ENVIRONMENT AGENCY

A SCOPING STUDY ON THE EPHEMEROPTERA OF SOUTHERN CHALK STREAMS

A Report to the Environment Agency

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Statement of Use
This short scientific review was commissioned to further a 'LEAP' action to investigate factors which potentially could contribute to an alleged decline in Ephemeroptera within the Avon catchment. The review has relevance to other chalk systems within the UK and should significantly contribute to the Agency's knowledge, enabling future monitoring to be focused on specific aspects which influence this group.

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EXECUTIVE SUMMARY

This scoping study was undertaken at the request of the Environment Agency, following expressions of concern from fishermen that some species of Ephemeroptera (mayflies) appear to have declined on the R.Wylye and on the upper reaches of the Hampshire Avon. The purpose of this scoping study is to provide a short scientific review of the mayfly fauna of southern chalk streams.

Forty nine species of mayflies are known to occur in Britain. The status of two additional species is uncertain. An appraisal of the RIVPACS III data-base yielded 42 high quality sites on southern chalk streams. Examination of the species lists for these sites confirmed that over 50% of the British species occur on southern chalk streams. Information is provided on the seasonal occurrence of the different species and their frequency of occurrence at the 42 sites.

Between four and fifteen species of mayflies were recorded per site, with an arithmetic mean of 9.12 per site. The most species-rich sites (12 or more species) occurred between 10 and 50 km from stream source. They included sites on such well known rivers as the R. Frome (Dorset), R. Itchen, R. Lambourn, Moors River (Dorset) and R.Test. The study includes information on the longitudinal occurrence of each species.

The RIVPACS III data-set also includes information on the log. categories of abundance of each family of mayfly in spring, summer and autumn, based on the standard RIVPACS pond-net samples. This provides a useful general guide on whether a given family is scarce, common or abundant in a given season. Members of the Baetidae were found to be important components of the mayfly fauna in spring, summer and autumn, but were particularly abundant at most sites in summer. Ephemerellidae were also very abundant at most sites in summer.

Notes are provided on the flight period and life cycles of each species, as far as these are known. The life cycles of some species show flexibility and some members of the Baetidae are capable of having several generations in a year. Hence, interpretation of the life cycle can pose problems.

Information on the habitats, habits and feeding behaviour of the larvae demonstrates that a wide variety of different habitats and food resources are exploited by mayfly larvae.

A consideration of the potential impact of flow regime on larval populations suggests that if changes in the flow regime affect the habitats and food resources within a stream, then there are likely to be consequences for the mayfly fauna. However, different members of the mayfly fauna may respond in different ways, given their various adaptations.

Low flows are of particular interest at present, and several short term studies on chalk streams, together with one long-term study on the R.Lambourn in the 1970's, are starting to provide scientific data on the way in which different components of the

mayfly fauna appear to respond to the discharge regime. Some provisional findings for the Baetidae, Ephemerellidae and Ephemeridae are given below.

A nine-year study on the R. Lambourn provided evidence that in early June, densities of larvae in the Baetidae (which may have included up to six species) were low in drought years (~500 m^{-2}) compared with some years with high discharge when densities were ~5,000 m^{-2}.

Densities of larvae in the Ephemerellidae (*Ephemerella ignita* only) were higher in the year following a drought.

Densities of larvae in the Ephemeridae (*Ephemera danica* only) did not appear to be related to the prevailing discharge regime in the R. Lambourn. Instead, cool damp conditions during the period of flight activity in May/June of one year resulted in very low larval densities of the next generation in December of that year. Over the next three generations (at intervals of two years), larval densities increased progressively in the December following oviposition.

Studies commissioned by the Environment Agency on a number of chalk stream sites first examined in the 1970's may soon provide further information on the response of mayflies to the flow regime.

Some chalk streams may be subject to organic pollution as a result of sewage effluent, fish farm effluent or farm wastes. Low levels of organic enrichment may not have adverse effects on the mayfly fauna, but more severe cases of organic pollution will result in the progressive elimination of the more sensitive species. Environment Agency biologists are well-versed in the detection of organic pollution using standard methodologies.

Although the time spent in the aerial phase of the life cycle is only a small fraction of the total life span, it is crucial for successful reproduction and dispersal. Despite predation and parasites, the subimagos and imagos normally find suitable shelter and terrain markers for swarming, thereby ensuring that mating and subsequent oviposition is successful. However, as previously indicated for *Ephemera danica*, there is circumstantial evidence that inclement weather is capable of disrupting this critical phase of the life cycle.

KEY WORDS

Chalk stream; Ephemeroptera; mayflies; distribution; low flows; pollution

1. INTRODUCTION

1.1. Background to the study

The need for this scoping study was identified during a meeting between staff from the Environment Agency (EA) and the Institute of Freshwater Ecology (IFE) which took place at the River Laboratory in late August 1997. EA staff indicated that there had been expressions of concern from fishermen, alleging a decline in Ephemeroptera (mayflies) within some tributaries of the Hampshire Avon (R.Wylye & Upper Avon). In particular, concern focused on poor hatches of mayflies in the family Baetidae.

As a result of the initial meeting, the IFE was asked to develop some proposals under three separate headings:

a). A short scientific review of the mayfly fauna of southern chalk streams.

b). An appraisal of a very limited data-set held by the IFE on the mayfly larvae of one or two sites on the R.Wylye and Upper Avon for the 1970's, to determine whether there was merit in repeating these surveys.

c). An outline proposal for the long-term monitoring of chalk stream mayflies, with particular regard to the emergent stage of the life cycle.

Following a consideration of these outline proposals from the IFE, the EA requested separate quotations for items a). and c). Funding for a short scientific review of the mayfly fauna of southern chalk streams (item a) was approved in November 1997 and forms the subject of the present report. The agreed specification for the review is given in Appendix 1.

1.2. The British Ephemeroptera (mayflies)

Worldwide, the insect order Ephemeroptera is quite small, with something in excess of 2,000 known species in approximately 200 genera and 19 families (Brittain, 1982). Until recently, the British list included 48 species in eighteen genera and just eight families (Elliott, Humpesch & Macan, 1988). However, two of the species on this list, *Arthroplea congener* Bengtsson and *Heptagenia longicauda* (Stephens), have not been recorded since the 1920's/1930's and may no longer occur in the British Isles (Bratton, 1990). Refer to Elliott, Humpesch & Macan (1988) for the checklist of 48 British species.

In the last few years, examination of specimens from many streams and rivers in Great Britain has revealed three additional species previously recognised on mainland Europe, but unknown in Britain. These are *Caenis pseudorivulorum* Kieffermuller (Gunn and Blackburn, 1997) and *Caenis beskidensis* Sowa (Gunn and Blackburn (in press)) in the family Caenidae and *Electrogena affinis* (Eaton) (Blackburn, Gunn and Hammett (in press)) in the Heptageniidae. Thus, at present, 49 species of mayflies are known to occur in Britain with two additional species of uncertain status.

2. THE EPHEMEROPTERA OF SOUTHERN CHALK STREAMS

2.1. Species characteristic of southern chalk streams

The RIVPACS III data-set, which includes species-level data for many chalk stream sites of high quality in southern England, was used to determine which species occurred in chalk streams. For the purposes of this scoping study, the EA nominated officer and IFE staff agreed that 'southern' chalk streams would be defined as occurring in three EA regions (Thames, Southern and South-West region) and that whereas the source waters would always be derived from chalk aquifers, sites would continue to be defined as chalk stream sites when the course of the river progressed over different geology (e.g. tertiary gravels). This protocol generated a total of 42 chalk stream sites which are listed in Appendix 2. In turn, these sites yielded 26 mayfly taxa (mainly species, but including two genera and two species 'groups') in six families. There were no records for two families (Siphlonuridae and Potamanthidae).

A list of the mayflies which were characteristic of chalk stream sites, together with their frequency of occurrence at the 42 sites is given in Table 2.1. The Baetidae, represented by 12 taxa in four genera, was by far the most taxon-rich family in southern chalk streams. All taxa were identified to species with the exception of the *Baetis scambus* group, which comprised both *B. scambus* Eaton and *B.fuscatus* (Linnaeus). These two species, which are difficult to separate as larvae, were always treated as a 'species group' in the RIVPACS project. Within the genus *Baetis*, one species (*B.digitatus*), is known from a very limited number of sites in Britain (including non-chalk stream sites) but others, such as *B.rhodani*, *B.vernus* and *B.scambus* group occurred in a majority of the chalk stream sites and normally formed an important element of the fauna. Additional species, including *B.muticus* and *B.niger* were frequent and *B. atrebatinus* and *B. buceratus* were also encountered quite frequently. Of the remaining species in the Baetidae, *Centroptilum luteolum* occurred in over half of the chalk stream sites, but *C. pennulatum*, *Procloeon bifidum* and *Cloeon dipterum* were less commonly encountered.

