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A FURTHER ECOLOGICAL STUDY OF THE RIVER RHEIDOL: THE FOOD OF THE COMMON INSECTS OF THE MAIN-STREAM

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(With 2 Figures in the Text)

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1. INTRODUCTION

The Rheidol, which flows into Cardigan Bay, is a good example of a swift, stony river of medium size. A number of papers have appeared, dealing with its history of pollution (Carpenter, 1924, 1925; Laurie & Jones, 1938; Newton, 1944), and recently the writer (1949*a*) has published a general account of the river describing the fauna of the main-stream and the backwaters, together with physiographical data. The present paper deals with the feeding habits of the characteristic insect species of the main-stream and is based on the examination of the gut contents of about 1300 specimens.

2. THE CONDITIONS OF EXISTENCE

The general environmental conditions of the fauna have been discussed in the earlier study (Jones, 1949*a*, pp. 67–78) and may be summarized as follows. The main-stream has a total fall of about 1750 ft., a length of about 28 miles and is for the most part about 100 ft. in width. The river draws most of its water from peaty land over 1000 ft. in altitude—the west and north-west slopes of Plynlimmon, and throughout its course, in many respects, has the general character of a large mountain stream. The water is very soft and acid, its pH varying from 6·4 at low level to 5·8 at full flood. The current is swift, exceeding 5 ft./sec. on the riffles even when the level of the river is low. Floods are frequent and violent; at full flood the level of the river, near Aberystwyth, rises about 2 ft. and the mid-stream current is nearly 6 ft./sec. In its upper reaches the stream-bed is largely rocky; in its lower reaches the bed is composed of pebbles and gravel and is very unstable so that the course of the river is continually changing. The river water is well oxygenated, but its turbulence permits only a small degree of supersaturation; the highest oxygen concentration recorded, on a sunny, spring day when the river bed was covered with green algal growth, is only 101·8%. Temperature conditions are favourable; the river rarely freezes and on cool, sunny days the water may be 2–3° C. warmer than the air. After many days of hot sunshine, however, the water temperature does not exceed 22° C.

In 1931–2, when the faunistic survey of Laurie & Jones (1938) was made, the river was still very slightly polluted with lead, carrying about 0·1 mg. Pb/l. in solution at full flood and 0·02–0·03 mg./l. at normal or low level. At this time there was no evidence that the pollution limited the invertebrate fauna to any degree, and during the last 17 years there has been at least no deterioration in the river's chemical condition; it has now been stocked with trout and the fishing is protected. There is no appreciable amount of sewage pollution, for its valley is thinly inhabited.

The insects of the river have few enemies apart from predatory members of their own group, the trout (*Salmo trutta*) and Hydracarina. Leeches are very rare in the main-stream and there are no large Crustacea. Newts are extremely rare; the stickleback (*Gasterosteus aculeatus*) occurs in fair numbers in the lower reaches of the river, mainly in the backwaters, but there are no other insectivorous fish such as the loach, gudgeon or bullhead, and eels are rare. Prior to the summer of 1949 minnows (*Phoxinus phoxinus*) were conspicuous by their absence, but in June 1949 small numbers appeared in the *Ranunculus* beds near Penybont. This addition to the fauna of the river is a further indication of its present freedom from pollution.

3. THE AVAILABLE SUPPLY OF VEGETABLE FOOD

The available supply of vegetable food may be classified into: (1) the macroflora—bryophytes and flowering plants growing in the water; (2) the algae or microflora; (3) detritus; and (4) plant material originating outside the river.

On the rocky bed in the upper and middle reaches of the river there is a fair growth of moss (*Fontinalis antipyretica* L.) and at some points, principally in rock pools in the gorge section, a liverwort (*Aplozia crenulata* Sm.) is common; but in its lower reaches the stony main-stream is for the most part destitute of bryophyte growth. It is probable that the instability of the river-bed is an obstacle, for where there are firmly fixed rough stones (around the foundations of the bridges) *Fontinalis* grows in abundance. *Ranunculus fluitans* and *Callitriche* sp. occur in the main-stream at points where the current is moderate and there are deposits of sand, and *Glyceria fluitans* is fairly common near Aberystwyth. Generally speaking, however, the macroflora of the river is poor, and for most of its course the main-stream has a bare and monotonous stony bed, with no plants other than the algae.

An account of the microflora of the river, with quantitative data for 1934 and 1935, has been given by Reese (1937); this refers mainly to its upper and middle reaches, stations B and D in the writer's survey (Jones, 1949*a*). The following notes on the microflora are based on Reese's data and observations made by the writer between February 1948 and July 1949.

Stigeoclonium falklandicum Kütz. is the dominant green alga throughout the course of the main-stream and occasionally appears in such abundance as to cover the river-bed with green growth. Other filamentous Chlorophyceae which occur from time to time are *Ulothrix*, *Microspora*, *Mougeotia*, *Draparnaldia*, *Zygnaema* and *Spirogyra*, but these never seem to rival the *Stigeoclonium* in abundance and are generally somewhat rare. The Chlorococcales are represented by *Ankistrodesmus falcatus* (Corda) Ralfs, *Selenastrum gracile* Reinsch, *Tetraëdron minimum* (A. Br.) Hansg. and *Scenedesmus obliquus* (Turp.) Kütz., but none is common.

A small species of *Closterium* (*C. subulatum* (Kütz.) Bréb.) is abundant in the main-stream in spring and early summer, on the stones of the stream-bed and among the leaves of macrophytes, but otherwise the desmids are rather rare. Species recorded include *Closterium Ehrenbergii* Menegh., *C. acerosum* (Schrank) Ehrenb. and *C. acutum* (Lyngb.) Bréb., *Euastrum binale* (Turp.) Ehrenb., *Cosmarium reniforme* (Ralfs) Arch., *Penium cucurbitinum* Biss, *Staurastrum polytrichum* Perty and *S. Kjellmani* Wille, *Arthrodesmus Incus* (Bréb.) Hass. and *A. octocornis* Ehrenb., *Gonatozygon monotaenium* De Bary, *Spondylosium papillosum* W. & G. S. West and *Hyalotheca dissiliens* (Sm.) Bréb. Desmids are named according to the monograph of W. and G. S. West (1904–23), the nomenclature of other algae follows Smith (1933).

The blue-green algae are represented chiefly by *Phormidium* and the Chamaesiphonales. Reese (1937, p. 405) recorded three abundant species—*Phormidium tenue* (Menegh.) Gom., *Chamaesiphon incrustans* Grun. and *Chamaesiphonopsis regularis* Fritsch; other blue-green algae are rare. Two species of Rhodophyceae—*Batrachospermum moniliforme* Roth and *Lemanea* (*Sacheria*) *mammillosa* Kütz. are common at all parts of the main-stream, particularly in winter and early spring. These 'red' algae grew in the river when it was heavily polluted with lead and almost destitute of plant life (Carpenter, 1924, p. 2) and, as will be shown later, they figure largely in the diet of some of the river's most abundant animals.

