THE HABITATS OF BRITISH EPHEMEROPTERA

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ABSTRACT

Forty-seven species of Ephemeroptera occur in Great Britain. This is many fewer than in Europe as a whole. During synoptic studies of freshwater ecosystems in Britain over 1000 different waters have been surveyed. Collections of zoobenthos were made at all sites and many included Ephemeroptera. A selection of the data have been analysed to describe quantitatively the habitats of British Ephemeroptera and the nature of the communities and ecosystems in which they do and do not occur. A small number of species are so rare that it is not possible to describe their habitats. Of the commoner species, some occur in a variety of waters, others in one particular type. The defining factors appear to be related to water flow, temperature regime, chemistry, exposure and other complex variables, some of them biotic. Association and other multiple analyses show that, although there are transitions, certain communities of Ephemeroptera can be defined. The value of the study in both the applied and the theoretical fields is discussed.

INTRODUCTION

This paper is an attempt to describe how the habitats of the British species of Ephemeroptera may be defined in quantitative terms, using data available from a large number of sites all over Great Britain. There is now, too, a considerable literature available on the ecology of the British Ephemeroptera covering their taxonomy (e.g. Macan 1949, 1950, 1951, etc.), distribution (e.g. Maitland 1965, Wise 1976), life cycles (e.g. Elliott 1967, Brittain 1972), food (e.g. Brown 1961) and general ecology (e.g. Minshall and Kuehne

1969). General descriptions of the habitat are included in many of these papers, but there is rarely any attempt to quantify these for individual species. The recent key to the nymphs of British Ephemeroptera by Macan (1979) summarises much of the available information and describes the habitat of each species in a general way.

METHODS

This study forms a small part of an extensive synoptic survey of the fresh waters of Great Britain, which is being carried out at present (Maitland 1979). The primary aim of this research is to provide a scientific background for the interpretation and classification of aquatic ecosystems in Great Britain, but there are a number of additional valuable facets to the work. These include the development of autecological and synecological studies of various important groups of organisms such as Ephemeroptera.

The initial phases of this research, which have mostly been completed, are desk studies aimed at describing the number and variety of fresh waters (Smith and Lyle 1979), the range of species of plants and animals which inhabit them (e.g. Maitland 1977), and the published literature relating to freshwater sites and organisms in Great Britain. Thus a comprehensive background is now available for detailed field studies of the type described below. For example, it is now known that the total number of standing waters in Great Britain is approximately 60,000, and of running waters approximately 8,000. About 3,800 species of freshwater animals (excluding Protozoa) occur in Great Britain, 47 of which are Ephemeroptera.

The field data for this paper orignate from three separate synoptic surveys of British fresh waters. The first of these followed a decision by the Nature Conservancy to make a thorough scientific appraisal of ecosystems of all types over the whole of Great Britain, in order to identify as certainly as possible those sites of outstanding value (Ratcliffe 1977). The initial selection of freshwater sites was based on a desk study of existing information on sites of all kinds. These were then classified according to size, depth and trophic status and most were visited between 1968 and 1970 to collect new data.

In 1974, a synoptic survey of the fresh waters of Shetland was initiated. Following a comprehensive study of topographical (1:63, 360) and geological maps, which located 1,596 standing waters and 1,970 running waters, a principal component analysis was carried out using the correlation matrix derived from values of a number of measured variables (e.g. altitude, size, catchment size, etc.). This analysis gave 16 clusters (plus 14 aberrant sites) and 14 clusters (plus 9 aberrant sites) for standing and running waters respectively. For field study a random sample of three sites from

each cluster together with the aberrant sites gave a total of 113 sites which were visited for sampling during the spring and autumn of 1974.

A third synoptic study was carried out during 1977 and 1978, on this occasion to survey the fresh waters of the Tayside Region of central Scotland. Initially an analysis and count of all the waters shown on 1:50,000 maps of the area concerned was carried out. This gave a total of about 950 standing waters and 10,300 stream segments. These were then classified using the following variables: geology (base poor, intermediate, base rich), size (five categories) and altitude (four categories). For field study, random selections of two sites from each class were made and this gave a total of 125 sites which were visited for sampling in the spring and autumn of 1977. A further 19 sites were studied during 1978.

In addition to comparable map information assembled for all the sites mentioned above, standard techniques were used in the field to collect data or samples covering a wide number of variables. These included physical features (e.g. substrate type, current speed, etc.), water chemistry (samples were deep frozen and taken back to the laboratory for the analyses of main ions), phytoplankton, macrophytes, zooplankton and zoobenthos. Samples of the latter were made in shallow water with a standard hand-net for a known period of time using a consitent collecting technique (Maitland 1966). In deeper water, an Ekman grab or a small dredge was used. These samples were preserved in the field using 4% formaldehyde and then sorted, counted and identified in the laboratory using, for Ephemeroptera, mainly the keys provided by Macan (1949, etc; 1961).