Members of the family Heptageniidae, are usually associated with fast-flowing upland streams, but one species, *Heptagenia sulphurea*, is characteristic of chalk stream sites. Two other genera were also represented, but were infrequent in the data-set. They were *Rhithrogena* sp.(either *R. germanica* or *R.semicolorata*) and *Ecdyonurus* sp. (four species in this genus). Within the RIVPACS project, an early decision was made not to attempt to distinguish the larvae of the different species in these two genera due to inherent problems with small specimens. Hence, the results are presented at generic level

The family Leptophlebiidae, includes three genera and all were represented in the chalk stream data-set. However, *Leptophlebia vespertina*, which is more characteristic of still waters, was recorded only once and *Habrophlebia fusca* was only recorded at two sites. All three species in the genus *Paraleptophlebia* were present and *Paraleptophlebia submarginata* was found at 20 of the 42 sites. In contrast, *P.cincta* was only recorded twice and *P. werneri*, a rare species with Red Data Book 3 status (Bratton, 1990), which is most characteristic of winterbourne streams (intermittent chalk streams), was found at a single site.

The Ephemeridae includes three British species but only *Ephemera danica*, the fisherman's mayfly, was a common and characteristic species of southern chalk streams.

Table 2.1 Listing of the mayflies recorded at 42 chalk stream sites, together with the number of sites at which each taxon was found. Data from RIVPACS samples (three seasons samples combined).

Family	Species	No. of Occurrences
Baetidae	*Baetis atrebatinus* Eaton	11
	Baetis buceratus Eaton	10
	Baetis digitatus Bengtsson	1
	Baetis muticus (L.)	17
	Baetis niger (L.)	17
	Baetis rhodani (Pictet)	41
	Baetis vernus Curtis	37
	Baetis scambus group[1]	30
	Centroptilum luteolum (Muller)	24
	Centroptilum pennulatum Eaton	6
	Cloeon dipterum (L.)	2
	Procloeon bifidum (Bengtsson)	3
Heptageniidae	*Rhithrogena* sp.	5
	Heptagenia sulphurea (Muller)	24
	Ecdyonurus sp.	4
Leptophlebiidae	*Leptophlebia vespertina* (L.)	1
	Paraleptophlebia cincta (Retzius)	2
	Paraleptophlebia submarginata (Stephens)	20
	Paraleptophlebia werneri Ulmer	1
	Habrophlebia fusca (Curtis)	2
Ephemeridae	*Ephemera danica* Muller	31
Ephemerellidae	*Ephemerella ignita* (Poda)	42
Caenidae[3]	*Brachycercus harrisella* Curtis	2
	Caenis horaria (L.)	1
	Caenis rivulorum Eaton	24
	Caenis luctuosa group[2]	25

[1] Includes *Baetis scambus* Eaton and *Baetis fuscatus* (Linnaeus)

[2] Includes *Caenis luctuosa* (Burmeister) and *Caenis macrura* Stephens

[3] Recently, *Caenis pusilla* was identified amongst Caenids in samples from the Test, Itchen & Hants Avon. However, the data-base has not yet been updated.

The family Ephemerellidae includes two species, of which just one, *Ephemerella ignita*, known to fishermen as the blue-winged olive, was present at every site.

Finally, members of the Caenidae, often referred to as the Angler's Curse, were represented by four taxa. Two of them (*Brachycercus harrisella* and *Caenis horaria*) were rarely recorded, being more characteristic of other types of flowing and standing waters. However, *Caenis rivulorum* and the *Caenis luctuosa* group (which includes both *C.luctuosa* (Burmeister) and *C. macrura* Stephens, which are difficult to separate as larvae) were both encountered at more than half of the chalk stream sites in the data-set.

A full listing of the mayflies recorded at each of the 42 chalk stream sites is given in Appendix 3. This list combines the records for the three seasons (spring, summer and autumn) in which the RIVPACS samples were collected, such that 1 indicates that a given taxon occurred in a single season, whereas 2 (or 3) indicates presence in two (or 3) seasons.

2.2. Seasonal occurrence of larvae

Each RIVPACS sample was collected by pond-net and involved sampling all available habitats in proportion to their occurrence over a period of 3 minutes in each of spring, summer and autumn. These seasons were broadly defined due to the scale of the sampling operation. They were spring (March - May), summer (June - August) and autumn (September - November).

The frequency of occurrence of each species by season is given in Table 2.2. The results provide a broad indication of the season or seasons in which the larvae of a given species may be found and whether they are common, frequent or rare in a chalk stream.

However, it would be unwise to over-interpret the information in the table without prior knowledge of the life cycles of the individual species (See Section 3 of this report). For example, both *Baetis rhodani* and *Ephemera danica* occur at many sites in spring, summer and autumn, but whereas in chalk streams, *B. rhodani* appears to have several generations per year (multivoltine), *E.danica* has one generation every two years (semivoltine). Again, *B.muticus* and *B. niger* overwinter as larvae and are most frequent in spring, whereas *B.vernus* and *B.scambus* group overwinter in the egg stage and are most frequent in summer.

In cases where there are few records for a species, it is even more important to be aware of the life cycle, because a single record in a given season may have very little or alternatively, considerable significance. An example of the latter is the single record of *Paraleptophlebia werneri* in spring. This species is characteristic of calcareous streams, and in particular winterbournes. When present in winterbournes, the larvae must complete their larval stage in spring and emerge before the stream dries up in summer. Resistant eggs in the stream bed then survive the period of drought through the autumn and early winter.

Table 2.2 Frequency of occurrence of mayfly larvae in 42 chalk stream sites by season.

Species	No. of Occurrences		
	Spring	Summer	Autumn
Baetis atrebatinus	4	6	6
Baetis buceratus	7	5	2
Baetis digitatus	0	1	0
Baetis muticus	15	11	5
Baetis niger	14	7	5
Baetis rhodani	35	33	34
Baetis vernus	14	33	27
Baetis scambus group	8	28	19
Centroptilum luteolum	13	13	11
Centroptilum pennulatum	0	5	3
Cloeon dipterum	0	1	1
Procloeon bifidum	0	3	0
Rhithrogena sp.	5	2	2
Heptagenia sulphurea	21	12	18
Ecdyonurus sp.	1	3	2
Leptophlebia vespertina	1	0	0
Paraleptophlebia cincta	0	2	0
Paraleptophlebia submarginata	10	3	17
Paraleptophlebia werneri	1	0	0
Habrophlebia fusca	1	1	1
Ephemera danica	28	23	26
Ephemerella ignita	25	41	28
Brachycercus harrisella	0	2	0
Caenis horaria	0	0	1
Caenis rivulorum	18	5	9
Caenis luctuosa group	9	18	11

2.3. Species richness at chalk stream sites

The number of mayfly taxa recorded in the combined seasons RIVPACS samples at the 42 sites varied from 4 to 15 with an arithmetic mean of 9.12 taxa per site (Fig.2.1). These numbers should not be regarded as the full compliment of species occurring at each site, but probably give a reasonable indication of site richness. For example, the three 3-minute RIVPACS samples for the R.Lambourn at Bagnor yielded 12 species. A very comprehensive sampling programme undertaken throughout the 1970's yielded just two additional species.

In view of the variation in the number of species found at different sites, there is a need to consider whether mayfly richness has a tendency to vary with location downstream.