The diatoms are represented by about fifty-six species. These are listed in Table 1, roughly classified in four orders of abundance. This list is based on ten samples taken from the lower reaches of the main-stream during the period October 1948–June 1949. During the winter *Tabellaria flocculosa* is generally the dominant species, but in spring and summer it may be surpassed in numbers by *Achnanthes minutissima*, *Meridion circulare* and *Gomphonema parvulum*. *Achnanthes* tends to be a dominant form on the pebbles, while *Meridion* and *Gomphonema* are abundant among the macrophytes. Some collections were made in the upper reaches of the river at station B (see Jones, 1949*a*, Fig. 1 for the location of collecting stations) in May and June 1949; nearly all the species listed in Table 1 were represented, and *Tabellaria flocculosa*, *Asterionella formosa*, *Eunotia arcus* and *Frustulia rhomboides* seemed to be rather more abundant than in the samples taken near Aberystwyth. For identification the diatom samples were treated with nitric acid, washed in the usual way and mounted preparations were made with Gurr's 'Clearax'.

The quantitative data for the River Tees given by Butcher, Longwell & Pentelow (1937) indicate that the microflora of swift, stony rivers, in which floods are frequent, undergoes violent and irregular variation in density. All types of algal growth are not

Table 1. *Diatoms collected in the lower reaches of the main-stream of the Rheidol, October 1948–June 1949*

The nomenclature is that of Hustedt, 1930

(1) The dominant species, present in all samples and usually abundant

Tabellaria flocculosa (Roth) Kütz.
Achnanthes minutissima Kütz. var. cryptocephala Grun.
Gomphonema parvulum (Kütz.) Grun.

(2) Sub-dominant species, occasionally abundant

Meridion circulare Ag. var. constricta (Ralfs) van Heurck
Diatoma hiemale var. mesodon (Ehr.) Grun.
Achnanthes microcephala Kütz.
Gomphonema angustatum (Kütz.) Rabh.

(3) Common; present in most samples in fair numbers

Fragilaria capucina Desmaz.
Eunotia lunaris (Ehr.) Grun.
Achnanthes linearis W. Smith.
Navicula Rotaeana (Rabh.) Grun.
Surirella ovata Kütz.
Pinnularia interrupta W. Smith

(4) Rare

Cyclotella sp.
Tabellaria fenestrata (Lyngb.) Kütz.
Meridion circulare Ag.
Ceratoneis arcus Kütz.
Fragilaria virescens Ralfs
F. undata W. Smith
Asterionella formosa Hassall
Synedra ulna (Nitzsch) Ehr.
S. acus Kütz.?
Eunotia pectinalis (Kütz.) Rabh.
E. pectinalis var. ventralis (Ehr.) Hust.
E. arcus Ehr. var. fallax Hust.
E. tridentula Ehr. var. perminuta Grun.
E. monodon Ehr. var. major (W. Smith) Hust.
E. praerupta Ehr.
Cocconeis placentula Ehr.
Achnanthes lanceolata Bréb.
Frustulia rhomboides (Ehr.) de Toni
F. vulgaris Thwaites
Gyrosigma acuminatum (Kütz.) Rabh.
Neidium iridis (Ehr.) Cleve fo. vernalis Reichelt
N. iridis var. amphigomphus (Ehr.) van Heurck
N. affine (Ehr.) Cleve
Stauroneis phoenicenteron Ehr.
Navicula rhyncocephala Kütz.
N. viridula Kütz.
N. gracilis Ehr.
Pinnularia borealis Ehr.
P. gibba Ehr.
P. viridis (Nitzsch) Ehr.
P. maior (Kütz.) Cleve
Amphora ovalis Kütz.
Cymbella cuspidata Kütz.
C. ventricosa Kütz.
C. sinuata Greg.
C. affinis Kütz.
C. cistula (Hempr.) Grun.
Gomphonema acuminatum Ehr.
G. acuminatum var. coronatum (Ehr.) W. Smith
G. gracile Ehr.
G. lanceolatum Ehr.
G. constrictum Ehr.
Nitzschia palea (Kütz.) W. Smith
N. acicularis W. Smith
N. linearis W. Smith
Surirella biseriata Bréb.

affected by floods to the same extent; encrusting forms like *Chamaesiphonopsis* and *Chamaesiphon* can survive very swift currents; the diatoms, which are insecurely attached, are swept away. Thus Reese (1937, p. 399) has recorded that a diatom population of 702/sq.mm. was reduced to 44/sq.mm. by flooding. The violent fluctuations that occur in the diatom population of the Rheidol are readily perceived; after a period of dry, sunny weather an abundant brown growth will develop on the pebbles in shallow water near the margins of the flood-beaches and may extend to cover almost the whole of the river-bed; a heavy flood will sweep all this away to leave the stones clean and grey. Generally speaking the microflora, particularly the diatoms, would appear to form a somewhat unreliable source of food at all seasons of the year.

A more reliable source of food is detritus—amorphous organic matter formed mainly by the disintegration and decay of plants. This accumulates among the stones and gravel of the stream-bed and is strained out of the flowing water by the phanerogams. Some of it is formed by the disintegration of vegetation growing in the water, some of it has its origin outside the river for much decaying terrestrial plant material must be washed into the river by rain. Whatever its source, it would appear that adequate supplies are always available, probably a maximum amount in late autumn and early winter.

Much of the valley of the Rheidol is well wooded, and great quantities of dead leaves find their way into the river to be deposited at the bottom of pools or trapped between stones on the riffles. Under the large stones in swiftly flowing water considerable accumulations of oak and elm leaves can be found during the winter. These form an important source of food: some insects feed on them by biting off pieces, others apparently swallow the fragments into which they are eventually broken by the grinding action of the stones and gravel. No other plant material growing outside the river appears to form a major food source except in so far as it contributes to the general supply of detritus.

4. LITERATURE AND TECHNIQUE

A brief review of the literature dealing with the feeding habits of aquatic insects is given in my paper dealing with the ecology of the River Sawdde (Jones, 1949*b*, pp. 151–2) and some additional works are referred to in the course of this paper. The methods adopted for the determination of the gut contents of specimens from the Rheidol followed closely those adopted in the work on the Sawdde fauna; to aid in the accurate identification of the prey of predatory species a comprehensive series of balsam slides was prepared illustrating the mouthparts, legs, gill lamellae, etc., of all the common insects of the main-stream and additional temporary preparations were made as required. Most of the material for examination was collected from the lower reaches of the river, near Aberystwyth; this could be transported to the laboratory very quickly and examination of the gut contents could be begun within 30 min. Speedy examination is advisable when plant material has to be identified; the chloroplasts of algae are quickly digested. Insect food is digested much more slowly and can be identified even if the specimen to be examined is kept alive in the laboratory for some hours before its gut is extracted.

In the case of the Ephemeroptera and Plecoptera, when specimens were picked out for examination, care was taken to avoid mature nymphs about to moult to the winged stage, for these almost invariably have the gut quite empty. Such cases are readily distinguished by the size and dark colour of the wing buds. Otherwise specimens were taken at random from the material collected.

In Tables 2–5, which summarize the results, *all figures*, except the number of specimens examined and their size range, are *percentages*, and indicate the percentages of the specimens examined in which the different 'foods' were found, the percentages which contained digested food only, and so on.

The presence of algae is indicated only when some, at least, of the cells contained chloroplasts, showing that the insect had been feeding on the living plant, and diatoms are indicated as present only when the gut contained what appeared to be a substantial number. Odd diatoms were present in most of the specimens examined, many are sometimes seen in the gut of predatory insects and these are usually part of the food of the prey. Many specimens contained plant material broken up into very small pieces; when these pieces were clearly of a cellular nature the gut contents were recorded as including 'fragmented leaf and stem tissue'. What appeared to be vegetable matter broken down into an amorphous mass mixed with grit is recorded as 'detritus'. It will be understood that the distinction between detritus and partially digested plant food of other types is frequently difficult. True detritus, however, always appears to include a considerable proportion of grit.

