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A FURTHER ECOLOGICAL STUDY OF CALCAREOUS STREAMS IN THE 'BLACK MOUNTAIN' DISTRICT OF SOUTH WALES

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(With Plates 4–6 and 2 figures in the text)

CONTENTS

1. INTRODUCTION

In a paper recently published in this *Journal* the writer (1948) has described the summer fauna of four torrential streams in the 'Black Mountain' district of south Wales. Of these four streams one has moderately calcareous water and a rich fauna including about 130 species; this is the river Clydach, which flows on the northern slopes. The three streams flowing on the southern slopes have very soft water which is rendered acid to varying degrees by drainage from peaty soils, and all have a much poorer fauna, including few species other than insects. This first paper dealt with variations in current speed, in the hydrogen-ion concentration and mineral salt content of the stream water and the relation between temperature and air temperature.

The present paper describes the summer fauna of the river Sawdde,* the main stream on the northern slopes of the Black Mountain, and of which the Clydach is a tributary. It includes, also, a qualitative study of the microflora of the Sawdde and the Clydach and some observations on the feeding habits of the dominant insects in this stream system, based upon the examination of the gut contents of about 600 specimens.

2. THE RIVER SAWDDE: TOPOGRAPHY, CHEMICAL NATURE, FAUNA

The river Sawdde is one of the finest trout streams in the district and is protected by the Towy Fishery Board. It has its source at an altitude of about 1700 ft. in Llyn-y-Fan-fach, a small lake lying beneath the western end of a long escarpment which $1\frac{1}{2}$ miles to the east rises to about 2500 ft. About 2 miles to the north-east is the source of the river Usk. For about a mile after leaving the lake the stream flows northwards and then turns west; at station A (Fig. 1) the river is about 25 ft. wide, its bed is composed of large stones and boulders with very little gravel or sand; the stream-bed gradient and current speed vary somewhat from place to place, but there are no pools. The stream is shaded by trees and bordered by narrow strips of cultivated land.

At B, the next collecting station, the river has widened to 35 ft. and its bed has become much more uniform in gradient, so that the water flows very steadily and is up to about a foot in depth at normal level. Here and there, near the banks, there are deposits of very coarse, red gravel. Most of the stones are 6–9 in. in diameter, some are grey and some are red, and in spring, when many of the stones are bright with green algal growth, the river has a striking appearance. The right bank is shaded by trees. About 2 miles farther on the Sawdde is joined by the Clydach, and now it enters upon a kind of gorge section about 3 miles in length; here the river has cut its bed down to a level 12–15 ft. below the valley floor, and at many points flows as a narrow, deep torrent between precipitous rocky banks. The valley itself is narrow and well wooded. In this section the river is so inaccessible that no attempt was made to study the fauna, but at one point (C) some riffles are accessible where there is a thick growth of submerged moss, and here some microflora samples were taken, as described in the next section.

* Approximate pronunciation Sou′they; *sou* as in 'south'.

