excursion Flora of the British Isles. Cambridge.

Insects—Kloet, G. S., and Hincks, W. D. (1945). A check list of British insects. Stockport. Leeches - Mann, K. H. (1954). A key to the British freshwater leeches. Sci. Publ. Freshw.

Biol. Ass., 14.
Snails—MACAN, T. T. (1949). A key to the British fresh- and brackish-water gastropods. Sci. Publ. Freshw. Biol. Ass., 13; and ELLIS, A. E. (1946-7). Freshwater bivalves. Synops. Brit. Fauna, 4 and 5.

Other groups-Mellanby, H. (1953). Animal life in freshwater. London.

The identity of the British Velia sp. as V. caprai was pointed out by Mr. J. Clegg, who also drew attention to the taxonomic confusion in Hydra and Spongilla and advised against their specific determination. The beetles were identified by Mr. J. W. F. Balfour-Browne, the snails were checked by Mr. L. W. Stratton, and Eucrangonyx gracilis was named at the British Museum.

Table 1. Analysis of water samples (F.B.A.) for pH and certain ions, from the three localities studied. (Figures are given as parts per million.)

								alkalinity	
Locality	Ca++	Mg++	Na+	\mathbf{K} +	Cl'	SO₄″	NO3'N	as CaCO ₃	pН
A	34.0	2.1	6.8	4.4	12.4	22.0	0.6	76·5	7.5
В	56·o	8.5		3.6			0.16		8.2
$\tilde{\mathbf{c}}$	59.2	5.5	8.5		14.2	32.7	0.24	145.0	8.2
_	JJ -	55	- 5	J -		J- 1		- 13	-

Table 2. Counts of animals in two microhabitats at Blakemere reach (Fig. 4, A)—two samples in each.

(Those species marked † are not strictly bottom dwellers and as collections were made in October had probably descended from plants and upper layers of water for overwintering.)

		S	ilt	Organic mud		
		Ι	II	I	II	
Tubifex	 	 1	52			
Ephemera vulgata	 	 15	32			
Sialis lutaria	 	 2	4	3	_	
Pisidium	 	 13	14	8	3	
Sphaerium	 	 1	I	14	7	
Chironomus plumosus	 	 	2	5	6	
†Asellus aquaticus	 	 _	I	14	19	
†Eucrangonyx gracilis	 	 	1	24	II	
†Erpobdella octoculata	 	 _		2	I	
†Bithynia leachii	 	 _	_	8	4	
†Planorbis vortex	 	 _	—.	4		
†Noterus clavicornis	 	 	_	5	2	

Table 3. List of vascular plant species in the three localities (A: Blakemere reach, B: Redwith/Maesbury Marsh reach, C: Redwith/Crickheath Wharf reach), arranged alphabetically under "ecological" headings.

The headings are defined as follows:

Aquatic plants are those which rely solely on the water for their support, and grow either floating or submerged.

Reedswamp plants have their leaves and stems fully emergent, but are rooted in standing water.

Marsh plants grow in damp soil just above the normal water level, but liable to periodic flooding.

Frequencies have been allotted to each species in each station where they occur, according to the usual convention:

(c.)d. (co-) dominant		o. occasional						
a. abundant								
f. frequent		l. locally						
Aquatic plants:			A.	В.	C.			
free-floating:								
Hydrocharis morsus-ranae			r.	c.d.	0.			
Lemna minor			r.	$\mathbf{c.d.}$,o.			
Lemna polyrhiza			r.	f.	0.			
Lemna trisulca (submerged)			r.	a.	0.			