5. THE PLECOPTERA

The observations on the Plecoptera are summarized in Table 2. It will be noted that *Perlodes** is mainly carnivorous, *Isoperla* and *Chloroperla* are omnivorous, while *Leuctra*, *Protonemura* and *Amphinemura* subsist almost entirely on vegetable food. During autumn and winter *Perlodes* is the dominant predatory insect in the river and is a most voracious animal; the crop in a large specimen measures about 9 by 2·5 mm. and in the majority of cases is fully distended with food. Usually the meal consists of a comparatively small number of insects of large size; 84 of the nymphs contained animal food totalling approximately 257 prey individuals, an average of about three per specimen. The *Leuctra* nymphs were mainly found in the specimens taken from the upper reaches of the river (station B); *Baëtis* and *Rhithrogena* were the chief prey in those captured near Aberystwyth. The smallest *Perlodes* examined measured about 10 mm., the diet of these specimens did not appear to differ from that of the large ones in any important respect; the prey tended to consist of smaller specimens of the same species.

Like *Perla* and *Dinocras*, *Perlodes* swallows its prey entire, and in a suitable running-water apparatus will feed in the laboratory. Small *Baetis* nymphs are seized and disappear from sight in a few seconds, but the consumption of a large *Rhithrogena* takes some time. The *Perlodes* seizes the *Rhithrogena* with a swift rushing movement, generally by the posterior end of the body and about one-third of the prey is swallowed immediately; then there is a pause during which the stonefly stops quite still or walks about with the captured insect protruding from its mouth. After a short time swallowing recommences; the mandibles and maxillae work to and fro gently gripping the mayfly nymph and drawing it into the throat. Several minutes after capture the prey disappears from sight, its mouthparts still moving feebly.

* All generic and specific names of British insects in this paper follow the check-list of Kloet & Hincks (1945).

Table 2. *Summary of observations on the gut contents of the plecopteran nymphs*

Explanation in the text, § 4

Species ...	*Perlodes mortoni* (Klap.)	*Isoperla grammatica* (Poda)	*Chloroperla tripunctata* (Scop.)	*Leuctra hippopus* Kemp.	*Protonemura meyeri* (Pict.)	*Amphinemura cinerea* (Oliv.)
Number of specimens examined	100	100	120	50	50	80
Size range (mm.)	10–25	6–12	4–9	6–8	6–8	3–6
Months	Oct.–Mar.	Jan.–Apr.	Nov.–Apr.	Feb.–Apr.	Nov.–Mar.	Feb.–Apr.
Collection stations	B, C, D, E	E	D, E	D, E	D, E	D, E
Anterior part of the gut empty	6	8	1	16	4	15
Gut contents digested	7	5	6	14	14	22
Gut contents:						
Detritus	4	2	33	62	34	38
Moss fragments (*Fontinalis*)	—	—	3	8	12	2
Other fragmented leaf and stem tissue	3	5	30	36	60	35
ALGAE						
Green algae						
Ulothrix	—	—	2	—	—	—
Microspora	—	1	4	2	8	1
Stigeoclonium	2	1	5	—	18	1
Mougeotia	—	—	1	—	2	—
Pleurotaenium	—	—	1	—	—	—
Closterium	—	—	4	—	2	—
Cosmarium	—	—	2	—	2	—
Gymnozyga	—	—	1	—	—	—
Green algae not identified	4	2	4	4	10	2
Lemanea	4	15	12	—	—	2
Batrachospermum	—	10	30	2	4	4
Diatoms	2	3	40	4	6	6
Phormidium	—	—	1	—	—	—
ROTIFERA	—	—	—	—	—	1
OLIGOCHAETA	—	3	10	—	—	—
COPEPODA						
Cyclops sp.	—	—	1	—	—	—
CLADOCERA	—	—	1	—	—	—
HYDRACARINA	—	—	1	—	—	—
PLECOPTERA (nymphs)						
Isoperla	1	1	—	—	—	—
Chloroperla	6	8	—	—	—	—
Leuctra	19	3	3	—	—	—
Protonemura	1	—	—	—	—	—
Amphinemura	1	—	—	—	—	—
Not identified	—	1	—	—	—	—
EPHEMEROPTERA (nymphs)						
Baëtis	32	18	18	—	—	1
Rhithrogena	27	22	7	—	—	—
Ecdyonuridae not determined	11	1	—	—	—	—
ODONATA (naiads)						
Ischnura (?)	1	—	—	—	—	—
Cordulegaster	1	—	—	—	—	—
TRICHOPTERA (larvae)						
Polycentropus	3	1	—	—	—	—
Hydropsyche	5	—	—	—	—	—
Limnophilidae	2	—	—	—	—	—
COLEOPTERA (larvae)						
Dytiscidae	3	—	—	—	—	—
Elminae	1	—	—	—	—	—

Table 2 (*continued*)

DIPTERA (larvae)						
Limnophila	—	1	—	—	—	—
Dicranota	—	—	1	—	—	—
Simulium	24	—	—	—	—	—
Chironomidae	10	30	12	—	—	—
DIPTERA (pupae)						
Simulium	1	—	—	—	—	—
Remains not identified	4	2	2	—	—	—
Animal food only	77	58	17	—	—	—
Animal and vegetable food	7	13	32	—	—	2
Vegetable food only	3	14	44	70	82	61
Anterior part of the gut empty, with its contents digested or with none of the contents identified	13	15	7	30	18	37

Isoperla appears to be more partial to plant food than *Perlodes*, for a number of the specimens contained masses of *Batrachospermum* and *Lemanea*, and the prey organisms tend to be smaller; chironomid larvae form a very large part of the diet, fifty prey individuals being found in the 100 nymphs examined, and there appears to be some tendency for the nymphs to become more carnivorous as they increase in size; fifty-five 6 mm. specimens were examined in January and February, of these forty-seven contained food and this was entirely animal in twenty-four cases; of the thirty 9–12 mm. specimens examined in April twenty-six contained food and this was entirely animal in twenty-four.

Chloroperla tripunctata is another abundant form during autumn, winter and spring. *C. torrentium* occurs also but is much less common. An important feature of the diet of the species studied is its great variety; almost any form of plant food is eaten, and in addition small nymphs of *Baëtis*, *Rhithrogena* and *Leuctra*, chironomid larvae and oligochaetes. Many specimens contained a substantial number of large diatoms such as *Pinnularia viridis* and *Surirella biseriata*. No significant difference was noted between the diet of 4–5 mm. nymphs examined in November and large specimens taken from the river in April.

Of the four species of *Leuctra* occurring in the Rheidol (*fusciventris* Steph., *inermis* Kemp., *nigra* Oliv. and *hippopus* Kemp.) the last is the most common and this species was chosen for study. In a typical 7 mm. specimen the 'stomach' is about 4 mm. in length; the anterior third usually contains a mass of finely divided plant material mixed with gritty detritus. It would appear that the vegetable matter is speedily digested and the mineral matter accumulates in the gut, the posterior third of which is usually packed with grit and little else. *Leuctra* does not seem to eat *Batrachospermum* or *Lemanea* even when there is an ample supply, and when *Chloroperla* nymphs collected from the same part of the river-bed, on the same occasion, have their crops filled with these algae.