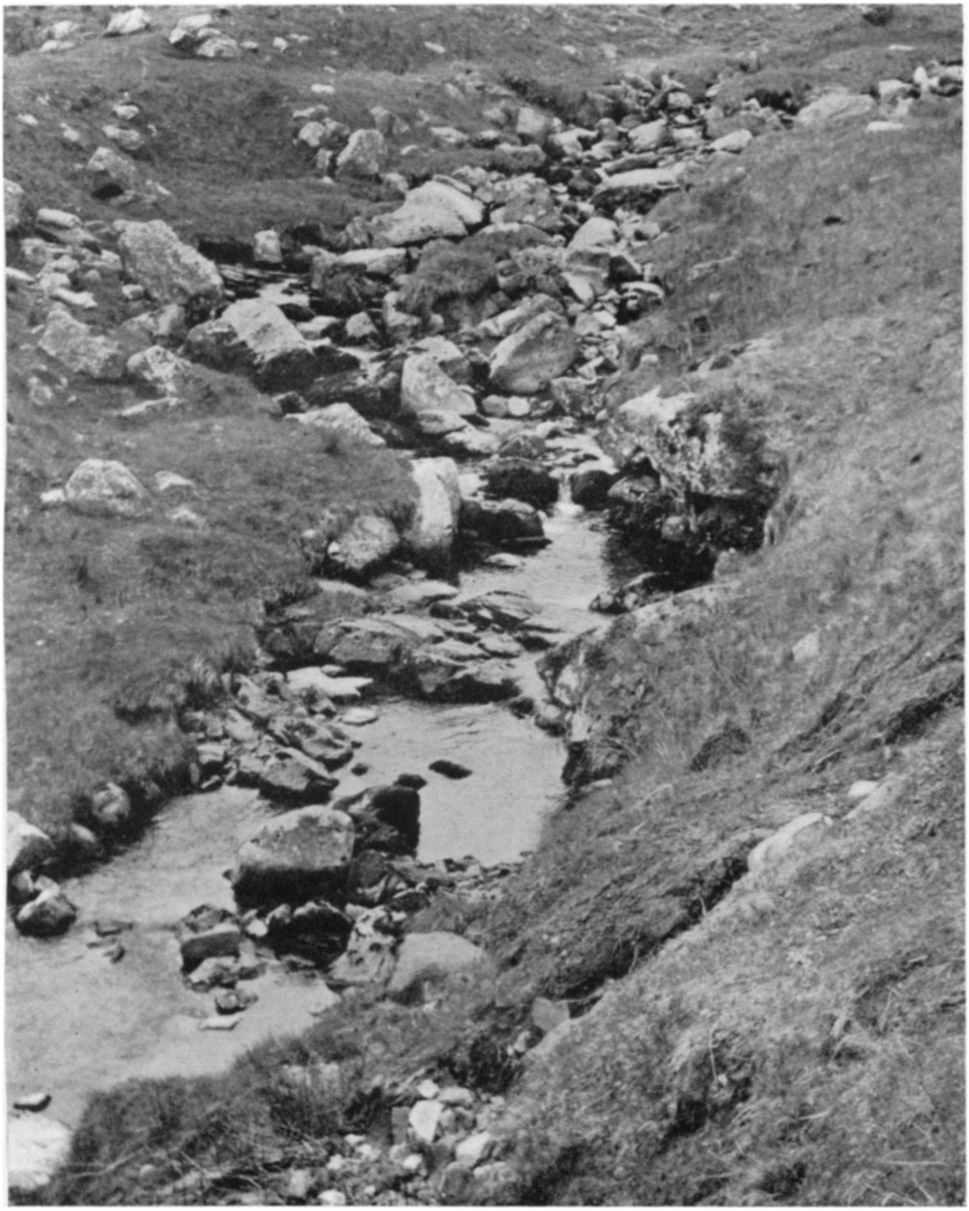

Photo 1. The river Clydach near station F (Pont Clydach).
The pools in the foreground are about 12 feet wide.

Photo 2. The river Sawdde at station B (Aberllechach).

Photo 3. The river Sawdde near station C (Pont-ar-llechau).
In the foreground the river is about 4 feet deep.

About 2 miles below station C the valley has widened and the river has left its 'gorge' section to flow 3–4 ft. below the level of the land, between banks of sandy soil. It is now 50–80 ft. in width and generally very shallow and swift flowing. At some points the water surface is broken from bank to bank, at others the water near the bank is almost motionless, and the stony bed is smothered with heavy deposits of silt. There is no tree shade at this station, in contrast to the other sampling stations above. About a mile below station D the Sawdde joins the river Towy, which opens to the sea near Carmarthen.

The Sawdde has an abundant flow of water which is not greatly diminished by long spells of dry weather, and very heavy rainfall is necessary to produce any substantial degree of flooding. The water is normally very clear, with no trace of peat colour, and completely free from any type of pollution. In Table 1 the result of some determinations of its main constituents are set out (for the methods employed see Jones, 1948, p. 54). The results show that the river water is moderately calcareous and has very much the same composition at all three stations. Many colorimetric pH determinations were made from time to time between April and November 1948; the results of a series made on 27 July 1948 are inserted in Fig. 1, and these show that the whole stream system is one of moderately alkaline water. On this occasion the water-level was about normal. When the river is swollen by rains its water becomes less alkaline; under conditions of slight flood the pH readings at stations A, B, C and D may change to 7·2, 7·4, 7·4 and 7·4, and a moderately heavy flood results in the pH at B, C and D dropping to 7·2. Similar changes occur in the tributary streams; chemical data for the Clydach are given in the earlier study (Jones, 1948, pp. 54–5). The oxygen determinations show that the river water is well oxygenated. These samples were taken on the afternoon of a dull November day and appear to indicate a high level of photosynthetic activity; the figure of 101·9% saturation at station D equals the highest values recorded by the writer for the river Rheidol at Aberystwyth on bright, spring days (Jones, 1949, p. 77).