rooted:	n+\					
(floating leaves always preser	,			_	f.(l.d.)	
Nuphar lutea	• •	• •	• •	r.		
Potamogeton natans		• •	• •		f.(l.d.)	r.
(floating leaves sometimes pr				_		
Callitriche intermedia	• •	• •	• •	0.		
Luronium natans	• •	• •	• •	0.		
Potamogeton alpinus	• •	• •	• • •	r.		
Sparganium c.f. emersum		• •	···	о.		_
(floating leaves never present				_		
Callitriche hermaphrodition		• •	• •	r.	- (1.4.)	
Ceratophyllum demersum		• •	• •	_	o.(l.d.)	
Elodea canadensis	• •	• •	• •		0.	_
Potamogeton compressus	• •	• •	• •	о.	о.	
Potamogeton crispus	• •	• •	• •	r.	_	-
Potamogeton friesii	• •	• •	• •	r.	о.	r.
Potamogeton obtusifolius	• •	• •	• •	r.	_	
Potamogeton perfoliatus	• •	• •	• •	о.		
Potamogeton praelongus	• •	• •	• •	r.		
Ranunculus circinatus	• •	• •	• •	_	r.	
D 1						
Reedswamp plants:					_	_
Alisma plantago-aquatica	• •	• •	• •	r.	0.	0.
Butomus umbellatus	• •	• •	• •	<u></u>	0	r.
Carex acutiformis	• •	• •	• •	l.f.	l.a.	о.
Carex riparia	• •	• •	• •	1.f.	1.6	_
Eleocharis palustris	• •	• •	• •	r.	1.f.	0.
Equisetum fluviatile	• •	• •	• •	r.	l.f.	r.
Glyceria maxima	• •	• •	• •	l.f.	d.	a.(l.d.)
Menyanthes trifoliata	• •	• •	• •	_	r.	r.
Oenanthe fistulosa	• •	• •	• •	r.	0.	O. ,
Rumex hydrolapathum	• •	• •	• •	r.	о.	0.
Solanum dulcamara	• •	• •	• •	r.	0.	0.
Sparganium erectum	• •	• •	• •	_	f.	a.(l.d.)
Manch Mante.						
Marsh plants:				l.f.	f.	f.
Agrostis stolonifera	• •	• •	• •			
Angelica sylvestris	• •	• •	• • .	0.	o. f.	o. f.
Apium nodiflorum	• •	• •	••.	0.	f.	f.
Berula erecta	• •	• •	• •	0.		1.
Bidens cernua	• •	• •	• •	r.	r.	0.
Caltha palustris	• •	• •	• •	0.	0.	0.
Cardamine pratensis	• •	• •	• •	r.	0.	
Carex hirta	• •	• •	• •	r.	r. r.	r. r.
Carex otrubae	• •	• •	• •	r.		
Carex paniculata	• •	• •	• •	r.	0.	0.
Carex remota	• •	• •	• •	r.	r.	
Catabrosa aquatica	• •	• •	• •	r.		
Cirsium palustre	• •	• •	• •	r. —	o.	r.
Epilobium hirsutum	• •	• •	• •		r.	0.
Epilobium parviflorum	• •	. •	• •	r.	o.	r.
Equisetum arvense	• •	• •	• •	о.	f.	f. —
Equisetum palustre	• •	• •	• •		r.	
Filipendula ulmaria	• •		• •	f.	0.	r.
Galium palustre	• •	• •	• •	0.	f.	f.
*Glyceria fluitans	• •	• •	• •	0.	r.	r.
Hydrocotyle vulgaris	• •	• •	• •	r.	l.f.	r.
Iris pseudacorus	• •	• •	• •	r.	0.	0.
Juncus acutiflorus	• •	• •	• •	0.	0.	0.
Juncus articulatus	• •	• •	• •	о.	о.	о.

Juncus effusus	 	 r.		_
Juncus inflexus	 	 _	0.	0.
Lotus uliginosus	 	 r.	r.	r.
Lycopus europaeus	 	 0.	f.	f.
Lysimachia nummularia	 	 r.	0.	r.
*Mentha arvensis	 	 0.	f.	f.
Mimulus guttatus	 	 f.	о.	о.
*Myosotis scorpioides	 	 0.	f.	f.
Oenanthe crocata	 	 r.	0.	ο.
Phalaris arundinacea	 	 r.	\mathbf{f} .	f.
Polygonum persicaria	 	 r.	r.	r.
Potentilla anserina	 	 r.	ο.	о.
Rumex conglomeratus	 	 r.	0.	ο.
Scutellaria galericulata	 	 0.	f.	f.
Senecio aquaticus	 	 _	r.	
Stachys palustris	 	 r.	ο.	о.
Valeriana officinalis	 	 r.	r.	r.

^{*} These species are difficult to distinguish vegetatively from close relatives. The record for Glyceria fluitans may include some G. plicata, for Mentha arvensis some M. aquatica, and for Myosotis scorpioides some M. caespitosa.

Table 4. List of freshwater invertebrates collected from the three localities, arranged alphabetically within major groups under headings descriptive of their modes of life and methods of locomotion.

The headings are loosely defined as follows:

Agabus bipustulatus...

Dytiscus marginalis...

SKATERS Insects

"Swimmers" are able to propel themselves freely under water.

"Burrowers" have restricted movement in or over the surface of loose bottom sediments.

An animal, even in its immature stages, may not be rigidly confined to one of these classes.

В.

C.

Gerris				+	+	+
Hydrometra stagnorum				+	_	_
Velia caprai				+	+	_
Gyrinus marinus	• •	••	• •	+	+	+
Swimmers						
Worms						
Stylaria				+	+	+
Arachnids						
Argyroneta aquatica					+	+
Hydrarachna				+	+	+
Hygrobates			• •		+	+
Megapus					+	
Crustaceans						
Eucrangonyx gracilis				+	+	+
Insects						
Corixa				+	+	+
Ilyocoris cimicoides				+	+	_
Notonecta				+	+	
Triaenodes (larvae)				+	_	

[&]quot;Skaters" are those animals which move over the surface film.