RESULTS

Even for a small group like Ephemeroptera it is only possible within the confines of this short paper to give a brief outline of some of the results of these studies and how they are being interpreted. As explained above, the main objectives of the overall programme are a comprehensive interpretation and classification of aquatic ecosystems in Great Britain using physical, chemical, botanical and zoological features. A computer study is at present being organised with these objectives. Selected data, such as those for Ephemeroptera, are also being subjected to a variety of individual analyses.

General Ephemeroptera Habitats

Although entirely aquatic for most of their life history, Ephemeroptera as a group are very versatile and occupy a wide range of freshwater habitats, both running and standing. However,

Table 1. The percentage occurrence of Ephemeroptera at freshwater sites in Great Britain as a whole, and in two specific areas of Great Britain - Tayside and Shetland.

Area	Number of Ephemeroptera Species Recorded															Number of Sites
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Great Britain (38 species)	19.8	18.5	15.4	16.4	9.7	8.1	2.7	2.7	2.7	1.7	1.0	0.3	0.3	0.7	0	300
Tayside (28 species)	11.2	19.2	14.4	12.8	8.0	14.4	6.4	7.2	2.4	2.4	0.8	0.8	0	0	0	125
Shetland (6 species)	56.9	31.9	11.2	0	0	0	0	0	0	0	0	0	0	0	0	116

they are not found at all under certain conditions and it is very relevant to an understanding of the general ecology of the group to see from what kinds of habitats they appear to be excluded. Table 1 shows the general occurrences of Ephemeroptera among sites examined during the three surveys described above. It can be seen that there is a considerable difference between Great Britain and Tayside on the one hand, and Shetland on the other.

Only six species were recorded from Shetland, and most of the sites studied (56.9%) contained no Ephemeroptera. The majority of the others (31.9%) included one species, though at a number of sites (11.2%) two species occurred. None of the sites ever included more than this. In Tayside and Great Britain as a whole, however, many more species were recorded (28 and 38 respectively) and relatively few sites contained no Ephemeroptera (11.2 and 19.8% respectively). In Tayside 34.4% and in Great Britain 20.2% of the sites contained five or more species, and in both areas sites with ten or more species occurred.

An analysis of the characteristics of sites in Tayside and Great Britain which have no Ephemeroptera shows that the majority fall into one of the following four categories: (1) Small water bodies of of any type which appear to be temporary and thus liable to periodic desiccation. (2) Estuarine reaches of running waters or standing waters sufficiently near the coast to have saline water. (3) Nutrient-poor upland waters in very exposed areas. (4) Nutrient-rich lowland waters subject to eutrophication and pollution. Very few natural waters outside these categories do not have Ephemeroptera, except in island areas like the Shetlands, where, apparently the extreme exposure to wind renders many habitats unavailable to this poorly flying group.

Most of the sites with large numbers of Ephemeroptera are in medium or low altitude areas of base rich geology away from dense human populations or intensive agriculture. Characteristically a wide variety of microhabitats are available at each site, a majority of which are running waters.

The 47 species of Ephemeroptera recorded from Great Britain are given in the check list included in Table 2. The numerical data in this table are based on the results from most of the sites in the Tayside and Great Britain surveys discussed above (a total of 425 sites - 216 standing and 209 running waters) together with (for the sake of completeness) data from the literature for a few species which were not recorded during the present surveys. It can be seen that there is a wide range of occurrences, from common species like *Baetis rhodani*, *Ephemerella ignita* and *Caenis horaria* which were found at about 20% or more of the sites examined, to rare species such as *Baetis digitatus* and *Arthroplea congener* which did not occur at any of the 425 sites included in the table and have only ever

Table 2. A check list of the British Ephemeroptera and their occurrence in standing (S) or running (R) water. This is expressed as a percentage of the total number of sites (N) at which each species was found. The data refer to collections from Great Britain (including Tayside), together with a few records for the less common species taken from the literature and included in the total number of sites*.