The bed of the river appears to be remarkably stable. On 12 September 1948 a week of wet weather culminated in many hours of torrential rain, when all the streams in the Black Mountain district became flooded to a most abnormal degree. In the Pedol, the Garw and the Amman (the acid streams of the southern side) the force and velocity of the current was such that the stones on the stream bed were moved about, producing a groaning sound which could be heard some distance away. An examination after the flood had subsided showed that all bryophyte growth had been dislodged and swept away; the fauna had suffered so severely that hardly an insect could be found. In the case of the Sawdde little disturbance of the stream-bed was evident, most of the moss remained, and the fauna appeared to have suffered comparatively little.

At stations A, B and D a qualitative survey of the fauna was made in the summer of 1948; the dates set out at the head of Table 2, in which the animals are listed, each represent about 2 hr. collecting. The methods of collecting employed and the literature used for identification are given in earlier papers (Jones, 1941, 1948, 1949). Insects are named according to the check list of Kloet & Hincks (1945). In frequency of occurrence the various species are roughly classified into four categories: v signifies that a single specimen was taken at the collecting station; r denotes species taken in small numbers; total number up to 10; C those more common, totalling up to 100 specimens; and A the dominant animals, of which 100–200 specimens could be collected in one sample.

Table 1. *Chemical data for the river Sawdde, 27 November 1948*

River level about normal for the season. Sky overcast throughout the day. Samples for oxygen content taken at 14.00–14.30 hr. G.M.T.

Station ...	B	C	D
Water temperature (° C.)	8·0	8·3	8·3
Oxygen (mg./l.)	12·10	11·83	12·08
Oxygen (% saturation)	101·3	99·8	101·9
pH (colorimetric)	7·4	7·6	7·6
Alkali reserve (normality)	0·00108	0·00112	0·00112
Calcium (mg./l.)	21·2	22·0	21·0
Cl′ (mg./l.)	8·5	7·2	8·0
Magnesium (mg./l.)	3·5	3·5	4·0
Fe'''		Not detected	
SO_4''		Less than 1 mg./l.	

The fauna list includes about 75 species, a much smaller number than that recorded for the Clydach (about 130). In numbers of Plecoptera, Ephemeroptera and Trichoptera the Sawdde list does not differ very much from the Clydach list, and differences are most evident when we consider the Hemiptera, Coleoptera and Diptera. The chief reason for the comparatively restricted nature of the Sawdde fauna appears to be the much more restricted range of habitat afforded by the larger stream. Whereas the Clydach is very variable in gradient and has numerous pools of various sizes, the Sawdde is very uniform in gradient and has very few pools. This probably accounts for the absence of the Gerridae, Corixidae and Odonata found in the Clydach, and the occurrence in the Sawdde of only four species of Dytiscidae and one hydrophilid. At all three stations where the fauna was studied the larger stream resembles the Clydach at station G, where the summer fauna includes about 70 species. The Sawdde fauna is, of course, essentially lithophilous; the typical lithophilous fauna, though it may be very rich in number of individuals, is not usually rich in number of species.

3. THE FLORA OF THE RIVERS SAWDDE AND CLYDACH

A qualitative survey of the flora of the Sawdde and the Clydach was begun in the spring of 1948; it was the writer's intention to determine the plant species that might afford food for the animals, and as it was soon discovered that the flora varied somewhat from time to time and from place to place, numerous examinations were made at all the collecting stations during the year. The examination dates are set out at the head of Table 3, which records all the plants seen; no quantitative sampling of the microflora was attempted; on each date specified notes were made on the distribution of *Ulothrix*, *Stigeoclonium*, *Cladophora* and other algae which could be seen with the naked eye, and scrapings were taken from stones and rocks and 'squeezings' from submerged bryophytes (as described by West & Fritsch, 1927, p. 13). On each occasion an adequate portion of the stream bed