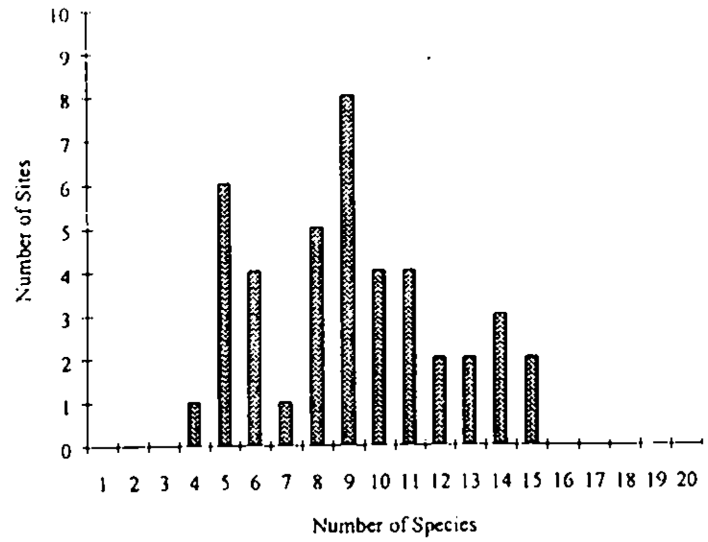
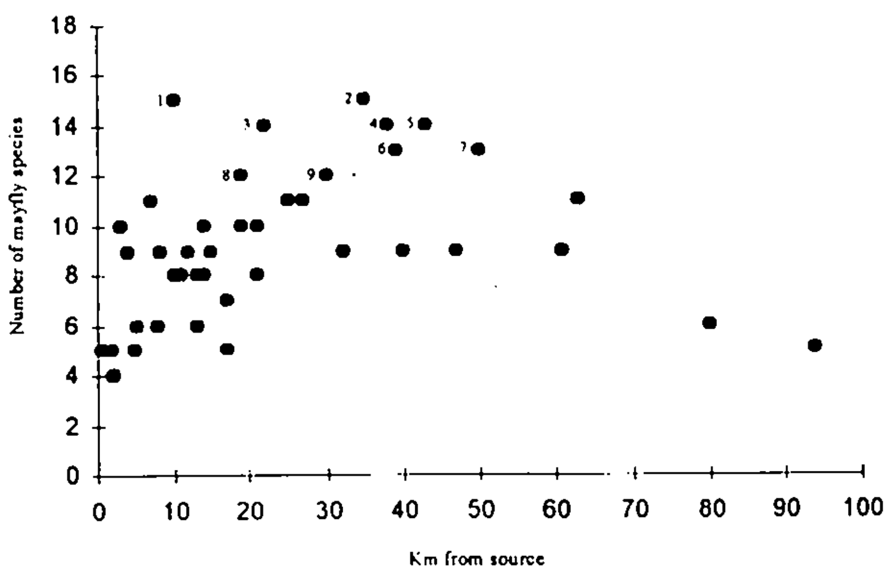


Figure 2.1 Number of species of mayfly larvae recorded at 42 chalk stream sites

Figure 2.2 presents site species richness in relation to distance downstream. It is apparent that sites with relatively low richness (say, six or fewer species) are most frequently encountered at locations less than 20km or over 75km from source.



1	Moors/Crane at Romford Bridge	6	Itchen d/s Chickenhall SDW
2	Frome at Moreton	7	Test at Skidmore
3	Itchen at Itchen St. Cross	8	Lambourn at Bagnor
4	Test at Lower Brook	9	Itchen at Otterbourne Water Works
5	Frome at East Stoke		

Figure 2.2 Mayfly species richness for 42 chalk stream sites in relation to location downstream.

In contrast, sites with twelve or more species only occurred between 10 and 50km from source. It is possible that some of the sites with just four or five species had experienced some form of natural or man-induced stress prior to sampling and may be capable of supporting more species. The most species rich sites have been labelled 1-9 and are identified in a footnote to Fig.2.2. They include a number of the most famous chalk streams in southern England (R. Frome in Dorset, R.Test, R.Itchen and R.Lambourn) and other rivers (R.Crane/Moors River) recognised for the high species richness of their macroinvertebrate assemblages (Wright *et al.* 1988).

2.4. Longitudinal occurrence of species

In order to investigate the basis of this variation in site richness, it is necessary to examine the longitudinal occurrence of the individual species. In Table 2.3 the 42 sites have been placed into a series of eight categories representing distance from source. The distance categories are <5, <10, <15, <20, <30, <40, < 60 and <100km from source. The total number of sites in each distance category is given at the head of the table and this is followed by information on the longitudinal occurrence of each species.

Within the Baetidae, *Baetis rhodani*, *B.vernus* and also *Centroptilum luteolum* were common or frequent in all distance categories. Several other species, including *B.muticus*, *B. niger* and *B. scambus* group were also widely distributed, although less frequent at sites <10 km from source. Additional species in the genus *Baetis* (*B. atrebatinus, buceratus and digitatus*) appeared most consistently in the middle and lower reaches of chalk streams, as did *C. pennulatum*, *Cloeon dipterum* and *Procloeon bifidum*.

In the Heptageniidae, whereas both *Heptagenia sulphurea* and *Ecdyonurus sp.* were widely distributed, *Rhithrogena sp.* was never recorded more than 15 km from source.

Similarly, within the Leptophlebiidae there was evidence of spatial separation of species. *Leptophlebia vespertina* is more characteristic of ponds, lakes and slow-flowing streams and hence the single record in the lower reaches of a chalk stream was to be not entirely unexpected. Whereas *Paraleptophlebia submarginata* is widespread in chalk streams, *P.cincta*, though occasionally recorded, is more frequent in other river systems. In contrast, *P.werneri*, which has RDB3 status, is normally found in winterbournes and the upper perennial sections of chalk streams. Although the single RIVPACS site record was at 5.1 km from source on the R.Crane, the species was also recorded at a further site 3.5 km from source on the R. Crane which dried out in summer and was rejected as a RIVPACS site. *Habrophlebia fusca* is also most frequently encountered in small streams.

Both the Ephemeridae and Ephemerellidae were represented by single species (*Ephemera danica* and *Ephemerella ignita* respectively), which were widely distributed along the length of southern chalk streams.

Finally, the four taxa within the Caenidae included two species (*Brachycentrus harrisella* and *Caenis horaria*) typical of silty rivers which were restricted to downstream locations and two others (*C. rivulorum* and *C. luctuosa* group) which were more widespread in their occurrence.

Table 2.3 Longitudinal occurrence of mayfly larvae at 42 chalk stream sites

Distance from Source (km)	<5	<10	<15	<20	<30	<40	<60	<100
Number of sites in category	6	5	8	5	5	5	4	4
Baetis atrebatinus	-	-	-	1	2	4	3	1
Baetis buceratus	1	-	1	1	1	2	-	4
Baetis digitatus	-	-	-	-	-	-	1	-
Baetis muticus	1	2	3	1	1	5	4	-
Baetis niger	1	1	5	1	3	4	2	-
Baetis rhodani	6	5	8	5	5	5	4	3
Baetis vernus	5	5	8	4	5	4	3	3
Baetis scambus group	1	1	5	5	5	5	4	4
Centroptilum luteolum	2	3	7	3	3	3	2	2
Centroptilum pennulatum	-	-	-	1	2	2	1	-
Cloeon dipterum	-	-	-	-	1	-	1	-
Procloeon bifidum	-	-	-	-	1	1	-	1
Rhithrogena sp.	1	2	2	-	-	-	-	-
Heptagenia sulphurea	2	2	5	2	4	5	3	1
Ecdyonurus sp.	1	-	1	1	-	-	1	-
Leptophlebia vespertina	-	-	-	-	-	-	1	-
Paraleptophlebia cincta	-	-	1	-	-	1	-	-
Paraleptophlebia submarginata	2	3	3	2	3	5	1	1
Paraleptophlebia werneri	-	1	-	-	-	-	-	-
Habrophlebia fusca	1	1	-	-	-	-	-	-
Ephemera danica	4	3	7	4	4	3	4	2
Ephemerella ignita	6	5	8	5	5	5	4	4
Brachycercus harrisella	-	-	-	-	1	1	-	-
Caenis horaria	-	-	-	-	-	1	-	-
Caenis rivulorum	3	2	5	2	4	4	3	1
Caenis luctuosa group	2	1	3	5	4	3	3	4

2.5. Abundance of families at chalk stream sites

The species-level data for mayflies at all RIVPACS sites is simply presence/absence data with no indication of whether the individual species are abundant, common or scarce at each site. Each 3-minute RIVPACS sample was obtained by pond-netting all available habitats, with the time roughly allocated in proportion to the area of each habitat. The resulting sample was therefore effort-dependant, and whilst it was NOT a quantitative sample, it did include crude information on whether taxa were common or scarce. In view of the potential value of this information, it was decided to estimate the abundance of every family of macroinvertebrate in each sample in terms of log categories of abundance (i.e. 1=less than 10 individuals per sample; 2=<100; 3=<1,000; 4=<10,000). This information is available for the six families of mayflies in each season at the 42 sites (Fig. 2.3). Although it is only at family level, it does provide a useful guide to the season(s) when a given family is scarce, common or abundant. For completeness, Fig. 2.3 also includes the number of sites at which a given family was not recorded in the sample for a given season.