Family		Genus	Species	S	R	N
SIPHLONURIDAE	1.	*Siphlonurus*	*armatus* Eaton	50	50	4*
	2.		*lacustris* Eaton	93	7	15
	3.		*linnaeanus* (Eaton)	60	40	5*
	4.	*Ameletus*	*inopinatus* Eaton	29	71	17
BAETIDAE	5.	*Baetis*	*fuscatus* (L.)	0	100	7
	6.		*scambus* Eaton	4	96	53
	7.		*vernus* Curtis	7	93	42
	8.		*buceratus* Eaton	0	100	11
	9.		*rhodani* (Pictet)	6	94	109
	10.		*atrebatinus* Eaton	0	100	4
	11.		*muticus* (L.)	0	100	66
	12.		*niger* (L.)	6	94	18
	13.		*digitatus* Bengtsson	0	100	1*
	14.	*Centroptilum*	*luteolum* (Muller)	35	65	79
	15.		*pennulatum* Eaton	0	100	8
	16.	*Cloeon*	*dipterum* (L.)	79	21	66
	17.		*simile* Eaton	89	11	54
	18.	*Procloeon*	*bifidum* Bengtsson	11	89	18
HEPTAGENIIDAE	19.	*Rhithrogena*	*semicolorata* (Curtis)	1	99	80
	20.		*germanica* Esben-Petersen	0	100	3*
	21.	*Heptagenia*	*sulphurea* (Muller)	0	100	17
	22.		*longicauda* (Stephens)	0	100	6*
	23.		*fuscogrisea* (Retzius)	50	50	2*
	24.		*lateralis* (Curtis)	3	97	34
	25.	*Arthroplea*	*congener* Bengtsson	0	100	1*
	26.	*Ecdyonurus*	*venosus* (Fabricius)	6	94	32
	27.		*torrentis* Kimmins	6	94	17
	28.		*dispar* (Curtis)	29	71	45
	29.		*insignis* (Eaton)	0	100	3*
LEPTOPHLEBIIDAE	30.	*Leptophlebia*	*marginata* (L.)	94	6	35
	31.		*vespertina* (L.)	94	6	35
	32.	*Paraleptophlebia*	*submarginata* (Stephens)	10	90	10
	33.		*cincta* (Retzius)	0	100	5*
	34.		*tumida* Bengtsson	0	100	5*
	35.	*Habrophlebia*	*fusca* (Curtis)	0	100	10
EPHEMERELLIDAE	36.	*Ephemerella*	*ignita* (Poda)	7	93	84
	37.		*notata* Eaton	0	100	8
POTAMANTHIDAE	38.	*Potamanthus*	*luteus* (L.)	0	100	4*
EPHEMERIDAE	39.	*Ephemera*	*vulgata* (L.)	0	100	3*
	40.		*danica* Muller	27	73	15
	41.		*lineata* Eaton	0	100	5*
CAENIDAE	42.	*Brachycercus*	*harrisella* Curtis	0	100	3*
	43.	*Caenis*	*macrura* Stephens	0	100	6*
	44.		*moesta* Bengtsson	56	44	72
	45.		*robusta* Eaton	50	50	6
	46.		*horaria* (L.)	74	26	81
	47.		*rivulorum* Eaton	0	100	27

been recorded once each in Great Britain - the former from the River Frome (Macan 1979) and the latter at Stanmore, Middlesex (Kimmins 1954).

Table 2 shows that there are no species which occur exclusively in standing waters, though there are a few which are found mainly in this habitat (e.g. *Leptophlebia marginata, L. vespertina* and *Cloeon simile*). On the other hand, many species appear to occur only in running water (e.g. *Baetis muticus, Caenis rivulorm* and *Heptagenia sulphurea*) or mainly so (*Baetis scambus, B. rhodani* and *Ephemerella ignita*) and indeed well over half of the British species can be described as showing a distinct preference for the lotic environment.

Ephemeroptera Associations and Ecodata

In order to describe the associations among different species in communities, Fager (1957) has suggested an index which relates the probabilities of the joint occurrence of any two species to the sum of their total occurrences This index does not consider negative associations and is a useful preliminary step to the delimitation of communities. An association analysis of the affinities among the 38 species of Ephemeroptera occurring at sites surveyed during the Great Britain survey described above has been carried out and the results are shown in Figure 1.

It can be seen from this figure that there are several strong groupings among the network of associations produced from the analysis. Two of these are large: one centred around *Baetis scambus/ Ephemerella ignita/B. rhodani*, the other around *Baetis buceratus/ B. niger*. Table 2 shows that both these groupings are dominated by running water species. There are two smaller groupings evident in Figure 1: one associated with *Leptophlebia vespertina/ L. marginata*, the other with *Cloeon simile/Caenis horaria*. From Table 2 it can be seen that these groupings are dominated by standing water species. The species linking these standing and running water groupings (e.g. *Ecdyonurus dispar* and *Caenis robusta*) are commonly found in both standing and running waters (Table 2).

Using the extensive background information available from the large number of sites surveyed during this study it is possible to define fairly clearly the conditions in which each species occurs Presumably these can be considered as associated with their tolerance limits for at least some factors. As an example, the values for altitude of the common Ephemeroptera occurring in Tayside are shown in Figure 2. It can be seen that the sites at which *Ameletus inopinatus* occurs have a mean altitude of 517 m, but that this species can occur at a considerable range around this. At the other end of the scale, *Ephemerella notata* occurs at sites which have a mean altitude of only 40 m and a range around this of 31 m.