Protonemura seems to have a more varied diet than *Leuctra*, but subsists mainly on leaves. Some variety of leaf tissue was seen in the specimens examined; in those taken from stones on the riffles the leaf fragments were very dark, bore numerous stellate hairs and were evidently pieces of dead leaves of deciduous trees. Fragments of moss were also seen and nymphs taken from vegetation at the margins of the river frequently had the gut filled with yellow and green pieces of *Glyceria*. The diet of *Amphinemura* is similar, but fewer specimens had fed on green algae.

In general, these observations on the Plecoptera are in agreement with those of Hynes (1941) who has studied the feeding habits of all the British species of this order. Hynes states, however, that usually from about 50 to 90% of the specimens he examined had no food in their alimentary canals (1941, p. 532). Table 2 shows that in the case of the Rheidol specimens the proportion which contained no food was much lower than this. Even in the case of *Amphinemura cinerea*, the species in which the greatest number of cases with no food occurred, the proportion of those which had recognizable food material in the anterior part of the gut always exceeded 50% and in the case of *Perlodes* about 80% of the specimens examined had taken an ample meal. Whether this indicates that in the Rheidol there is less competition for the food supply available cannot be decided without further investigation.

Grau (1926) examined the gut contents of a number of plecopteran nymphs including *Perlodes dispar* Rmb., which was found to feed mainly on Ephemerid nymphs, chironomid larvae and *Gammarus*. Frison (1929, 1935) has discussed the feeding habits of the nymphs of North American species of Plecoptera; he concludes that in Illinois all the fall and winter stoneflies are herbivorous (1935, p. 301) and that the carnivorous Perlidae comprise a group of species essentially belonging to the late spring and early summer. This seems a curious reversal of the conditions in the Rheidol where the carnivorous species are predominant during the winter. The chief predatory British species of Plecoptera whose nymphs occur during the summer are *Dinocras cephalotes* (Curt.) and *Perla carlukiana* Klap., but these do not occur in the Rheidol. The reasons for their absence are not understood. According to Hynes (1941, p. 529, Fig. 19) *Dinocras* (*Perla cephalotes* in Hynes's nomenclature) likes stony rivers with a stable substratum while *Perla carlukiana* is common in rivers in which the bottom is unstable. Both species occur in smaller streams and over a wide altitude range. *P. carlukiana* occurs in the Towy, the Teifi and the Dovey, all larger rivers than the Rheidol but with less acid water.

6. THE EPHEMEROPTERA

The observations on the Ephemeroptera are summarized in Table 3. As in the case of the Plecoptera each species was studied during that period of the year when large numbers of nymphs of moderate to large size could be collected; *Baëtis rhodani* occurs in fair numbers in most months of the year, the others have fairly definite seasons (see Jones, 1949*a*, p. 85).

Rhithrogena and *Heptagenia* are essentially detritus feeders, and in typical cases the anterior part of the gut contains a smooth mass of amorphous matter and grit. In this some very small leaf fragments, pieces of *Batrachospermum*, or a few diatoms may be seen, but the relative amount of such matter is always small. As in the case of *Leuctra* the organic matter appears to be digested quickly and the mineral matter accumulates at the posterior end of the gut, which is usually packed with a mass of grit; this sometimes contains so little organic matter as to appear very light coloured. Unlike *Ecdyonurus*, which lives near the margins of streams and thus seems to escape the predatory Plecoptera (Jones, 1949*b*, p. 156), *Rhithrogena* likes fairly deep water and a swift current; hence it is preyed upon by *Perlodes*. *Heptagenia* appears later in the year than *Rhithrogena*, after *Perlodes* has bred out, and does not seem to have any stonefly enemy.

Table 3. *The Ephemeroptera*

Species ...	*Ephemerella notata* Eaton	*Baëtis rhodani* (Pict.)	*Siphlonurus lacustris* Eaton	*Rhithrogena semicolorata* (Curt.)	*Heptagenia lateralis* (Curt.)
Number of specimens examined	40	80	40	50	30
Size range (mm.)	5–10	6–10	8–14	7–13	3–7
Months	June	Jan.–Mar.	Apr.–May	Jan.–Mar.	Mar.–Apr.
Collection station	E	E	E	E	E
Anterior part of the gut empty	5	2	2	2	7
Gut contents digested	—	8	15	6	20
Gut contents:					
Detritus	82	86	75	92	73
Fragmented leaf and stem tissue	17	2	72	8	7
ALGAE					
Green algae					
Stigeoclonium	60	—	2	—	—
Spirogyra	2	—	—	—	—
Closterium	35	—	—	—	—
Cosmarium, Staurastrum and other desmids	5	—	12	—	—
Batrachospermum (including Chantransia stage)	—	43	—	4	—
Diatoms	55	16	13	4	10
Algae not identified	—	—	5	6	—
Other material not identified	—	—	—	1	—

Baëtis also seems to subsist mainly on detritus, but a high proportion of the specimens examined contained a considerable amount of *Batrachospermum*. In the nymphs collected in January and February numerous small pieces of the 'chantransia' juvenile stage of this alga were seen in the gut contents; in March some specimens contained tightly packed pure masses of the mature thallus. A few contained myriads of *Achnanthes* and other diatoms. It is probable that *Baëtis* will eat almost any type of vegetable food.

The gut of the *Siphlonurus* nymphs usually contained detritus mixed with small pieces of leaf tissue and other fragmented plant matter. In many specimens the chief food appeared to be narrow strips of *Glyceria*, and perhaps other grasses; some contained many desmids and diatoms. The favourite habitat of *Siphlonurus* is phanerogamic vegetation in gently flowing water; the masses of *Ranunculus* and *Callitriche* appear to strain out vegetable particles brought along by the current and amid their leaves desmids and diatoms multiply to form, with the accumulating debris, a kind of thick vegetable soup upon which the nymphs feed voraciously. They will also live in small pools, eating vegetable debris which accumulates on the bottom. Whether these nymphs can bite fresh vegetable material into pieces seems rather doubtful, most of the plant tissue they consume is probably fragmented by decay and the grinding action of the stones and gravel.

Ephemerella notata is the chief mayfly of the summer months and nymphs 4–5 mm. in length usually appear towards the end of May. Shallow, gently flowing water is the favourite habitat and the nymphs flourish in warm, sunny weather when the river-bed becomes covered with a thick growth of green algae and diatoms. The specimens were collected during such a period, and *Stigeoclonium*, *Closterium* and other desmids formed the greater part of their food. Of the specimens studied 82% are recorded as having fed on detritus. The amount of undigested food in the gut appeared to be much greater in specimens taken from the river early in the morning than in those collected during the afternoon, which suggests that these insects feed at night, or very early in the day.

Wissmeyer (1926), who studied the gut contents of a number of species of Ephemeroptera states that the food of *Ephemerella* includes plant tissue, *Sphagnum*, *Scenedesmus*, *Oedogonium*, *Ulothrix*, *Stigeoclonium*, diatoms and detritus. In the River Sawdde (Jones, 1949*b*, p. 153) *Ephemerella* seems to eat *Ulothrix* when a plentiful supply of this is available; the moss *Fontinalis antipyretica* is eaten when the green alga is scarce.