Baetidae were present at almost all sites in each of spring, summer and autumn. They were also a dominant element of the mayfly fauna in most seasons, particularly in summer when over 30 sites recorded log category 3 abundance (i.e. between 100 and 999 specimens per 3-minute sample).

The Heptageniidae were dominated by a single species, *Heptagenia sulphurea* and summer emergence dictated that densities of larvae would be lowest at this time.

The Leptophlebiidae were also dominated by a single species (*Paraleptophlebia submarginata*) and once again, early summer emergence resulted in lower densities of larvae at this time before the next generation appeared in autumn.

Ephemera danica, the only species of Ephemeridae recorded at the 42 chalk stream sites, has a two year life cycle and therefore, apart from the emergence of some larvae in the second half of May resulting in lower abundances in summer, the changes in abundance were relatively damped.

Once again, the Ephemerellidae were represented by a single species, the ubiquitous *Ephemerella ignita*. Although this species was recorded at every site (Table 2.1), the life cycle resulted in most sites having their highest abundances of this important member of the mayfly fauna in summer.

Finally, the Caenidae, with four taxa included in the data-set (plus the recently recorded *C.pusilla*), appeared to be progressively less abundant from spring to autumn. The number of sites at which they occurred also decreased with season.

Standard RIVPACS samples, as collected and processed by the Environment Agency, frequently have log. abundance categories ascribed to each BMWP family, including the six families of Ephemeroptera featured above. The information presented in Fig. 2.3 provides a record of the range of abundance categories observed over 42 different chalk stream sites in three seasons. Previously unsampled chalk stream sites which are examined in a given season could exhibit any of the results shown in the figure. However, at high quality sites, some results are more likely than others, and for example, there are very few chalk stream sites in Fig. 2.3 in which the Baetidae are not abundant in summer. Hence, used with caution, this Figure may offer some early clues on whether newly sampled sites are poorly represented in terms of their mayfly larvae Note, however, that the use of full RIVPACS predictions at the family abundance level will provide more detailed predictions tailored to the specific attributes of new sites.

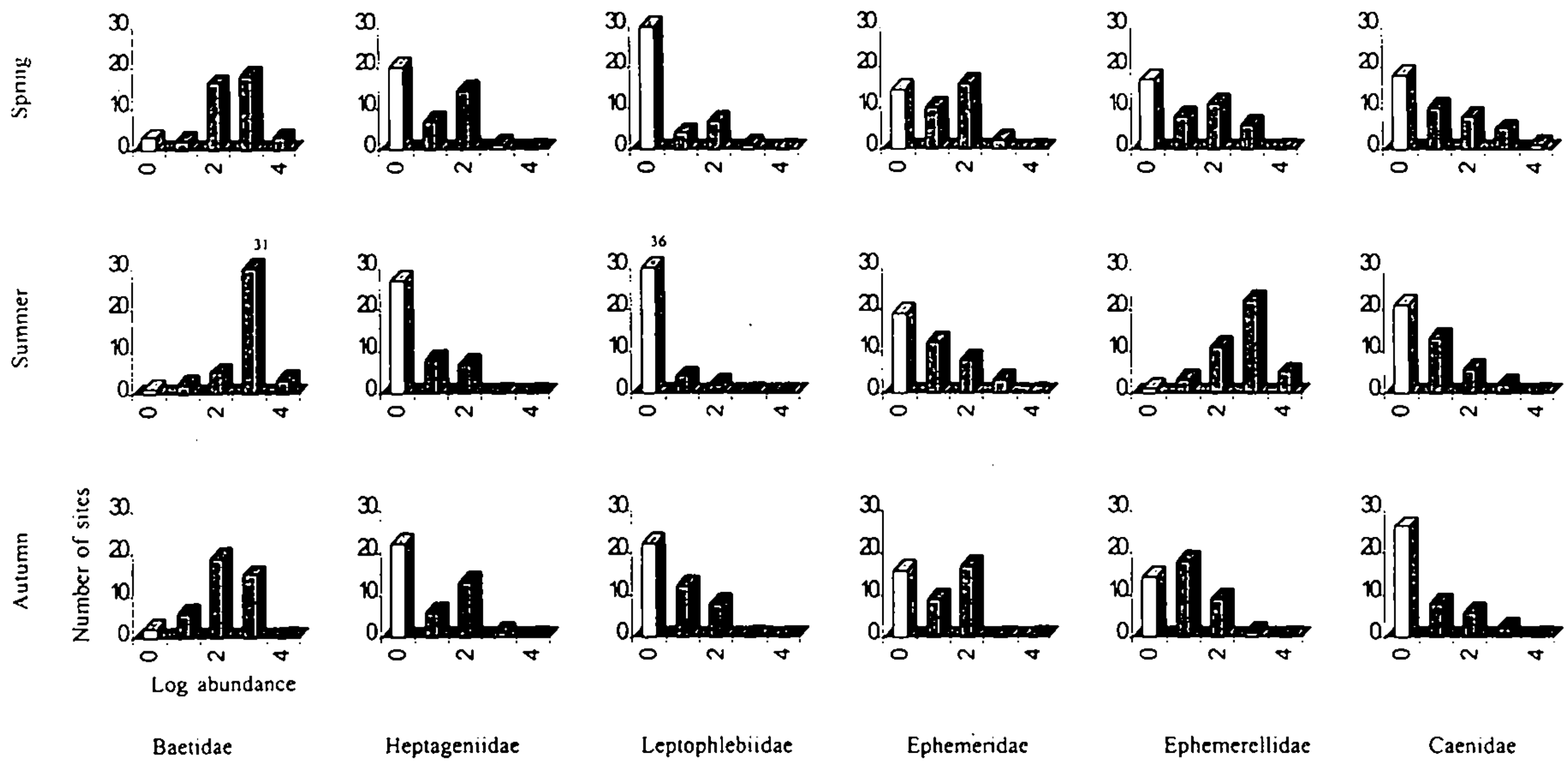


Fig 2.3 The log category abundance data for each mayfly family at 42 chalk stream sites in spring, summer and autumn. The '0' log abundance category (unshaded) indicates the number of sites at which the family was absent in a given season. Log category 1 = <10 individuals per sample; 2 = <100; 3 = < 1,000; 4 = <10,000.

3. NOTES ON THE LIFE CYCLES OF EACH SPECIES

Despite the fact that a very substantial number of studies have been conducted on the life cycles of mayflies in Europe, our knowledge is far from complete. This is, in part, due to the fact that in some mayflies the life cycle shows flexibility, depending on the environmental conditions. In addition, where a species is capable of having several generations in a year, interpretation of the life cycle can be problematic when based on field observations alone. Hence, many workers in this field emphasize the importance of both field and laboratory studies (egg hatching and larval growth) for the correct interpretation of the life cycles (Brittain, 1982, Elliott *et al.* 1988)

Elliott and Humpesch (1983) and Elliott *et al.* (1988) have collated the extensive European literature on the flight periods and life cycles of mayflies found in Britain. Information from these two publications is reproduced in Table 3.1 for the 26 taxa being considered in this report. Note that the flight periods include observations from many varied streams and rivers within Europe and so, flight periods in southern chalk streams may be more restricted in some cases. An example is *Ephemera danica*, which is normally observed in May/June, although emergence at other times of the year is not unknown.

Elliott *et al.* (1988) classify the life cycles of the British species into five broad categories, which are listed and defined in a footnote to Table 3.1. Groups 1A and 1B are both univoltine (one generation per year) but whereas 1A overwinters in the egg stage, 1B overwinters in the larval stage. Groups 2A and 2B are bivoltine (two generations) or multivoltine (more than two generations per year) but again, 2A overwinters in the egg and 2B overwinters in the larval stage. Finally, group 3 has one generation every two years (every three years in some northern latitudes). Note that more than one category is offered for some species (where life cycle varies with river type or geographical location) and that a question mark is used where uncertainty remains.

The final column in Table 3.1 is reserved for additional notes on some species whose flight periods/life cycles have been studied in southern chalk streams.

The Baetidae in particular, display a considerable degree of life cycle flexibility throughout their distributional range (Brittain, 1982). For example, *Baetis rhodani* may have a single overwintering generation in northern Europe and in mountainous areas further south. However, a winter generation followed by a summer generation is typical of less extreme conditions and in more southerly locations there may be additional summer generations. Elliott *et al.* (1988) point out that the combination of the long flight period, the long period when eggs are present and the multivoltine life cycle are the major factors which enable this species to dominate the mayfly fauna of most streams and rivers in Britain.