[&]quot;Crawlers" have restricted movement over the surface of plants and stones, "Clingers" are sedentary upon them.

				<i>I</i>		
Haliplus lineolatus				+	+	_
Hyphydrus ovatus				÷	+	+
Laccophilus hyalinus				$\dot{+}$	<u>.</u>	+ + - + + + +
Noterus capricornis				<u>.</u>	+	+
Noterus clavicornis			• •	+	<u>'</u>	
Platambus maculatus				1	_	
Anopheles (larvae)			• •	T		
Chaoborus (larvae)		• •	• •		_	Ţ
Chironomus sp. (larvae oth	 ortho	n (C n)	•••	\	— + + + +	†
		-	umosus	, +	<u>†</u>	+
Culex (larvae)	• •	• •	• •	+	†	+
Dixa (larvae)	• •	• •	• •	+	+	+
Forcipomyia (larvae)	• •	• •	• •	+	+	
CRAWLERS AND CLINGERS						
Hydroids						
Hydra				+	+	_
_ '	• •	• •	• • •	,	1	7
Sponges						
Spongilla	• •	• •	• •	+	+	
Flatworms						
Bdellocephala punctata				+	+	+
Dendrocoelum lacteum			• • •	<u> </u>	+	<u> </u>
Planaria lugubris	• •	••	• •	÷	1	<u></u>
Polycelis nigra		• •	• •	1	+	T
	• •	• •	• •	,	T	т
Leeches						
Erpodella octoculata				+	+	+
Erpodella testacea				+	+	+
Glossiphonia complanata				+	 + + + +	
Glossiphonia heteroclita				+	+	+
Haemopis sanguisuga				+	+	
Helobdella stagnalis				+	+	+
Hemiclepsis marginata				_	<u> </u>	
Piscicola geometra				+	· ·	++ + + + +
TD)				÷		_
Snails				'		
				,		
Ancylus lacustris	• •	• •	• •	+	÷	+
Bithynia leachii	• •	• •	• •	+	+	+
Bithynia tentaculata	• •	• •	• •	÷	+	+
Hydrobia jenkinsii	• •	• •	• •	+		_
Limnaea auricularia	• •	• •	• •	+	+	_
Limnaea pereger	• •	• •		+	+	+
Limnaea stagnalis	• •	• •	• •	+	+	+
Physa fontinalis	• •	• •	• •	+	+	+
Planorbis albus		• •	• •	+	÷	+++ ++ +
Planorbis carinatus				+	+	+
Planorbis complanatus	• •			+	. + + +	+
Planorbis corneus				+	+	_
Planorbis crista	• 1•			_	+	_
Planorbis laevis				+	+	_
Planorbis vortex				+	+	+
Viviparus viviparus				+		
Crustaceans						
Asellus aquaticus	• •	• •	• •	+	+	+
Insects						
Aeshna grandis (nymphs)				+	+	
Coenagrion puellum (nym				+	÷	+
				+	+	+ + —
Agravlea (larvae)				<u>.</u>	<u> </u>	
Anabolia nervosa (larvae)				+	<u>'</u>	_
(()		. •	- •	•		