7. THE TRICHOPTERA

Table 4 summarizes the observations made on trichopteran larvae during the period October 1948–June 1949. *Polycentropus flavomaculatus* is the chief carnivorous type and feeds on a fair variety of insects, but the sixty specimens examined, which contained food, had accounted for only ninety-eight prey, an average of less than two per specimen. The other carnivorous trichopteran larvae found in the Rheidol include *Plectrocnemia conspersa* and *Rhyacophila dorsalis*. *Plectrocnemia* is rare, except in the uppermost reaches of the river (station A), and no specimens of this species were examined; some observations on its diet are included in the work on the River Sawdde (Jones, 1949*b*, p. 154). *Rhyacophila dorsalis* was common in the river during the spring and early summer of 1948. In May 1948, 12 specimens from station D were examined; all of these had been feeding on *Simulium* larvae and pupae which were so fragmented that it was extremely difficult to count the number eaten; a cautious estimate would be two to three larvae or pupae each. During the period October 1948–June 1949 *Rhyacophila* was very rare and only eight specimens were found. Of these five contained food, including *Leuctra*, *Hydropsyche* and *Velia*.

For the greater part of the same period *Hydropsyche* larvae were rare also, but in May 1949 large numbers of *H. instabilis* appeared in the Ponterwyd region (station B); thirty of these were examined with the result set out in Table 4. Some contained animal food but none had fed on animal food exclusively, and the majority appeared to be feeding on the abundant algal vegetation then growing on the river-bed. Generally the gut was filled with *Lemanea*, *Stigeoclonium*, *Microspora* and myriads of diatoms. The green algae were present in tangled masses, the *Lemanea* in the form of short, cleanly bitten off, cylindrical pieces. *Hydropsyche* larvae are said to trap their food with the nets they spin and also pick up food from the substratum; when algal food is abundant, as in the present instance, it would seem that the latter method is employed.

The larva of *Glossosoma boltoni* is one of the most abundant animals in the lower reaches of the main-stream. Large numbers of young larvae appeared early in May on stones in shallow, gently flowing water. These stones were thickly speckled with the small, dark patches of an encrusting blue-green alga which grows abundantly in the river and is probably the *Chamaesiphonopsis regularis* Fritsch recorded by Reese (1937, p. 405). Its cells are very small, tightly packed together, and so firmly attached to the stone that they are not removed without considerable friction. Ten of the *Glossosoma* larvae were examined and in every one the gut was found to be packed with pure masses of this alga and a little grit. On this diet the larvae seemed to grow rapidly, for by 8 June the majority had pupated. Rousseau (1921, p. 422), writing of the larvae of the Glossosomatinae says 'leur régime est typiquement carné' (régime carné = meat diet) but this appears doubtful; the scraper type mandibles of the larva and the ventral opening to its stony house seem peculiarly adapted for feeding on encrusting algae. Lloyd (1921, p. 116) states that he examined the stomach contents of a large number of specimens of *Glossosoma americanum*, and that all contained a 'light-coloured material', the cellular nature of which could not be determined.

Table 4. *The Trichoptera*

Species ...	*Polycentropus flavomaculatus* (Pict.)	*Glossosoma boltoni* Curt.	*Hydropsyche instabilis* (Curt.)	*Anabolia nervosa* (Curt.)	*Halesus radiatus* (Curt.)	*Sericostoma personatum* (Spence)
Number of specimens examined	70	10	30	45	40	50
Size range (mm.)	No record	6–8	8–15	3–16	12–18	No record
Months	Oct.–Apr.	May	May	Feb.–June	Feb.–Apr.	Oct.–May
Collection stations	A, B, D	E	B	E	E	D, E
Anterior part of the gut empty	3	—	3	—	—	2
Gut contents digested	11	—	—	9	—	22
Gut contents:						
Detritus	—	—	33	55	35	32
Leaf fragments (*Fontinalis*)	—	—	7	—	—	—
Leaf fragments (*Glyceria*)	—	—	3	73	60	—
Other fragmented leaf and stem tissue	—	—	17	28	50	58
Undetermined vegetable matter	—	—	—	4	—	26
Algae						
Green algae						
Palmodictyon	—	—	26	—	—	—
Microspora	—	—	60	2	—	2
Stigeoclonium	—	—	87	13	5	—
Scenedesmus	—	—	—	—	—	2
Mougeotia	—	—	3	—	—	—
Closterium	—	—	3	7	—	2
Staurastrum	—	—	—	—	—	2
Other green algae	—	—	—	15	5	4
Batrachospermum	—	—	7	2	15	2
Lemanea	—	—	70	2	20	—
Diatoms	—	—	80	40	40	10
Chamaesiphonopsis (?)	—	100	—	—	—	—
Nematoda	—	—	3	—	—	—
Oligochaeta	—	—	3	—	—	—
Cladocera						
Eurycercus lamellatus	1	—	—	—	—	—
Species not identified	—	—	3	—	—	—
Copepoda	—	—	7	—	—	—
Plecoptera (nymphs)						
Chloroperla	4	—	—	—	—	—
Leuctra	13	—	—	—	—	—
Protonemura	—	—	—	—	—	2
Ephemeroptera (nymphs)						
Baëtis	23	—	7	—	—	—
Rhithrogena	24	—	—	—	—	—
Trichoptera (larvae)						
Hydropsyche	4	—	—	—	—	—
Species not identified	3	—	—	—	—	2
Trichoptera (imagines)						
Species not identified	—	—	—	—	—	2
Coleoptera						
Dytiscid larvae	3	—	—	—	—	—
Diptera (larvae)						
Simulium	6	—	3	—	—	—
Pentaneura	4	—	—	—	—	—
Anatopynia	1	—	—	—	—	—
Cricotopus	6	—	—	—	—	—
Chironomus	1	—	—	—	—	—
Tanytarsus	1	—	—	—	—	—
Other chironomidae	14	—	13	—	—	2
Insect remains not identified	3	—	—	—	—	—
Animal food only	86	—	—	—	—	—
Animal and vegetable food	—	—	37	—	—	6
Vegetable food only	—	100	60	91	100	70
Anterior part of the gut empty or its contents digested	14	—	3	9	—	24