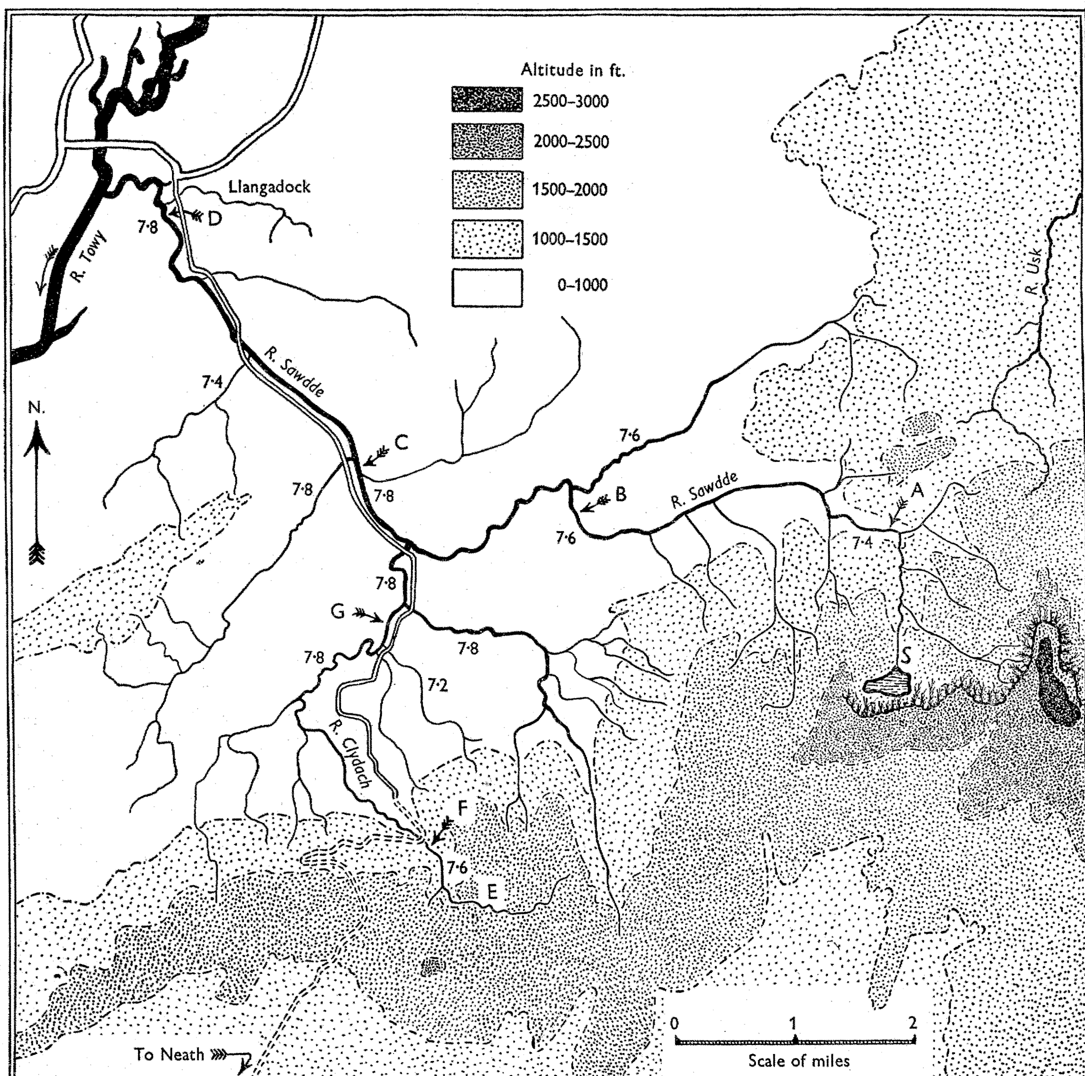

Fig. 1. Map of the river Sawdde and its tributaries. The centre of the area figured lies about 20 miles due north of Swansea Bay. Contours are drawn for 1000, 1500, 2000 and 2500 ft. A, B, C, D, E, F, G: collecting stations. *S* is the source of the river at Llyn-y-Fan-fach. The figures are a series of pH determinations made on 27 July 1948 with the river and its tributaries approximately at normal level.

Table 2. *The summer fauna of the river Sawdde*

v, very rare; r, rare; C, common; A, abundant; as explained in the text.