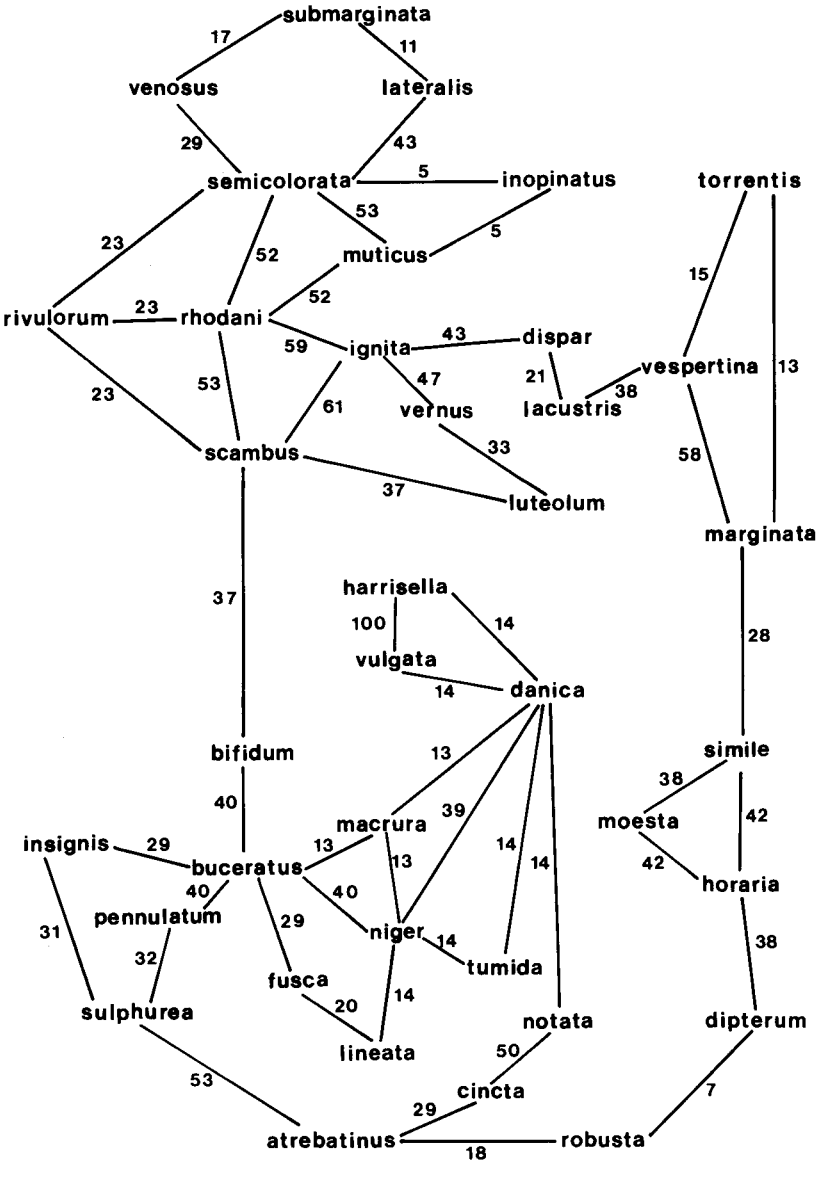

Figure 1. An association network for Ephemeroptera recorded during a survey of 300 sites (150 standing and 150 running waters) in Great Britain. The association values (indicated by the figures between species) were obtained as recommended by Fager (1957) and the network has been produced by linking each species with the two others with which it is most highly associated.