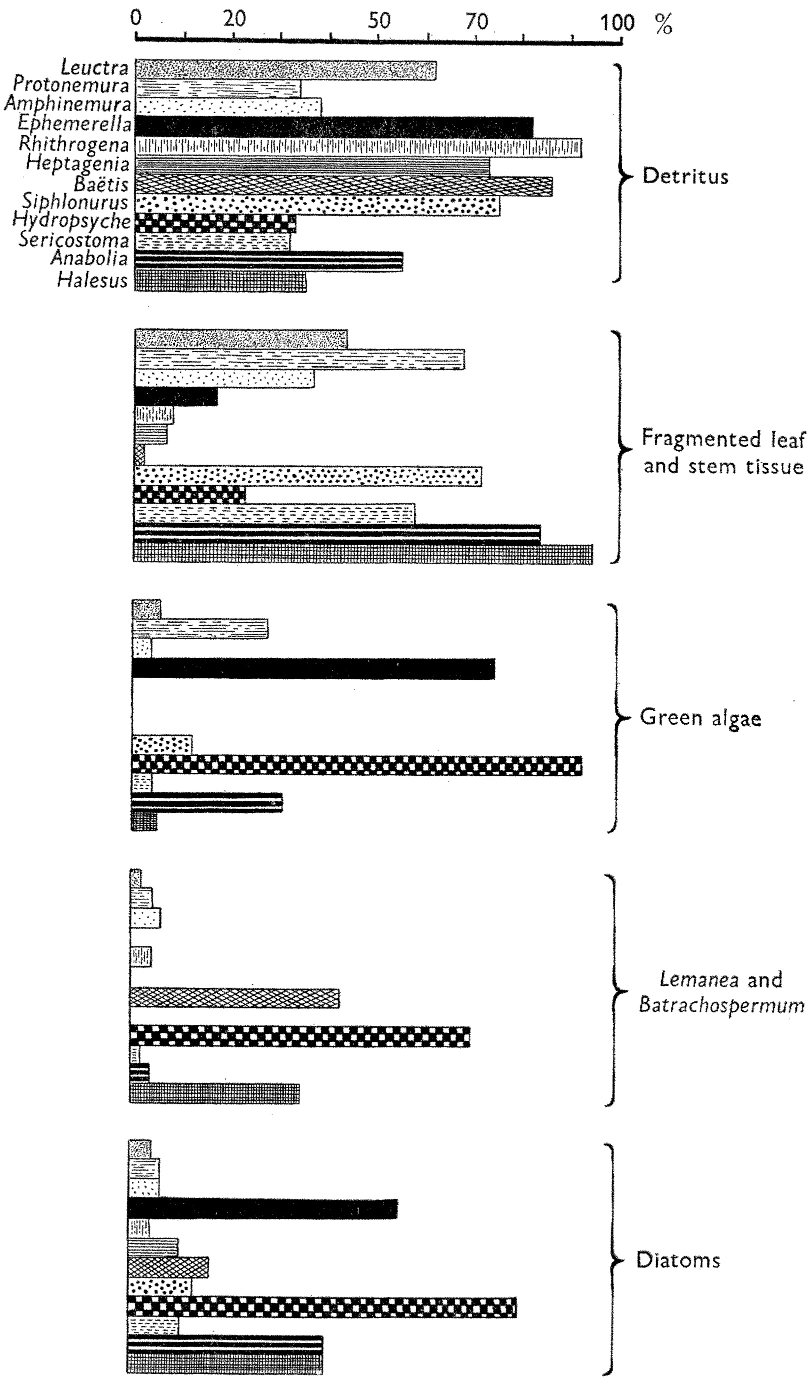

Fig. 1. The food of the phytophagous species. This includes all the species in which none of the specimens examined had fed on animal food only, with the exception of *Glossosoma boltoni*. The figures give the percentages of the specimens examined, in which food of the class indicated was found in the gut contents. 'Fragmented leaf and stem tissue' here includes dead leaves, *Glyceria*, other higher plant tissue and moss, but not the 'undetermined vegetable matter' cited in Table 4.

Anabolia nervosa is the most common limnophilid larva, and its favourite habitat in the main-stream is the *Glyceria* which grows at the margins and from which the young larvae build their cases. The gut contents, which are very bulky, are generally made up of yellow and green pieces of this grass, other fragmented leaf and stem tissue, gritty detritus and diatoms. Green algae are sometimes present, but not in significant amount. The diet of small (4 mm.) larvae examined in February and March appeared to be essentially the same as that of the large specimens taken from the river in June.

The diet of *Halesus radiatus*, which occurs during the winter in the *Glyceria* beds, is very similar; in both species the gut usually contains a fair amount of diatoms, for the most part these are epiphytes on the *Glyceria* leaves and swallowed with them or grazed off; if a leaf is taken from the habitat, its surface scraped and the scraping examined an assemblage of diatoms is discovered similar to that seen in the larva's gut.

The larva of *Sericostoma personatum* lives among stones in flowing water and among debris at the bottom of pools. Here again the gut contents are usually made up of vegetable fragments, ranging from clean cut, roughly square pieces of dead leaves to tiny parings of plant tissue one cell thick. Some specimens contained small, shapeless and opaque lumps of matter which could not be identified, but may have been scrapings from wood.

These observations are not in complete agreement with those of Slack (1936). According to Slack's table (p. 107) only four out of the eighteen *Anabolia nervosa* larvae examined had fed on leaves and 7 had eaten *Baëtis* nymphs; again in seven out of nine specimens of *Rhyacophila dorsalis* the gut contained 'mineral and organic debris'. This may have been part of the gut contents of prey eaten. There is ample evidence, of course, that trichopteran larvae may display a marked change in diet when their conditions of existence are altered; limnophilid larvae which are altogether herbivorous under natural conditions may become carnivorous or cannibalistic when confined in aquaria (Lloyd, 1921, p. 39).

8. THE COLEOPTERA

The fauna of the river includes a fair number of Coleoptera, but the larger Dytiscidae are rare except in the backwaters, and the chief species of the main-stream are the five for which gut contents data are set out in Table 5. It will be seen that *Deronectes elegans* and the three species of *Oreodytes* have a similar diet, *Baëtis* and chironomid larvae being the chief prey. *Hydroporus lepidus* collected from rock pools in the gorge section of the river, where this beetle is very common, feeds to some extent on Copepods and Cladocera.

Identification of the prey was somewhat difficult as the insects found in the beetles' crops were much fragmented and frequently the greater part of the animal eaten would be missing; in some cases only the middle part of the body of a *Baëtis* nymph would be present, the head and tail missing, and the chironomid larvae were seldom complete, some specimens containing head ends and some tail ends. Only about twenty-two of the 290 beetles examined contained pieces of more than one prey organism and cases in which a number of prey were found in the crop were very rare; one specimen of *Deronectes* had eaten four small *Baëtis* and a chironomid larva.

It would appear from the results set out in Table 5 that these small Dytiscidae feed very irregularly, for the percentage of specimens with the crop empty or with its contents digested is very high. Some specific differences are apparent; in the case of *Oreodytes davisii* only 36% of the specimens had no recognizable food in the gut and 22% had the crop full of food, while in *O. septentrionalis* 74% contained digested food or nothing and only 6% had full crops. In the case of each species the specimens were examined in batches of 5–30 on various dates. *O. septentrionalis* was one of the species studied in the work on the River Sawdde; here 22 out of 41 contained no recognizable food.

The way in which these small Dytiscidae feed is uncertain. It is stated that the Dytiscidae are voracious and insatiable carnivores which have a preference for living prey but will content themselves, on occasion, with dead animal matter. They hold captured insects with the fore- and mid-legs while the mandibles rupture their chitinous body wall and extract the soft internal tissues (Guignot, 1947, p. 24). If there is this tendency to swallow the soft parts only it would explain why the fore gut so frequently contains no recognizable matter. Many cases occurred, however, in which the prey, though fragmented, had all been eaten.

9. OTHER INSECTS

Though fairly common in the backwaters, the Odonata are somewhat rare in the main-stream of the river. The gut contents of some specimens of *Cordulegaster boltonii* (Donov.) were examined; only 11 naiads could be found, the food of which included *Halesus* larvae, *Siphlonurus*, *Baëtis*, a large dytiscid larva and one *Deronectes elegans*. The last is notable in being the only instance, in this investigation, of an adult beetle being found in the gut of another insect.