Habitats are given in the last column according to the following index. Where more than one figure is given the first indicates the favourite habitat and the others refer to situations where the species is less commonly found:

1. Large stones in swiftly flowing water.
2. Large stones with heavy growth of moss, in swiftly flowing water.
3. Stones and pebbles in moderately swift water.
4. Stones with dense algal growth, in moderately swift water.
5. Stones and coarse gravel in slack water near the banks.
6. Stones in still water at the river margin, with heavy deposits of silt.
7. Moss, grass and other vegetation immersed at the margins of the stream.
8. Small pools with silt-covered bottom, and heavy growth of *Cladophora*.

Collecting station ...	A	B	D	
Collecting dates (1948) ...	29 July 27 Aug. 14 Sept.	29 July 17 Aug. 14 Sept. 22 Sept.	1 Aug. 14 Aug. 30 Aug. 14 Sept.	Habitat
PLATYHELMIA				
Planaria alpina (Dana)	r	.	v	1, 3
OLIGOCHAETA				
Nais sp.	r	.	r	5
Chaetogaster sp.	.	.	r	5
CRUSTACEA				
Gammarus pulex (L.)	r	.	.	5
Candona sp.	.	.	r	5
MOLLUSCA				
Ancylastrum fluviatile (Müll.)	.	C	C	3
Hydrobia jenkinsi Smith	.	.	r	8
HYDRACARINA				
Protzia exemia (Protz.)	r	r	.	3
Sperchon brevirostris Koen.	r	r	r	3
S. glandulosus Koen.	r	C	r	3
Diplodontus despiciens (Müll.)	.	.	r	3
Lebertia celtica Sig Thor	r	C	r	4, 5
Attractides brevirostris Halb.	C	r	A	4, 3
Hygrobates naicus (Jonst.)	r	.	r	3, 2
Megapus spinipes (C. L. Koch)	.	.	v	1
Ljania bipapillata Sig Thor	r	.	.	?
COLLEMBOLA				
Podura sp.	.	r	.	7
PLECOPTERA				
Dinocras cephalotes (Curt.)	C	r	r	1
Perla carlukiana Klap.	C	C	A	1
Perlodes mortoni (Klap.)	v	.	.	1
Isoperla grammatica (Poda)	.	.	r	3
Leuctra fusciventris Steph.	C	C	A	3, 5
L. geniculata Steph.	.	.	A	6
Protonemura meyeri (Pict.)	C	r	.	3
Amphinemura cinerea (Oliv.)		.	r	3, 4, 5
EPHEMEROPTERA				
Ephemera danica Müll.	.	.	r	5
Ephemerella notata Eaton	C	C	C	2, 4
Baetis rhodani (Pict.)	A	A	A	1, 2, 3, 4
Rhithrogena semicolorata (Curt.)	.	.	r	1, 3
Ecdyonurus venosus (Fab.)	C	C	r	5, 6

Table 2. (*cont.*)

Collecting station ...	A	B	D	
Collecting dates (1948) ...	29 July 27 Aug. 14 Sept.	29 July 17 Aug. 14 Sept. 22 Sept.	1 Aug. 14 Aug. 30 Aug. 14 Sept.	Habitat
HEMIPTERA				
Velia currens (Fab.)	r	C	C	5
TRICHOPTERA				
Stenophylax stellatus (Curt.) (pupae)	.	C	.	5
Sericostoma personatum (Spence)	r	C	r	5
Goera pilosa (Fab.)	r	r	.	5
Odontocerum albicorne (Scop.)	r	r	v	5
Hydropsyche instabilis (Curt.)	C	r	r	3
Plectrocnemia conspersa (Curt.)	r	r	C	6, 4
Polycentropus flavomaculatus (Pict.)	.	.	r	3
Philopotamus montanus (Donov.)	.	r	r	2
Glossosoma boltoni Curt. (pupae)	r	A	A	3
Rhyacophila obliterata McLachl.	r	C	C	1, 3
COLEOPTERA (imagines)				
Haliplus lineatocollis (Marsh.)	.	.	v	7
Oreodytes davisii (Curt.)	.	v	.	5, 3
O. septentrionalis (Gyll.)	.	r	C	6, 5, 3
O. rivalis (Gyll.)	r	r	r	5, 3
Platambus maculatus (L.)	.	.	v	8
Gyrinus natator (L.) var. substriatus Steph.	.	r	.	5
Orectochilus villosus (Müll.)	.	.	r	6
Hydraena gracilis Germ.	.	r	r	3, 2
Elmis maugei Bed.	r	v	.	3
Esolus parallelopipedus (Müll.)	C	r	r	3, 2
Limnius tuberculatus Müll.	.	r	r	2
Latelmis volkmari (Pz.)	r	r	.	3
COLEOPTERA (larvae)				
Dytiscidae	r	C	C	5
Gyrinidae	.	r	r	3
Helmidae	r	r	r	2
Helodidae	r	r	.	?
DIPTERA				
Tipula sp.	.	.	r	6
Dicranota	.	r	r	5
Limnophila sp.	.	r	r	5
Dixa sp.	C	r	r	7
Pentaneura sp.	C	C	C	3
Anatopynia sp.	.	.	r	6
Procladius sp.	.	.	v	?
Syndiamesa sp.	v	.	.	?
Cricotopus sp.	.	r	C	4
Hydrobaenus sp.	r	C	C	4
Chironomus spp.				
s.g. Endochironomus	r	r	.	4
s.g. Microtendipes	.	r	.	4
Tanytarsus sp.	.	.	r	6
Ceratopogonidae	.	v	.	5
Simulium spp. (mainly S. tuberosum Lundstr.)	C	C	r	3
Tabanus sp.	.	.	r	6
PISCES				
Phoxinus phoxinus (L.) (minnow)	.	.	C	8
Gasterosteus aculeatus L. (three-spined stickleback)	.	.	r	8
Cottus gobio L. (bullhead)	.	.	r	3
Salmo trutta L. (brown trout) S. salar L. (salmon)	Present, but not taken in the samples			