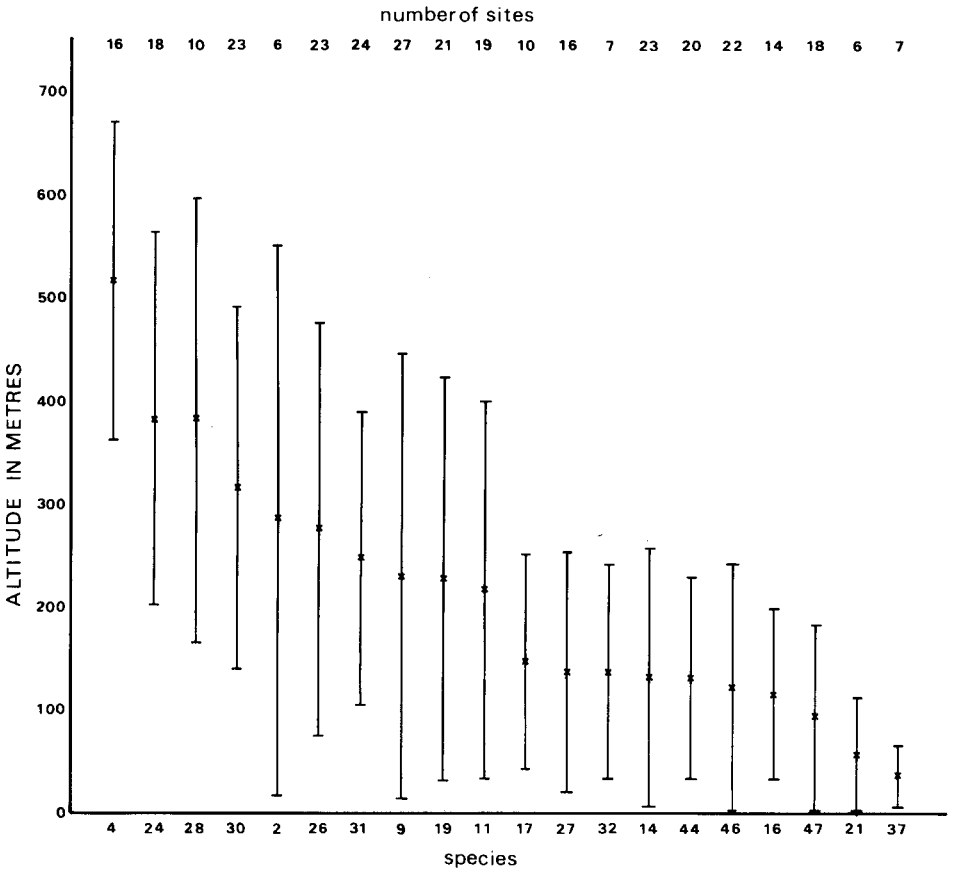

Figure 2. The means and standard deviations of the altitudes of sites in the Tayside Region at which common species of Ephemeroptera occurred. Only those occurring at six or more sites are figured. The numbers at the top of the figure refer to the number of sites; the numbers at the bottom to the species listed in Table 2.

If the altitude values for the species shown in Figure 2 are related to the species associations given in Figure 1, it can be seen that the running water *scambus/ignita/rhodani* and standing water *vespertina/marginata* groupings are dominated by high altitude species. In contrast, the running water *buceratus/niger* and standing water *simile/horaria* groupings are dominated by low altitude species. Thus it seems that the ecodata concerned are relevant to defining the nature of the communities of Ephemeroptera involved and that further more sophisticated, multivariate analyses are likely to be profitable.

Species Ecodata and Econiches

It will be clear from the methodology and the results described so far that a large data bank of information on individual Ephemeroptera and their habitats in Great Britain is now available. In this short paper it is only possible to indicate by example how these ecodata may be used in autecological studies. A single species has been selected for this purpose: *Cloeon simile*. It has already been shown that this is primarily a standing water species (Table 2), associated over Great Britain as a whole with *Caenis horaria* and *Caenis moesta* (Fig. 1) and occurring at low to medium altitudes (Fig. 2).

The distribution of *C. simile* at sites surveyed within Great Britain (excluding the Tayside and Shetland surveys) is indicated in Figure 3. It is clearly a widespread species. Even in Shetland where Ephemeroptera are relatively uncommon it occurred at 16 out of the 66 standing water sites studied: it was never found in running water there. The characteristics of the sites at which it occurred are indicated in Table 3 and these are contrasted there with the means of all the standing waters surveyed. The differences between the two sets of means are assumed to indicate something of the preferences of the species concerned, though naturally the casual relationships are not apparent.

At all the lochs on Shetland at least three samples (usually more) of zoobenthos from the dominant microhabitats were collected. The general results from the 16 lochs in which *C. simile* occurred are shown in Table 4. It is clearly a littoral species and occurred in none of the profundal samples collected. Within the littoral zone it occurred in a variety of microhabitats and apparently showed no special preference for one particular type of substrate. However, when the data for abundance are examined (Fig. 4) it is very clear that high densities occurred only in shallow water in areas of fine silt.

DISCUSSION

One of the important and original aspects of the surveys described in this paper, especially those of Shetland and Tayside is that they have attempted a more or less complete coverage of all the types of water body occurring in the areas concerned. Thus ditches, temporary pools, and high altitude waters (normally ignored in ecological surveys in Great Britain) have been included. The data therefore provide a firm basis for the assessment of the habitat of any one species. The large total number of sites which have now been surveyed is also relevant here.