Simulium reptans (L.) was not so abundant in the spring of 1949 as in 1948 and no large numbers of

Table 5. *The Coleoptera*

Species ...	*Deronectes elegans* (Panz)	*Oreodytes davisii* (Curt.)	*Oreodytes rivalis* (Gyll.)	*Oreodytes septentrionalis* (Gyll.)	*Hydroporus lepidus* (Oliv.)
Number of specimens examined	100	50	50	70	20
Months	May	May–June	May–June	May–June	Nov.
Collection stations	E	E	B	E	C
Crop empty	55	20	36	64	35
Crop contents digested	8	16	6	10	—
Crop full and distended	8	22	12	6	No record
Gut contents:					
COPEPODA	1	—	—	—	10
CLADOCERA	—	—	—	—	5
PLECOPTERA (nymphs)					
Leuctra	—	—	2	—	—
Species not identified	1	2	4	—	15
EPHEMEROPTERA (nymphs)					
Baëtis	14	10	16	17	—
Siphlonurus (?)	2	2	—	—	—
Rhithrogena (?)	1	—	2	—	—
TRICHOPTERA (larvae)					
Hydropsyche	1	—	4	—	—
Polycentropus (?)	—	—	2	—	—
COLEOPTERA					
Dytiscid larva	—	2	—	—	—
DIPTERA (larvae)					
Dicranota	—	2	—	—	—
Dixa	—	2	—	—	5
Tanypodinae	—	—	2	—	—
Corynoneura	—	—	—	1	—
Cricotopus	—	—	4	—	—
Tanytarsus	—	—	2	—	—
Other chironomidae	17	40	18	8	30
Simulium	—	2	—	—	—
DIPTERA (pupae)					
Simulium	—	—	2	—	—
Remains not identified	4	6	4	2	15

larvae appeared until June. Twenty specimens were examined on 10 June; in every case the gut contents were very similar, consisting mainly of grit, tiny leaf fragments, *Closterium*, *Scenedesmus*, short pieces of *Stigeoclonium*, *Microspora* and other green algae, and a fair variety of diatoms. The food of *Simulium* larvae seems to depend mainly on what is available. Puri (1925, p. 298) states that larvae of different species collected from the same locality always show more or less the same type of gut contents.

10. GENERAL OBSERVATIONS

Information on the extent to which different vegetable foods are utilized is summarized in Fig. 1. During the autumn, winter and early spring of the period of observation it was evident that detritus, fragmented plant tissue, dead leaves, *Glyceria*, *Lemanea* and *Batrachospermum* were the chief foods of the common phytophagous and omnivorous insects and that the green algae and the diatoms were comparatively unimportant, though some species, *Chloroperla tripunctata* for example, would feed upon them if they were available. In 1949 the green algae and the diatoms did not appear in abundance in the river until early in May, by which time the stoneflies had bred out and *Siphlonurus* and *Ephemerella* had replaced *Rhithrogena* and *Heptagenia*. In 1948 a luxuriant growth of *Stigeoclonium* developed in the last week of February and persisted until May, but this is probably exceptional; Reese (1937), whose observations on the microflora of the Rheidol covered the period November 1933 to December 1935, found that the *Stigeoclonium* appeared in April and her quantitative data (1937, p. 395) indicate that February and March were months of sparse algal growth. Unfortunately the extent to which this very early growth of green alga in 1948 was utilized as food by the winter Ephemeroptera and Plecoptera was not investigated, though the gut contents of some *Chloroperla* nymphs examined at this time showed that they were feeding on it.

January and February 1948 were months of heavy rainfall and it is possible that the abundance of the March growth may have been related to depletion of the benthic insects by the floods. The extent to which the plant growth of the river is limited by the feeding of the insects deserves further study. In the Rheidol, as in other rivers, the mature thallus of *Lemanea mammillosa* only develops abundantly where the current is swiftest though the alga will begin to grow on almost any part of the stream-bed where there are stones for attachment. *Lemanea* is eaten in such quantities by *Chloroperla*, *Isoperla* and *Hydropsyche* that it is possible that growth developing where the current is gentle or moderate is completely grazed down and that the plant flourishes in the most turbulent parts of the stream because here the risk of being swept away deters these insects from feeding upon it.

During the late spring and summer the green algae, particularly *Stigeoclonium*, *Microspora* and *Closterium*, become important sources of food, and some species, *Ephemerella notata* and *Hydropsyche instabilis* in particular, also feed extensively on diatoms. However, the fauna of the river does not seem to include any numerous insects in which the diatoms form the chief or only food. *Philopotamus montanus* (Donov.), which in my observation feeds mainly on diatoms, does not occur in the Rheidol, nor does *Silo nigricornis* (Pict.) which, according to Slack (1936), has a similar diet. *Silo pallipes* (Fab.) is one of the dominant insects in the Melindwr, one of the tributaries of the Rheidol (Jones, 1940, p. 194), but is very rare in the main river. The blue-green algae appear to be of no importance except in the case of *Glossosoma* already discussed; *Phormidium* was seen in the gut contents of a single specimen only (*Chloroperla*).

In the case of the Sawdde it was noted that some of the common animals of the river appeared to have some means of escaping attack by predatory species and further instances may be distinguished in the Rheidol. No Mollusca were found in any of the specimens examined; this is to be expected, for *Limnaea pereger* is extremely rare in the main-stream and the only common species, *Ancylastrum fluviatile*, is evidently protected by its shell and its ability to cling tightly to stones. The common Hemiptera of the main-stream, *Velia currens* and *Gerris najas*, live on the surface where they cannot be attacked by the predatory Plecoptera and Trichoptera. The stony case of *Glossosoma boltoni* appears to be an admirable protection against insects, though it does not prevent it being eaten by trout—Frost (1939, p. 180) in her study of the food of trout in the River Liffey found that *G. boltoni* larvae formed 9·8 % of the trichopteran larvae eaten at Straffan. The other cased trichopteran larvae of the Rheidol appear to escape attack also; this may be due partly to the protection afforded by their cases, but it is probable that their comparative immunity is mainly due to the fact that they live, for the most part, in vegetation in slowly flowing water or at the bottom of debris-laden pools, whereas the predatory Plecoptera and Trichoptera prefer the stony bed and a swift current. *Siphlonurus lacustris* is another insect which avoids these regions of danger.

In the majority of the species studied the food chain is short and uncomplicated. The general scheme for *Perlodes mortoni*, which is rather more elaborate, is shown in Fig. 2. This scheme is a little simplified by the omission, in the case of some species, of 'foods' occurring in less than 5 % of the specimens examined. It will be understood that this 'food chain' scheme applies more particularly to the Rheidol and other rivers of similar type. At the time of writing this paper a similar investigation is in progress dealing with the River Towy, a much larger river than the Rheidol and the Sawdde, with a stable bed, soft but nearly neutral water and a very rich algal and phanerogamic flora. It is hoped to present the results of this investigation in a subsequent paper together with a general discussion of the observations made on the three types of river examined in detail, but at this stage certain general conclusions may be framed. In the case of the predatory species it is evident that the polyphagous habit is general; the predatory insects feed upon the more numerous and defenceless animals; these are generally phytophagous and in swallowing its victims entire the predator obtains some supply of partially digested food, the food of the prey. This may form a considerable part of the gut contents of the carnivorous insects. The meal tends to consist of a comparatively small number of prey of large size rather than a large number of small animals, and it is possible to distinguish, at least in the Plecoptera, between species like *Perlodes mortoni* whose rapid growth appears to be associated with regular feeding so that the crop is almost always full of food, and species of slow growth (e.g. *Perla carlukiana*, whose life cycle occupies 3 years), in which feeding takes place much more irregularly, a high proportion of the specimens having the crop empty. Generally speaking, also, the predatory insects are types of high oxygen demand, living in swift, shallow water; the selection of other habitats by phytophagous species secures some degree of safety.