Table 3.1 indicates that all members of the Baetidae are capable of having two or more generations per year (Groups 2A & 2B). Clearly, those with overwintering larvae

(Group 2B) will have greater capacity for early spring emergence than those which overwinter in the egg stage (Group 2A). Note that *B. vernus* & *B. scambus* group,

Table 3.1 Information on the flight periods and life cycles of mayflies abstracted from Elliott and Humpesch, (1983) and Elliott *et al.* (1988) respectively, together with additional observations made in southern chalk streams.

Species	Flight Period	Life Cycle	Notes
Baetis atrebatinus	May - Oct	2B(?)	-
Baetis buceratus	Apr - Oct	2B	-
Baetis digitatus	May - Sep	?	-
Baetis muticus	Apr - Oct	2B	-
Baetis niger	Apr - Oct	2B	-
Baetis rhodani	Jan - Dec	2B	Multivoltine (Welton *et al.* 1982) Pre-emergent larvae Mar - Dec[1]
Baetis vernus	Apr - Oct	1A/2A	Pre-emergent larvae April -Dec[1]
Baetis scambus group	Feb - Nov	1A/2A	Pre-emergent larvae May - Dec[1]
Centroptilum luteolum	Apr - Nov	2B	2 or possibly 3 generations (Welton *et al.* 1982)
Centroptilum pennulatum	May - Oct	2A(?)	-
Cloeon dipterum	May - Oct	2B	-
Procloeon bifidum	Apr - Oct	2A(?)	-
Rhithrogena sp.	Mar - Sep	1B	-
Heptagenia sulphurea	May - Oct	1B	-
Ecdyonurus sp.	Mar - Oct	1B	-
Leptophlebia vespertina	Apr - Aug	1B	-
Paraleptophlebia cincta	May - Aug	1A(?)/1B(?)	-
Paraleptophlebia submarginata	Apr - Jul	1B	Univoltine (Welton *et al.* 1982)
Paraleptophlebia werneri	May - Jun	1A(?)	Univoltine in Winterbournes
Habrophlebia fusca	May - Sep	1B	-
Ephemera danica	Apr - Nov	1B/3	Semivoltine (Wright et al. 1981)
Ephemerella ignita	Apr - Sept	1A/1B/2B	Pre-emergent larvae Apr - Nov[1] See also Bass (1976) & Welton *et al.* (1982)
Brachycercus harrisella	? - July -?	1A(?)	-
Caenis horaria	May - Sep	1B/2B	-
Caenis rivulorum	Apr - Sep	1B	Univoltine (Welton *et al.* 1982) Pre-emergent larvae May -June[1]
Caenis luctuosa group	May - Sep	1B/2B	-

Group 1A. Univoltine (one generation per year), overwintering in egg stage.
Group 1B. Univoltine, overwintering in larval stage.
Group 2A. Bivoltine (two generations per year) or multivoltine (more than two generations per year), overwintering in egg stage.
Group 2B. Bivoltine or multivoltine, overwintering in larval stage.
Group 3. Semivoltine (one generation every two years or even every three years).

[1] Data on the occurrence of pre-emergent larvae taken from University of Reading (1978)

which have overwintering eggs, (and also *C. pennulatum* & *Procloeon bifidum* which are believed to have overwintering eggs), are less frequently encountered in spring samples in relation to those collected in summer and autumn (see Table 2.2).

Welton *et al.*(1982) studied the growth and production of five species of mayflies in a recirculating channel fed by borehole water whose chemistry was similar to local chalk streams in Dorset. The most abundant species was *B.rhodani*, and they were able to recognise five cohorts through the year. Their study also included *C. luteolum*, which had two and possibly three cohorts per year. In a separate study conducted at seven chalk stream sites during the mid-1970's (University of Reading, 1978) 5-minute pond-net samples were collected each week and pre-emergent larvae (with darkened wing-buds) were removed to document emergence patterns and attempt to recognise discrete generations. Pre-emergent larvae belonging to *B.rhodani*, *B.vernus* and *B.scambus* group began to appear at various times in spring (Table 3.1) and were sometimes recorded into December. In all cases there was convincing evidence of at least two generations.

In general, those Heptageniidae and Leptophlebiidae represented in Table 3.1 appear to have simple univoltine life cycles with overwintering larvae in most cases. However *Paraleptophlebia werneri*, which is believed to overwinter in the egg stage, *must* adopt this strategy in winterbourne streams, which dry out in summer leaving the resistant eggs within the stream bed. After the springs break in winter, the eggs can then hatch in early spring and rapid larval growth allows emergence to take place before the stream dries out once more.

In southern chalk streams, *Ephemera danica* has been shown to have a two year life cycle (Wright *et al.* 1981), with emergence in late May/ early June.

Whereas *Ephemerella ignita* is univoltine with overwintering eggs in many streams in Britain, larvae occur throughout the year in southern chalk streams (Bass, 1976). University of Reading (1978) recorded pre-emergent larvae from April to November and Kite (1962) observed adults on the wing in all months of the year in southern England. The reason for these differences is related to egg hatching. Elliott *et al.* (1988) demonstrated that in cool streams, a small proportion of eggs do hatch through the autumn and winter, but the main egg hatching period is between March and May, resulting in emergence between April and September. Chalk streams remain relatively warm through the autumn and winter months, allowing a higher percentage of eggs to hatch. Nevertheless, the highest densities of larvae recorded in small chalk streams were in April (Welton *et al.* 1982) or May (Bass 1976) and the peak densities of pre-emergent larvae in the seven chalk streams examined by University of Reading (1978) were observed between May and July.

Information is limited for the Caenidae. The single generation of *Caenis rivulorum* studied in the recirculating channel (Welton *et al.* 1982) started to emerge in May, and University of Reading (1978) only recorded pre-emergent nymphs in May and June. The seasonal occurrence of *C. luctuosa* group (Table 2.2) in which specimens were recorded at most sites in summer suggests somewhat later emergence than *C. rivulorum*

4. FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF EPHEMEROPTERA

4.1. Habitats, habits and feeding behaviour of the larvae

Elliott *et al.* (1988) provide a summary of the habitats, habits and feeding behaviour of the British Ephemeroptera. More recently, Wright *et al.* (1993) undertook a survey of macroinvertebrate-habitat associations at 76 lowland running-water sites in England and Wales. A large number of different habitats were sampled within three broad categories: non-macrophyte, submerged macrophyte and emergent macrophyte. Early analyses, based on these categories and using mayflies at family level only, demonstrated statistically significant positive associations between submerged macrophytes (Baetidae & Ephemerellidae), emergent macrophytes (Leptophlebiidae), non-macrophytes (Heptageniidae & Ephemeridae) and no significant associations for Caenidae (Wright *et al.* 1994). The habitat preferences of the individual species of mayflies in this study (Wright *et al.* 1993) are given in italics in Table 4.1. All other details on habit and feeding behaviour are taken directly from Elliott *et al.* (1988).

The descriptions of 'habit' need brief explanation. 'Swimmers', including many Baetidae, have a torpedo-shaped body whereas 'clingers' (e.g Heptageniidae) are dorso-ventrally flattened and have large curved tarsal claws. Sprawlers (e.g Caenidae) are poor swimmers and live in the surface layers of fine sediment or on the surface of macrophytes. 'Climbers' (eg *Centroptilum* spp.) are adapted to life amongst the stems of macrophytes whilst burrowers such as *Paraleptophlebia* spp. and *Ephemera danica* live in river sediments. Larvae of all the British species of mayflies are herbivores and feed on detritus or periphyton (algae and associated material on macrophytes and non-macrophyte substrata). 'Scrapers' exploit periphyton, 'collector gatherers' eat fine deposited detritus, whilst 'collector filterers' feed on fine detritus in suspension. Note that the diet of larvae is not fixed but may vary with the stage of development, time of year and the habitat/river in which the species occurs. Further information on both habits and feeding types may be found in Elliott *et al.* 1988.

Table 4.1 Running-water habitats (from Wright *et al.* 1993), together with habits and feeding behaviour (from Elliott *et al.* 1988) for the mayflies found in southern chalk streams. See text for further explanation.