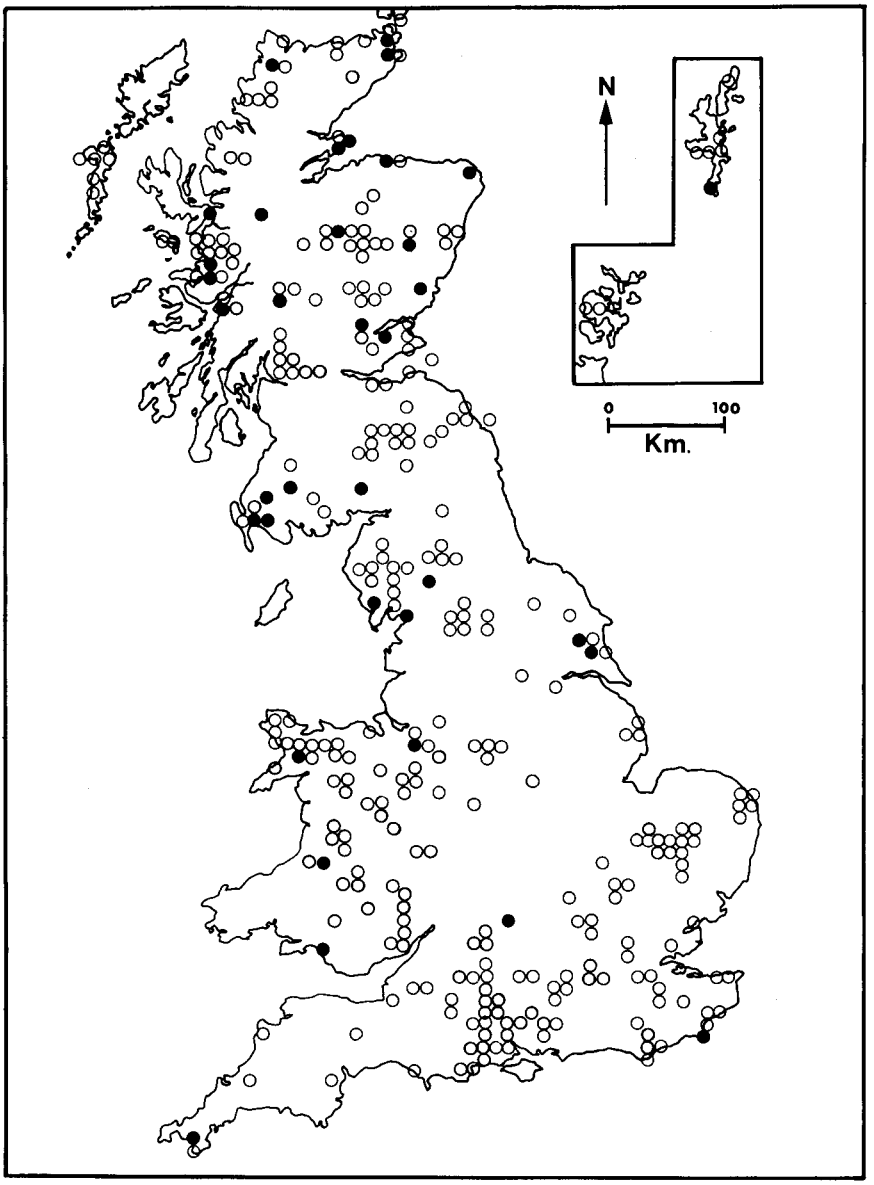

Figure 3. The occurrence of *Cloeon simile* at freshwater sites surveyed in Great Britain. Positive records are indicated by closed symbols.

Table 3. Sample ecodata for *Cloeon similie* on Shetland. This species does not occur in running waters there so the data refer to standing waters only.

	Feature	Background		+ve Occurrences	
		Mean	S.D.	Mean	S.D.
1.	National Grid Reference	4184/11773	0103/0243	4328/11599	0076/0161
2.	Surface Area (ha)	8.9	15.9	17.5	27.6
3.	Altitude (m)	60.2	46.1	39.0	28.2
4.	Catch. Altitude (m)	135.5	111.8	121.6	80.4
5.	% Arable	7.8	21.4	5.6	14.1
6.	% Forest	0	0	0	0
7.	% Peat	36.6	42.6	21.8	30.9
8.	% Water	3.6	6.7	6.9	8.6
9.	Nos. People	1.3	3.6	8.3	28.4
10.	Area (ha)	112.3	178.5	227.4	435.3
11.	Rainfall (cm)	110.4	10.7	103.1	11.3
12.	Distance from Sea (km)	0.95	0.76	0.80	0.81
13.	% Weed Cover	36.2	32.3	38.9	29.2
14.	Mean Depth (m)	1.12	1.47	1.92	1.89
15.	Maximum Depth (m)	3.12	4.29	4.16	5.34
16.	pH	6.6	1.6	6.8	1.0
17.	Calcium (mg/l)	8.1	8.4	7.8	5.1
18.	Alkalinity (mg/l)	26.4	26.2	23.4	19.4
19.	Phosphorus (mg/l)	0.027	0.083	0.070	0.040
20.	% Shore with Trees	0	0	0	0
21.	Water Colour (Hazen Units)	53.1	62.7	29.0	20.4
22.	Suspended Solids (mg/l)	0.025	0.032	0.012	0.014
23.	Sodium (mg/l)	46.1	15.6	50.5	18.9
24.	Conductivity (μS)	295.9	121.1	304.4	130.9