was examined, and care was taken to collect a representative sample of the microscopic forms by taking scrapings and squeezings from many points at the collecting station, including shallow and moderately deep, swift and slack water. In the laboratory the material collected in this way was mixed, and many portions of the mixture were examined at once in order to determine the more abundant algae present. Later the material was allowed to settle, and the rarer diatoms were determined by boiling the deposits with hydrochloric and nitric acids, separating the diatoms by sedimentation in the usual way, and mounting in Gurr's Clearax. At station D masses of diatoms could be collected from stones in slack water near the banks, particularly in September and October, but this could not be done at the other collecting stations where the submerged bryophytes yielded most of the algae.

In the identification of green and blue-green algae West & Fritsch (1927) and Smith (1933) were the principal works consulted; the literature used for the identification of diatoms included Boyer (1927), Van Heurck (1880–5) and Hustedt (1930). The diatom nomenclature is that of Hustedt.

No examination of plankton was made; it would appear that in shallow rivers the plankton represents 'a pale image of the benthos', from which it is almost entirely derived (Butcher, 1940, p. 210). According to their regularity of appearance in the different samples and the numbers or quantity seen, the plant species are classified as 'abundant', 'common', 'rare' or 'very rare'. A species denoted as abundant is one seen in every examination of the region specified and sometimes sufficiently abundant to be a dominant form; those denoted as common were present in moderate quantity in all or most of the samples, but were never clearly dominant types. Plants of more irregular occurrence and greater rarity are indicated as rare or very rare; diatoms classified as very rare were only seen after systematic search of the prepared slides.

This classification is, of course, very rough and covers an enormous range of abundance; thus in the case of *Gyrosigma spenceri* only two specimens were seen, while at the other extreme *Diatoma vulgare* occurred in all the samples taken at station D and usually in masses containing millions of frustules.

Of the filamentous green algae, *Ulothrix* is most widespread, and from time to time during the year was abundant at stations D and F. Growth was usually more scanty at the tree-shaded stations. At D the spring growth of this alga rendered the whole stream bed green. Two species appear to occur, one has large cells with thick walls (probably *U. zonata*), the other has small, thin-walled cells and may be *U. subtilis*. A species of *Zygnema* was seen growing abundantly at E and F on boulders and rocks over which the water pours in a thin trickle. *Stigeoclonium* appeared sporadically at C and D, but never equalled the *Ulothrix* in abundance, and its distribution was very patchy. *Spyrogyra* occurred in small, sand-bottomed pools and E and F in summer. Desmids are not common, as might be expected from the calcareous nature of the water; the only species at all common and well distributed is *Closterium leibleinii*, the commonest desmid of the Tees (Butcher *et al.* 1937, p. 118). Smith (1933, p. 565) states that rich collections of desmids are usually made only when the water has a pH of 5·0–6·0. It is probable that these plants do not flourish in swiftly flowing water even if this is somewhat acid; thus Reese (1937) found that desmids are rather rare in the river Rheidol, which has very soft water of pH 5·8–6·4. *Lemanea* was only seen at station A in spring, when it formed an abundant growth on some of the boulders. *Phormidium* occurred mainly on large, immovable stones and flat boulders in swift, shallow water. At station B patches up to 8 in. square were found. Apart from *Phormidium* the blue-green algae are comparatively rare.