In the case of the phytophagous insects it is evident that detritus forms the most reliable supply of food, but it would appear that the two rivers so far described belong to very different types as far as the origin of the detritus is concerned. In the Sawdde system where the stream-bed is occupied by great masses of bryophyte growth, much of it decaying, where flooding is infrequent and much of the water has its source in springs it is probable that the greater part of the detritus available as animal food is formed from plants growing in the water; in the Rheidol, whose shifting bed supports a much more scanty macroflora, it would appear that a high proportion of the detritus is of terrestrial origin. Frequent floods seem to ensure an ample supply, which accumulates among the loose stones on the river-bed; the amount available is probably a maximum in late autumn and winter, the season of the year when a detritus-feeding mayfly nymph peculiarly adapted for living in streams with a very swift current (*Rithrogena*) is one of the dominant animals.

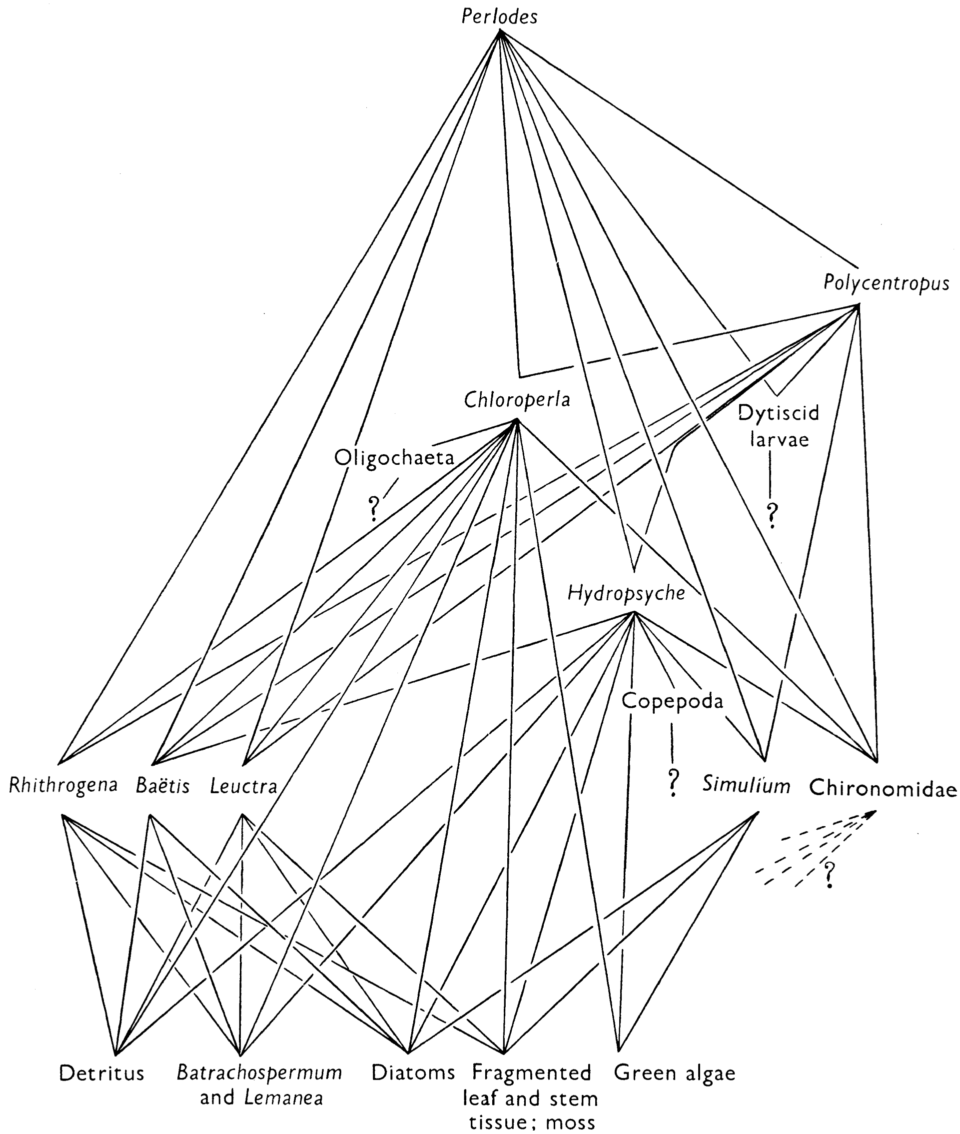

Fig. 2. The main features of the food chain of *Perlodes mortoni* and its chief prey. Based on Tables 2–5.

Containing, as it does, a high proportion of cellulose and valueless mineral matter detritus would not seem to form a nourishing diet. Insects feeding upon it have very capacious alimentary canals, feed continually and yet may display slow growth. Living algal food material is probably much more nutritious, the apparently very rapid development of *Glossosoma* larvae feeding on an almost pure diet of blue-green alga having been mentioned earlier in this paper. Some of the most successful species, *Siphlonurus lacustris* and *Baëtis rhodani*, for example, will eat detritus and almost any type of algal food, but whether a diet of living plant material results in more rapid growth has not been demonstrated. Here there would appear to be scope for observation and experiment.

11. SUMMARY

1. This paper deals with the food of the common insects in a swift, shallow, stony river with soft, acid water and is based on the examination of the gut contents of about 1300 specimens including 25 species.

2. The vegetable foods and the chief insects feeding on them are: (*a*) detritus (most phytophagous species); (*b*) dead leaves (*Protonemura meyeri*, *Amphinemura cinerea* and *Sericostoma personatum*); (*c*) *Glyceria fluitans* (*Halesus radiatus* and *Anabolia nervosa*); (*d*) fragmented leaf and stem tissue (*Leuctra hippopus* and *Siphlonurus lacustris*); (*e*) green algae (*Hydropsyche instabilis* and *Ephemerella notata*); (*f*) *Lemanea* and *Batrachospermum* (*Hydropsyche instabilis*, *Baëtis rhodani*, *Chloroperla tripunctata* and *Isoperla grammatica*); (*g*) diatoms (*Hydropsyche instabilis* and *Ephemerella notata*); and (*h*) encrusting blue-green algae (*Glossosoma boltoni*).

3. *Perlodes mortoni*, *Isoperla grammatica* and *Polycentropus flavomaculatus* are the chief predatory species; *Baetis*, *Rhithrogena*, *Leuctra* and chironomid larvae are the chief insects preyed upon. *Deronectes elegans* and the other small Dytiscidae of the main-stream feed mainly on *Baetis* and chironomid larvae. Very few animals other than insects are eaten by the predators.

Table 6. *Data on which Fig.* 1 *is based*

Species	Percentage of the specimens examined which contained vegetable food of the following types: Detritus	Fragmented leaf and stem tissue; moss, etc.	Green algae	*Lemanea* and *Batrachospermum*	Diatoms
Leuctra hippopus	62	44	6	2	4
Protonemura meyeri	34	68	28	4	6
Amphinemura cinerea	38	37	4	6	6
Ephemerella notata	82	17	75	—	55
Rhithrogena semicolorata	92	8	—	4	4
Heptagenia lateralis	73	7	—	—	10
Baëtis rhodani	86	2	—	43	16
Siphlonurus lacustris	75	72	12	—	13
Hydropsyche instabilis	33	23	93	70	80
Sericostoma personatum	32	58	4	2	10
Anabolia nervosa	55	84	31	4	40
Halesus radiatus	35	95	5	35	40

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