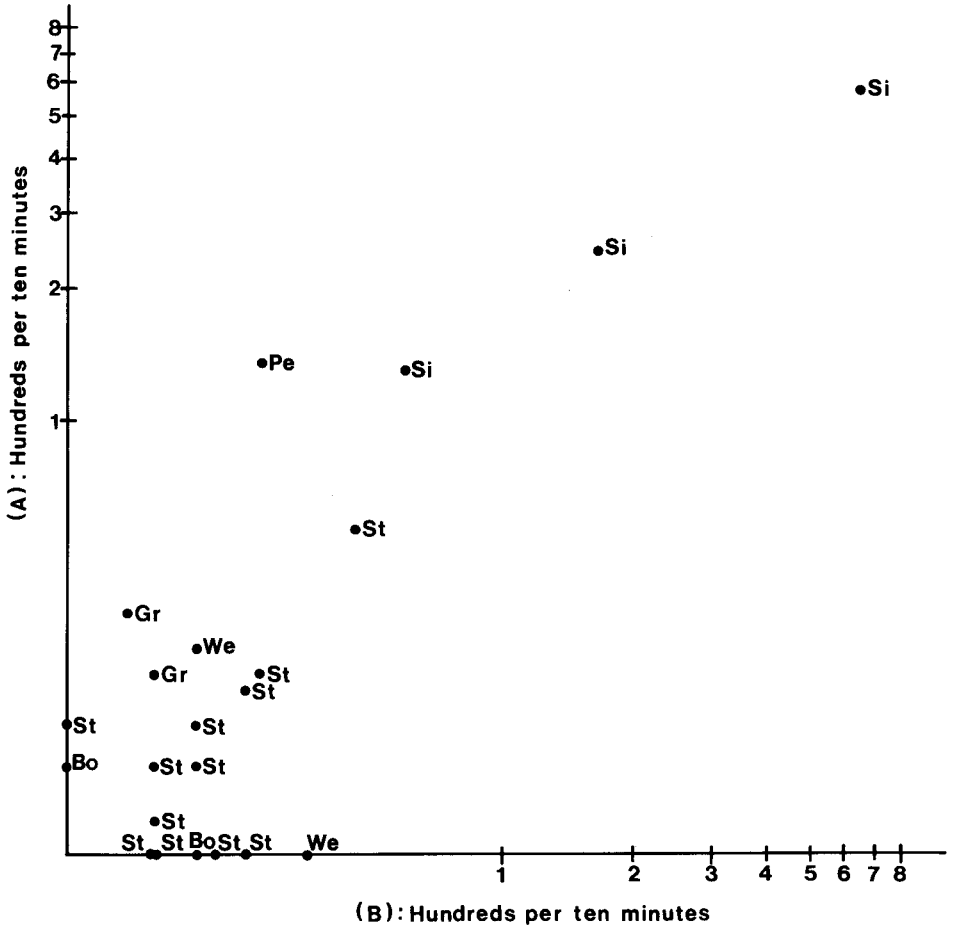

Figure 4. Plots of the numbers of *Cloeon simile* (per 10 minute collection) in pairs of samples (A and B) taken from various substrates in lochs on Shetland (Si: silt; Pe: peat; Gr: gravel; St: stones; Bo: boulders; We: weed). Only those pairs in which *C. simile* occurred in at least one sample are plotted.

Though not mentioned in the results presented above, it must be remembered that data on other aspects of the biota of these sites are also available. These include information on algae, higher aquatic plants, zooplankton and the other zoobenthos. Thus for example, an association diagram for the common Shetland zoobenthos, similar to that for the British Ephemeroptera (Fig. 1) is now available (Maitland 1979). In it, the association of the Shetland

Ephemeroptera with the other zoobenthos is clearly seen. *Baetis rhodani* is a characteristic memeber of the running water community there, and *Cloeon simile* and *Caenis horaria* of the standing water one.

This brief account indicates the strategy and tactics of the synoptic work at present in progress. The amount of data potentially available offers scope for a wide variety of analyses in many different fields. It is already evident that considerable interest has been generated by the project and that demands from other scientists and user organisations are likely to increase.

It is the eventual aim of the study that all parts of the data bank which are relevant to synoptic analyses will be computerised. So far, only selected portions of the data have been stored and analysed by computer, mainly with specific objectives in mind. Currently, the bulk of the data are stored by conventional manual filing systems, largely on a site basis using standard pro formas, or increasingly, edge notched cards. This system has proved invaluable for a number of purposes and will be maintained even after computerisation. Its prime use is the speed and ease with which full site information may be retrieved for examination.