Cyrnus (larv	rae)						+	
		atus (la	arvae)			+		_
						<u> </u>		
					••			_
			,		• •			
					• •		_	_
					• •	T	_	_
					• •	_	+	_
Nymphula n	lympna	cata (arvae)	• •	• •	-	+	_
Anacaena III	mata	•••			• •	+	_	_
					• •	+	_	
Tabanus (la	rvae)	• •		• •		+	+	
ROWERS								
						.1.	· L	
			••	• •	• •	Ŧ	+	7
Tubifor		atus	• •	• •	• •	Ţ	+	Ţ
	• •	• •	• •	• •	• •	+	+	+
Anodonta cy	gnea					+	+	_
Pisidium						+	+	+
Sphaerium						+	+	+
sects								-
	ia (nyr	nnhe\						
				••	• •			
			-		••	Ţ		_
						Ţ	T	+
				• •	• •	+		
			,	• •	• •	+	+	+
i ipuia (larva	ae)	• •	• •		• •	+	+	+
	Limnephilus Limnephilus Limnephilus Limnephilus Phryganea (Polycentropi Cataclysta le Nymphula n Anacaena li Hydroporus Tabanus (la ROWERS Tabanu	Limnephilus flavico Limnephilus rhomb Phryganea (larvae) Polycentropus (larv Cataclysta lemnata Nymphula nympha Anacaena limata Hydroporus (=Gra Tabanus (larvae) ROWERS Torms Eiseniella Lumbriculus varieg Tubifex Tubifex Tubifex Tubifex Tubifex Tubifex Sphaerium Sphaerium Sphaerium Sphaerium Ssett Caenis horaria (nyr Ephemera vulgata Sialis lutaria (larvae Molanna angustata Chironomus plumo	Limnephilus extricatus (la Limnephilus flavicornis (la Limnephilus flavicornis (la Limnephilus rhombicus (la Phryganea (larvae) Polycentropus (larvae) Polycentropus (larvae) Cataclysta lemnata (larvae) Nymphula nymphacata (la Anacaena limata Hydroporus (= Graptody Tabanus (larvae) Tabanus (larvae) ROWERS Torms Eiseniella Lumbriculus variegatus Tubifex Lumbriculus variegatus Tubifex Sphaerium	Limnephilus extricatus (larvae) Limnephilus flavicornis (larvae) Limnephilus flavicornis (larvae) Limnephilus rhombicus (larvae) Phryganea (larvae) Polycentropus (larvae) Cataclysta lemnata (larvae) Nymphula nymphaeata (larvae) Anacaena limata Hydroporus (=Graptodytes) pic Tabanus (larvae) ROWERS Torms Eiseniella Lumbriculus variegatus Tubifex Limbriculus variegatus Pisidium Sphaerium Sphaerium Sects Caenis horaria (nymphs) Sialis lutaria (larvae) Molanna angustata (larvae) Chironomus plumosus (larvae)	Limnephilus extricatus (larvae) Limnephilus flavicornis (larvae) Limnephilus flavicornis (larvae) Limnephilus rhombicus (larvae) Phryganea (larvae) Polycentropus (larvae) Cataclysta lemnata (larvae) Nymphula nymphaeata (larvae) Anacaena limata Hydroporus (= Graptodytes) pictus Tabanus (larvae) ROWERS Tabanus (larvae) ROWERS Tabanus (larvae) ROWERS Tabanus (larvae) ROWERS Tubifex Lumbriculus variegatus Tubifex Lumbriculus variegatus Tubifex Lumbriculus variegatus Tubifex Lumbriculus variegatus Sectis Caenis horaria (nymphs) Sphaerium Sectis Caenis horaria (nymphs) Sialis lutaria (larvae) Molanna angustata (larvae) Chironomus plumosus (larvae)	Limnephilus extricatus (larvae) Limnephilus flavicornis (larvae) Limnephilus rhombicus (larvae) Phryganea (larvae) Polycentropus (larvae) Cataclysta lemnata (larvae) Nymphula nymphaeata (larvae) Anacaena limata Hydroporus (= Graptodytes) pictus Tabanus (larvae) ROWERS Tabanus (larvae) Lumbriculus variegatus Tubifex Lumbriculus variegatus Tubifex Disidium Sphaerium Sects Caenis horaria (nymphs) Ephemera vulgata (nymphs) Sialis lutaria (larvae) Molanna angustata (larvae) Chironomus plumosus (larvae)	Limnephilus extricatus (larvae)	Limnephilus extricatus (larvae)

Note:

It is of some interest to compare the molluscs recorded in the present work with those listed by Boycott and Oldham in 1936. There is a considerable measure of agreement between the lists. It should be pointed out that while their work covered many miles of canal, the present studies were confined to a few hundred yards at each locality. My station A lies just outside their stretch A on the Ellesmere branch; my B and C are within their B. For this reason new records are likely to be more significant than failure to confirm old ones. The most striking changes are in the Llanymynech branch, which was then still in intermittent use and relatively weedless. The ease of overlooking the larger bivalves, buried in mud, has been enhanced by the overgrowth of vegetation: some of them may still be there, undetected. All the additions are pulmonates, depending on aquatic plants. Ancylus lacustris, whose presence was suspected by Boycott and Oldham, has now been found in both branches. Planorbis albus has not been seem in the Ellesmere branch, although it is given as one of the commonest species in 1936. Sphaerium spp. and Pisidium spp. have not been identified to species in the present work.

Collected in 1936 only:

A
Ancylastrum (Ancylus) fluviatile
Limnaea palustris
Planorbis albus
Valvata cristata
Valvata piscinalis
Unio tumidus

Collected in 1958 only

Ancylus lacustris Planorbis laevis Anodonta cygnea B
Limnaea palustris
Viviparus (Paludina) viriparus
Andonta anatina
Dreissena polymorpha
Pseudanodonta sp.
Unio pictorum

Ancylus lacustris Physa fontinalis Planorbis complanatus Planorbis corneus Planorbis crista Planorbis laevis