Species	Running water habitat	Habit	Feeding Behaviour
Baetis atrebatinus	*Submerged & emergent macrophytes*	Swimmer	Scraper & collector- gatherer
Baetis buceratus	*Submerged macrophytes*	Swimmer	Scraper & collector- gatherer
Baetis digitatus	*Submerged macrophytes*	Swimmer/ climber	Scraper & collector- gatherer
Baetis muticus	*Submerged & emergent macrophytes*	Burrower	Scraper-gatherer/(scraper?)
Baetis niger	*Submerged & emergent macrophytes*	Swimmer/climber	Scraper and -gatherer

Baetis rhodani	*Submerged & emergent macrophytes plus non-macrophytes*	Swimmer	Scraper and collector-gatherer
Baetis vernus	*Submerged & emergent macrophytes*	Swimmer	Scraper and collector-gatherer
Baetis scambus group	*Submerged & emergent macrophytes*	Swimmer/Climber	Scraper and collector-gatherer
Centroptilum luteolum	*Emergent macrophytes*	Swimmer/Climber	Collector-gatherer
Centroptilum pennulatum	*Emergent macrophytes*	Swimmer/Climber	Collector-gatherer
Cloeon dipterum	*Emergent macrophytes*	Swimmer/Climber	Collector-gatherer
Procloeon bifidum	*Emergent & submerged macrophytes plus non-macrophytes*	Swimmer/Climber	Collector-gatherer
Rhithrogena sp.	*Non-macrophytes*	Clinger	Scraper and collector-gatherer
Heptagenia sulphurea	*Submerged macrophytes*	Clinger & swimmer	Scraper and collector-gatherer
Ecdyonurus sp.	*Non-macrophytes*	Clinger & swimmer	Scraper and collector-gatherer
Leptophlebia vespertina	Running water (pools/margins and on macrophytes)	Sprawler & climber	Collector-gatherer
Paraleptophlebia cincta	*Submerged & emergent macrophytes*	Burrower	Collector-gatherer
Paraleptophlebia submarginata	*Submerged macrophytes*	Burrower	Collector-gatherer
Paraleptophlebia werneri	*Emergent macrophytes*	Burrower	Collector-gatherer
Habrophlebia fusca	*Emergent & submerged macrophytes plus non-macrophytes*	Sprawler & climber	Collector-gatherer
Ephemera danica	*Non-macrophytes plus submerged &emergent macrophytes*	Burrower	Collector-filterer
Ephemerella ignita	*Submerged macrophytes*	Clinger & sprawler	Collector-gatherer
Brachycercus harrisella	*Submerged & emergent macrophytes plus non-macrophytes*	Sprawler	Collector-gatherer
Caenis horaria	*Emergent macrophytes*	Sprawler	Collector-gatherer
Caenis rivulorum	*Non-macrophytes plus submerged & emergent macrophytes*	Sprawler	Collector-gatherer
Caenis luctuosa group	*Non-macrophytes plus emergent & submerged macrophytes*	Sprawler	Collector-gatherer

4.2. The impact of discharge regime

From the previous section it is apparent that the many species of mayfly larvae found in southern chalk streams exploit a wide range of habitats and rely on different food sources. Chalk streams exhibit a number of characteristic features which are critical to the maintenance of the habitats and food resources used by the entire macroinvertebrate fauna, including the mayflies. These features are well documented (Berrie 1992) and include:

1). The relatively stable flow regime within the perennial section, with peak flows in late winter followed by a falling hydrograph through the summer and autumn.
2). The seasonal nature of the flow regime in the winterbourne section above the perennial head, where flow is dependant upon replenishment of the chalk aquifer in winter.
3). The appearance of water from the chalk aquifer at a temperature of ~11°C throughout the year, resulting in chalk streams being warm in winter and cool in summer relative to streams which lack a groundwater component.
4). The presence of crystal-clear water with a high calcium content, due to the slow filtration of the rain water through the cracks and fissures in the chalk.

These varied features allow the development and maintenance of the submerged and emergent macrophytes which contribute to the wide diversity of habitats found within chalk streams. They also provide an enormous surface area on which algae can grow and within which both fine and coarse organic matter, including autumn-shed tree leaves, can be trapped. In this way, chalk streams normally maintain varied habitats and food resources year-round, resulting in both species-rich assemblages and high densities of individuals.

Some variation in the flow regime can be expected from year to year, and the fauna is adapted to tolerate a range of conditions. Chalk streams, by their very nature, are not prone to flood events, and the pattern of discharge most likely to cause concern is a low flow regime. Low flows can be the result of natural droughts and/or man-made abstraction. The impact of a natural drought on a chalk stream ecosystem will depend upon many factors, including the length and severity of the drought and also the season in which it starts and ends. Similarly, the ecological effects of abstraction will depend on the extent to which the natural hydrograph is modified and whether the river is already experiencing a natural drought.

In view of the fact that the different species of mayfly found in chalk steams are adapted to a variety of habitats and exploit different food resources, they can be expected to give different responses to low flow conditions. These may be direct responses to changes in the physical environment (e.g. current velocity, temperature regime or siltation) or indirect responses mediated through changes in the available habitat or food resources.

Studies in both N.America and Europe have noted an increase in invertebrate drift in response to conditions of low discharge, low current velocity and increased sediment loading (Brittain 1982, Brittain & Eikeland 1988, Elliott *et al.* 1988). In particular, Corrarino & Brunsven (1983) observed catastrophic drift in *Baetis* (and *Simulium*) in experimental channels subjected to reduced stream discharge, whilst Zelinka (1984) demonstrated that low discharge, which gave rise to low current speeds and siltation, led to loss of mayfly populations in experimental brooks.

The impact of low flows on the macrophytes and other habitats in chalk stream has been documented in a number of studies. In the 1970's, long-term studies of the aquatic macrophytes of shaded (Ham et al 1982) and unshaded sites (Ham et al 1981) in the lower perennial of the R.Lambourn included both minor (1973) and major (1976) drought events. Another unshaded site in the upper perennial of the R.Lambourn was monitored during the 1976 drought, as were three more sites on the R.Kennet (Wright & Berrie 1987). Growth of *Ranunculus*, an important habitat for many species of mayfly larvae, was poor during the drought of 1976, and was frequently accompanied by siltation of the river bed. Such major changes in the availability of the dominant habitats and their contained food resources would be expected to have significance for all macroinvertebrates, including mayfly larvae.

Ladle & Bass (1981) examine the flora and fauna of a small chalk stream in Dorset between 1973 & 1974, and during their study the 1973 drought transformed an essentially perennial discharge regime into an intermittent one between September and December 1993, with striking consequences. Following the return of water in 1974, the density of *Ephemerella ignita* reached over 9,000 m^{-2} in May, compared to a little over 2,000 m^{-2} the previous May.

More recently, Wood & Petts (1994) studied a small chalk stream, the Little Stour, in Kent. They monitored the ecological effects of a protracted drought, exacerbated by groundwater abstraction, and the subsequent partial recovery of the stream in 1993. In both 1992 and 1993 just six species of mayfly larvae occurred, but whereas in 1992 *Baetis rhodani* was scarce on just three sites, in 1993 higher numbers were recorded at eight study sites.

The detailed studies undertaken on the R.Lambourn in the 1970's (Wright 1992, Wright & Symes in press) are crucial to an understanding of the impact of the discharge regime on mayfly larvae. Only through long-term studies which include years of high and low discharge will patterns emerge which provide reliable data. Between 1971 & 1979 quantitative samples were taken on each of five habitats (Gravel, *Ranunculus*, *Berula*, *Callitriche* and silt) and on each of two sites (shaded and unshaded) in June and December each year. In each month, data were also available on the area of stream bed occupied by each major habitat. Wright and Symes (in press) present data for the shaded site in which the densities of a number of important families of macroinvertebrates are weighted according to their density on each habitat and also the area of each habitat on the river bed. This provides the best overall estimate of density for the site, given the complexity of habitats present.

The main findings for the three families of mayflies of greatest interest to fishermen (Baetidae, Ephemerellidae and Ephemeridae) are as follows:

Baetidae - (~ six species) In drought years (1973 & 1976) weighted mean densities of larvae in June were low (~ 500 m^{-2}) compared to some years with high discharge

(1975 & 1977) where densities were around 5,000 m^{-2}. Most other years had intermediate densities, although 1979 was rather low for the discharge regime as a result of the restricted area of macrophyte. In 1992, densities were abnormally low, as a consequence of hatch repairs during the spring which disrupted the normal pattern of flow through the study site.

Ephemerellidae (i.e. *Ephemerella ignita*) - densities of larvae could not be related to the discharge regime and in June, rarely exceeded ~2,500 m^{-2}. However, in the year following a drought, higher densities were found with ~ 4,000 m^{-2} in 1974 and ~ 9,000 m^{-2} in 1977.