Beyond the value of access to information on individual sites lies the goal of a full synopsis of British fresh waters. A major part of this will be comprehensive classification system covering the full range of aquatic habitats in Great Britain. The evidence so far, from both running waters (e.g. Maitland 1966) and standing waters, indicates that the framework for such a classification will be an arbitrary one - its limits bound by the range of fresh waters

Table 4. The occurrence of *Cloeon simile* in samples taken from different microhabitats in those Shetland lochs in which this species occurred.

	Profundal	Littoral			
	Silt	Silt/ Peat	Sand/ Gravel	Stones/ Boulders	Weed/ Silt
No. of samples	16	10	8	38	4
No. with *C. simile*	0	8	4	22	3
% with *C. simile*	0	80	50	58	75
C. simile per 10 mins: mean	0	199.0	6.5	8.2	14.0
: S.D.	0	236.8	9.6	11.9	11.4

occurring in Great Britain, its classes defined partly by natural boundaries and partly by convenient ones proposed by limnologists. This is because there appears to be a more or less complete transition from one extreme type of water to another with intermediate types occurring throughout the range.

Synecological studies of animal and plant communities appear to confirm that a critical definition of discrete communities is not possible, and rather that a continuum exists along which there are important, probably stable, nodes which can be described in detail. Apart from the scientific interest and value of synecological studies, the accurate description and quantification of the natural communities has a number of applied values, particularly in relation to impact studies.

The data derived from the studies in synoptic limnology described offer a promising field for autecological research. The definition of natural species niches and apparent tolerances to a wide variety of environmental parameters is a relatively straightforward exercise from the comprehensive data available, and such analyses lead naturally to comparisons of the ecological requirements of different species. Again, such studies have both pure and applied values - e.g. in the case of a species proposed for introduction to any area it is invaluable to have detailed figures for its natural range of habitat.

Finally, the predictive value of synoptic limnology must be emphasised, especially in the fields of conservation and resource management. One of the realistic developments of the synecological and autecological studies described above is that it should eventually be possible to predict, for example, the type of community found in any water whose geographic position and main physical characters are defined. Likewise the probability of a particular animal or plant species thriving at a new site or an existing site under new conditions should be estimated. Naturally, as in all biological situations, such predictions could never be completely accurate, nevertheless they must represent one of the most promising methods available to ecologists.

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RESUME

Quarante-sept espèces d'éphéméroptères se rencontrent en Grande-Bretagne, ce qui est beaucoup moins que dans l'ensemble de l'Europe. Au cours d'études synoptiques d'écosystèmes d'eau douce de l'Angleterre, on a analysé plus de mille plans d'eau. On a recueilli des échantillons de faune zoobenthique à tous les endroits et plusieurs contenaient des éphéméroptères. On procéda ensuite à l'analyse de données sélectionnées pour faire une description quantitative des habitats des éphéméroptères britanniques ainsi que de la nature des populations et des écosystèmes au sein desquelles ils vivent ou non. Quelques espèces sont si rares qu'il n'est pas possible de décrire leur habitat. D'autres espèces plus communes se recontrent dans toutes sortes d'eaux, d'autres encoure dans un seul type particulier. Les facteurs déterminants paraissent liés au courant, à la température, à la composition chimique, à l'exposition de l'eau et à d'autres variables complexes, certains de types biotiques. L'association ainsi que d'autres analyses multiples montrent que, malgré l'existence de transitions, certaines populations d'éphéméroptères peuvent être définies. L'auteur parle de la valeur de ses recherches dans le domaine des sciences pures et des sciences appliquées.

ZUSSAMENFASSUNG

In Groβorittannien gibt es 47 Ephemeropterenarten. Das sind viel weniger als in Europa insgesamt. Während synoptischer Studien von Süβwasser Ökosystemen in England wurder über tausend verschiedene Gewässer überprüft. An allen Stellan wurden zoobehtische Proben genommen und viele davon enthielten Ephemeropteren. Eine Auswahl von Daten wurde analysiert, um quantitativ die Heimat der britischen Ephemeropteren und die Art der Kommunitäten zu beschreiben, in welchen sie sich befinden oder nicht auftreten. Eien klein Anzahl von Arten ist so selten, daβ es nicht möglich wäre, ihre Beheimatung darzustellen. Von den gewöhnlicheren Arten treten einige in verschiedenartigen Gewässern auf, andere nur in einem bestimmten Typ von Wasser. Die definierenden Faktoren scheinen in Beziehung zu stehen zu Wasserfluβ, vorherrschender Temperatur, Chemie, Lage und anderen komplexen Variablen, von denen einige biotischer Art sind. Assoziation und andere multiple Analysen zeigen, daβ, obwohl es Ubergänge gibt, einige Ephemeropterengemeinschaften definiert werden können. Der praktische unde theoretische Wert der Untersuchung wird in der vorliegenden Arbeit erörtert.

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