Ephemeridae (i.e. *Ephemera danica*) - densities of larvae were at a high level at the outset of the study, but following emergence in late May 1972, larval densities were very low in December 1972, suggesting poor recruitment as a result of the cool damp conditions during the period of flight activity. The recruitment observed in subsequent generations (December 1974, 1976 & 1978) was progressively higher in each generation, suggesting that the discharge regime was not the most critical factor in this semivoltine species (See Wright *et al.* 1981 and also section 4.4. for further details)

(Note: In 1997, the Environment Agency commissioned further studies on the macrophytes and macroinvertebrates of sites on the R.Lambourn and R.Kennet first examined during the 1970's (R.Lambourn at Bagnor and the R.Kennet at Littlecote and at Savernake).The sampling regime for June and December 1997 was identical to that used in the 1970's and should provide further information of relevance to an understanding of the response of the fauna to the recent prolonged drought).

4.3. The impact of pollution

Mayfly larvae have been used as indicators of water quality, because of their widespread occurrence, importance in aquatic food webs and sensitivity to a wide range of pollutants. For example, they have been used in the detection of organic pollution, heavy metals, detergents, pesticides, petroleum products, pulp mill effluent and the effects of acidification (Brittain 1982). Fortunately, many of these problems are irrelevant or of relatively minor concern when considering the case of chalk streams. Early recognition of the importance of game fisheries on chalk streams and sustained interest and vigilance to ensure that these unique systems are not compromised has helped to minimize point source pollution inputs. However, in this heavily populated country, there will inevitably be cases of organic pollution on some chalk streams, whether through sewage effluent, fish farm effluent or farm wastes.

The BMWP score system (National Water Council, 1981) gives scores to families of macroinvertebrates (including the six mayfly families considered in this report) such that a high score represents intolerance to organic pollution and a low score represents increasing tolerance (score range is 10-1).

The relevant scores are as follows;

10 - Ephemerellidae	10 - Leptophlebiidae
10 - Ephemeridae	7 - Caenidae
10 - Heptageniidae	4 - Baetidae

Thus, in the BMWP system, most families of mayflies are regarded as very pollution intolerant, and only the Caenidae and more particularly the Baetidae have some tolerance to organic pollution. Within the Baetidae, *Baetis rhodani* has normally been regarded as the most pollution tolerant species (Woodiwiss, 1964).

Hellawell (1986) also provides information on the pollution tolerances of common European macroinvertebrates, derived largely from their position in published tables based on the 'Saprobien system'. Interestingly, the position of some of the individual species of relevance to this study does not link directly to the cruder BMWP categories given above. Thus:

Species largely intolerant of organic pollution (oligosaprobic)
Ecdyonurus sp
Rhithrogena sp.
Paraleptophlebia submarginata

Species tolerant of moderate organic enrichment (beta-mesosaprobic)
Baetis rhodani
Brachycercus harrisella
Caenis luctuosa
Cloeon dipterum
Ephemera danica
Ephemerella ignita
Heptagenia sulphurea

Species tolerant of severe organic pollution (alpha-mesosaprobic)
Baetis vernus
Caenis horaria

Pinder & Farr (1987) examined a number of sites on the R.Frome in Dorset at which there was visible evidence of organic pollution by sewage, fish farm effluent and farm waste. In practice, the low levels of organic enrichment they encountered did not have an adverse effect on faunal associations within the river and diversity indices were positively correlated with dissolved organic carbon.

In a recent study by Quinn & Hickey (1993), the response of benthic invertebrates to domestic sewage waste stabilization lagoon effluent was examined by sampling upstream & downstream of the discharges in eight streams in New Zealand. Whereas at low organic solids loadings the densities of Ephemeroptera, Plecoptera and Trichoptera increased by up to 50%, at higher loadings there was more than a 50% reduction in the densities of sensitive taxa in these three groups. In addition, trout farm effluent has been shown to decrease the taxon richness of Ephemeroptera, Plecoptera and Trichoptera below and for at least 1.5 km downstream of the outfall from three commercial trout farms in North America (Loch, West & Perlmutter 1996).

In cases where organic pollution leads to the elimination of BMWP families, biologists within the Environment Agency are familiar with standard techniques based on RIVPACS (Wright 1995, Murray-Bligh *et al.* 1997) which use observed/expected ratios for the number of BMWP taxa and Average Score Per Taxon (ASPT) for the detection of environmental stress. Finally, it is important to bear in mind that the impact of pollution may be exacerbated under conditions of low flow.

4.4. Factors affecting the terrestrial (adult) phase

Mayflies represent the oldest of the existing winged insects and are unique in possessing two winged adult stages, the subimago and the imago (commonly referred to as 'duns' and 'spinners' by fishermen). The adult stages do not feed, and therefore depend upon energy reserves acquired by the larvae. In some species, adults only live for 1-2 hours, in others the life span is from a few days to a maximum of two weeks. Mating takes place during aerial flight, but the dispersive potential of mayflies is only moderate (Brittain 1982, 1990). Thus, only a small fraction of the life span is spent as the adult, but nevertheless, this stage is crucial for successful reproduction and dispersal.

Elliott and Humpesch (1983) provide a detailed account of the adult phase under the following three headings: 1).Emergence and flight period. 2). Flight behaviour and mating. 3). Fecundity and oviposition behaviour, including egg development. Their review collates data on the behaviour and ecology of many of the species occurring in chalk streams and includes information on emergence behaviour and timing, factors affecting emergence, time when males swarm, fecundity of the different species and oviposition behaviour. In view of the detailed information readily available in this publication, it will not be repeated here. It is, however, worth mentioning that different authors, working on the same species, often disagree on the time of day at which emergence takes place, probably because variations in the diel cycle of water temperature and light intensity affect emergence (Elliot and Humpesch 1983).

Given that the characteristic behaviour and ecology of the pre-emergent larvae and the adults of each species has evolved to maximize the chance that females will be successful in laying eggs to ensure the next generation, what is known of factors which may cause significant disruption to this phase of the life cycle? The answer would appear to be very little. The larval stage occupies a high proportion of the life span and much attention has focused on factors affecting the distribution and abundance of larvae. In contrast, the assumption is normally made that if sufficient larvae reach the adult stage, then the high fecundity of most species will ensure the next generation. In the vast majority of cases this must be true, but not before the pre-emergent nymphs and adults have survived a number of obstacles. At emergence, the mature larva is particularly vulnerable to predation by fish. The response of trout to the emergence of *Ephemera danica* is well recorded by fishermen. After emergence, the subimago normally flies away from the river to shelter amongst vegetation where it moults to the imago. Swarming (limited to males except in the Caenidae) often occurs in relation to bushes or trees near water and females then fly into the male swarm in order to mate. During the life of both subimago and imago, further predation by dragonflies, birds and even bats may influence the numbers of females able to return to water to lay their eggs. Apparently, a number of different parasites of mayflies exploit these food chain links in order to complete their own life cycles (Brittain 1982).

Despite the need to minimize losses due to predation and parasitism and find suitable habitat for shelter and terrain markers for swarming, the terrestrial phase is normally effective at performing its essential role. However, inclement weather in the form of low temperatures, high winds and rain may have the potential to disrupt mating swarms and subsequent oviposition. This view has often been taken by fishermen (Macan 1969, and references in Wright *et al.* 1981) and now, circumstantial evidence based on larval populations is available to support this viewpoint (Wright *et al.* 1981). On four sampling occasions in 1971, the weighted mean density of *Ephemera danica* on the R. Lambourn at Bagnor (shaded site) was around 500 m^{-2} (Wright & Symes in press), but following cold damp weather during the period of flight activity in May/June 1972, the densities of larvae recorded in December 1972 were very low (~ 27 m^{-2}). Recovery to high densities took several generations and weighted mean densities for December 1974, 1976 and 1978 were estimated at ~71, ~142 and 2,300 m^{-2}. Whelan (1980) also records that in 1972, gale force winds drowned large numbers of emerging *E.danica* on lakes in Ireland, and prevented those that survived from making their egg-laying flight to the lake margin.

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Appendix 1. Specification for the scientific review of the mayfly fauna of southern chalkstreams

Background

Staff at the River Laboratory have access to a wide range of published and unpublished information on the Ephemeroptera (mayflies) of chalk streams. The available sources of information include:

a). The RIVPACS III data-base, which has species-level data for many chalk stream sites in southern England.

b). Lambourn Project data, including a run of 9 years data (1971-79) on the macroinvertebrate fauna of two study sites on the R.Lambourn. (This includes the drought year of 1976). Information is also available on the occurrence of pre-emergent mayfly nymphs at 11 chalk stream sites in southern England over a period of 1 or, at some sites, 2 years in the mid-1970's.

c) Information on the occurrence of mayfly nymphs on different habitat types in lowland streams, including some chalk stream sites.

d). Scientific papers on the ecology of mayflies in chalk streams. These include papers written by River Laboratory staff on the taxonomy, distribution, abundance, life cycles and production of mayflies and their response to adverse environmental conditions such as low flows.

The review will refer to southern chalk streams in general and include the following:

List of mayflies which are characteristic of southern chalkstreams.
Overall frequency of occurrence of each species at chalk stream sites of high biological quality (from the RIVPACS III data-set).
Variation in the number of species recorded at chalk stream sites in the RIVPACS III data-set.
Occurrence of species by season (using gross categories of spring, summer and autumn) and in relation to location along the watercourse.
Family level data with attached log categories of abundance based RIVPACS samples in spring, summer and autumn for chalk stream sites (from the RIVPACS data-set).
A brief statement on the life cycle of each species.

The above information should provide an indication of the range of species which may be expected at a given chalk stream site in the absence of environmental stress.

The report will also include a thorough review of the factors, both natural and resulting from man's activities, which may have deleterious effects on the distribution and abundance of mayflies.

Appendix 2. The 42 southern chalk stream sites from which RIVPACS samples have been obtained.

River	EA Region	Site	NGR
Allen	South-West	Walford Mill	SU 010 006
Avon	South-West	Breamore	SU 163 174
Avon	South-West	Bulford	SU 163 437
Avon	South-West	Christchurch	SZ 158 933
Avon	South-West	Moortown	SU 149 035
Avon	South-West	Patney	SU 071 585
Avon	South-West	Rushall	SU 132 558
Avon	South-West	Stratford-Sub-Castle	SU 129 330
Bere Stream	South-West	Middle Bere	SY 858 923
Candover	Southern	Abbotstone	SU 565 345
Chess	Thames	u/s R. Colne	TQ 066 947
Ed	South-West	Pains Moor	SU 074 105
Ed	South-West	Upper Farm	SU 067 112
Frome	South-West	Chantmarle	ST 589 023
Frome	South-West	East Stoke	SY 866 867
Frome	South-West	Frampton	SY 623 949
Frome	South-West	Lower Bockhampton	SY 721 904
Frome	South-West	Moreton	SY 806 895
Itchen	Southern	Chilland	SU 523 325
Itchen	Southern	d/s Chickenhall SDW	SU 466 175
Itchen	Southern	Itchen St.Cross	SU 481 282
Itchen	Southern	Otterbourne Water Works	SU 470 233
Kennet	Thames	u/s Aldershot Water	SU 544 659
Lambourn	Thames	Bagnor	SU 453 691
Mimram	Thames	Codicote Bottom	TL 208 180
Mimram	Thames	Panshanger	TL 282 134
Moors/Crane	South-West	d/s Cranborne	SU 062 129
Moors/Crane	South-West	East Moors Farm	SU 101 029
Moors/Crane	South-West	Great Rhymes Copse	SU 077 121
Moors/Crane	South-West	King's Farm	SU 105 064
Moors/Crane	South-West	Pinnocks Moor	SU 077 112
Moors/Crane	South-West	Redmans Hill	SU 074 079
Moors/Crane	South-West	Romford Bridge	SU 075 094
Moors/Crane	South-West	Verwood	SU 088 075
Piddle	South-West	Brockhill Bridge	SY 839 928
Piddle	South-West	Druce	SY 744 951
Piddle	South-West	Piddletrenthide	ST 703 010
Piddle	South-West	Wareham	SY 919 876
Test	Southern	Lower Brook	SU 338 276
Test	Southern	Romsey	SU 352 204
Test	Southern	Skidmore	SU 354 178
Wool Stream	South-West	Wool	SY 848 869

Species	Allen at Walford Mill	Avon at Breamore	Avon at Bulford	Avon at Christchurch	Avon at Moortown	Avon at Patney	Avon at Rushall	Avon at Stratford-Sub-Castle	Bere Stream at Middle Bere	Candover Brook at Abbotstone	Chess u/s R_ Colne	Ed at Pains Moor	Ed at Upper Farm	Frome at Chantmarle	Frome at East Stoke	Frome at Frampton	Frome at Lower Bockhampton	Frome at Moreton	Itchen at Chilland	Itchen d/s Chickenhall SDW	Itchen at Itchen St_Cross	Itchen at Otterbourne Water Works	Kennet u/s Aldershot Water	Lambourn at Bagnor	Mimram at Codicote Bottom	Mimram at Panshanger	Moors/Crane d/s Cranborne	Moors/Crane at East Moors Farm	Moors/Crane at Great Rhymes Copse	Moors/Crane at King's Farm	Moors/Crane at Pinnocks Moor	Moors/Crane at Redmans Hill	Moors/Crane at Rumford Bridge	Moors/Crane at Verwood	Piddle at Brockhill Bridge	Piddle at Druce	Piddle at Piddletrenthide	Piddle at Wareham	Test at Lower Brook	Test at Romsey	Test at Skidmore	Wool Stream at Wool	Total
Baetis atrebatinus Eaton	1	1													1		1	1		3	2	1																	3	1	1		11
Baetis buceratus Eaton		1		2	3													2					1					1		1			1					1				1	10
Baetis digitatus Bengtsson															1																												1
Baetis muticus (L.)	1							1		2					3			3	2	3	2	3							1		1	1	2					1	1	2	2		17
Baetis niger (L.)														2	1	2	1	2	1	3	2	2		1					1			1	2	1	1				2		1		17
Baetis rhodani (Pictet)	2	1	3	3	3	3	2	3	2	3	3	1	3	3	2	3	2	2	3	3	3	3		2	2	3	1	1	1	2	2	3	3	3	3	3	3	3	3	3	3	2	41
Baetis vernus Curtis		1	2		2	2	2		2	3	2	1	3		1	2	1		3	2	3	3	2	1	1	3	1	2	3	2	2	3	2	2	2	3	3	1	2	1	2	1	37
Baetis scambus group	1	2	2	1	2		2	2		1	2				2	2	1	3	2	3	3	3	3	1	1	1		1		1		2	1		2			2	2	2	2		30
Centroptilum luteolum (Muller)	1	1	1				2				1			2	1	2	1	1	2	3	2		2	1	1		1		1			3	2	1		1			3		1		24
Centroptilum pennulatum Eaton			1															1			2			1															2		1		6
Cloeon dipterum (L.)															1													1															2
Procloeon bifidum Bengtsson																		1			1		1																				3
Rhithrogena														2					1										1		3		2										5
Heptagenia sulphurea (Muller)			3					3	3	2	2				3	2	2	2	2	2	3	3	1	2					1		3		1		3	1	1	3	1		2		24
Ecdyonurus	1							1						3																			1										4
Leptophlebia vespertina (L.)															1																												1
Paraleptophlebia cincta (Retzius)																																	1					1					2
Paraleptophlebia submarginata (Stephens)						1	1		1	1	2			3	2		3	1		2	1	1	1	1					1		1		2		2			1	2				20
Paraleptophlebia werneri Ulmer																											1																1
Habrophlebia fusca (Curtis)						1								2																													2
Ephemera danica Muller	2	2	1				1	1	3		3	3	3	3	3	2	3	3				3	3	3			1	1	3	2	3	3	3	3	3	2			3	2	3	3	31
Ephemerella ignita (Poda)	2	3	3	1	2	1	1	3	3	3	2	1	3	2	2	3	2	1	3	3	3	3	3	2	3	2	2	1	3	1	2	3	3	2	2	2	3	1	2	2	2	3	42
Brachycercus harrisella Curtis			1															1																									2
Caenis horaria (L.)																				1																							1
Caenis rivulorum Eaton	1		1					3	2	1			1	2			1	1	2	2	1	1	1	1					1		2	1	2		1	1			1	1	1		24
Caenis luctuosa group	2	1	2	1	1		3	1	2	2	3	1								1	1	2	3	1	1	1		2		1					2	1			1	1	1		25
Total	10	9	11	5	6	5	8	9	8	9	9	5	5	10	14	8	11	15	10	13	14	12	11	12	6	5	6	8	11	7	9	9	15	6	10	8	4	9	14	9	13	5	

Appendix 3. Mayflies found at each of the 42 chalk stream sites. Data for the three seasons are combined. 1 indicates taxon occurrence in a single season, whereas 2 (or 3) indicates presence in two or three seasons.

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