The diatom flora includes about 85 species, but not many of these are common. In the Sawdde *Ceratoneis arcus* was an abundant spring species, but comparatively rare in the summer samples; this diatom was very variable in size and shape, and many curiously distorted frustules were seen. In August, *Diatoma vulgare* and *Achnanthes minutissima* appeared to be the most numerous species, and *Cocconeis placentula* was very common, except at station A. At station D the *Cocconeis* covered most of the *Cladophora*. The *Diatoma* frustules were variable in size but very constant in form, and the elongate varieties of the Tees (Butcher *et al.* 1937, pl. 8, 3*a*–3*d*) were not seen. *Achnanthes microcephala*, or at least the type form of this species, was rare except at station A.

The October samples at stations C and D contained great numbers of *Navicula viridula*, and in November this species, *Nitzschia dissipata* and *Melosira varians* seemed to have become the dominant types. Other common and well-distributed species in the Sawdde are *Synedra ulna*, *Cymbella ventricosa* and *Gomphonema olivaceum*, all three very variable in size and form. At station D the very large diatom *Didymosphenia gemminata* was abundant in August, epiphytic on the *Cladophora*.

In the Clydach the diatom samples varied from time to time and from station to station far more than those taken from the Sawdde, and tended to be characterized more by variety of species than by the dominance of particular types. *Tabellaria flocculosa* was common from time to time, and *Diatoma hiemale* var. *mesodon* was abundant in spring and autumn.

In some respects the microflora of the Sawdde-Clydach system resembles that of the upper reaches

Table 3. *The flora of the rivers Sawdde and Clydach*

v, very rare; r, rare or infrequent; C, common; A, abundant; as explained in the text.

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April 27 Aug. 14 Sept. 10 Nov.	10 April 29 July 17 Aug. 14 Sept. 23 Sept. 28 Dec.	24 March 1 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov.	24 March 1 Aug. 14 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov. 28 Dec.	10 July 19 Aug. 6 Sept. 20 Sept.	24 March 14 July 28 July 22 Aug. 16 Sept. 2 Oct. 10 Nov.	24 March 26 July 30 Aug. 9 Sept. 10 Nov.
PHANEROGAMA							
Potamogeton sp.	.	.	.	.	r	.	.
BRYOPHYTA							
Aplozia riparia (Tayl.)	r	.	.	.	r	r	.
Fontinalis antipyretica L.	C	C	C	r	r	A	C
CHLOROPHYCEAE							
Ulothrix spp.	C	C	r	A	r	A	C
Microspora sp.	.	.	.	.	r	C	.
Stigeoclonium spp.	.	.	r	C	.	.	.
Cladophora sp.	r	r	r	C	.	r	r
Ankistrodesmus falcatus (Corda) Ralfs	v	v	r	r	.	.	.
Scenedesmus obliquus (Turp.) Kütz.	v	.	.	.	.	.	.
Mougeotia sp.	.	.	.	.	A	C	.
Zygnema sp.	.	.	.	.	A	A	.
Spirogyra sp.	.	.	.	.	r	r	.
Gonatozygon sp.	v	.	.	.	r	.	.
Netrium digitus (Ehr.) Itz. & Rothe	.	.	.	.	v	v	.
Roya sp.	.	.	.	.	r	.	.
Closterium spp. (mainly C. leibleinii Kütz.)	C	r	r	r	r	r	r
Tetmemorus granulatus (Bréb.) Ralfs	.	v	.	.	.	.	.
Euastrum verrucosum Ehr.	v	.	.	.	.	.	.
E. elegans Bréb.	v	.	.	.	.	.	.
E. didelta (Turp.) Ralfs	.	.	.	.	r	.	.
Cosmarium spp.	r	r	r	r	r	r	r
Micrasterias truncata (Corda) Bréb.	.	.	.	.	.	.	v
M. denticulata Bréb.	.	.	.	.	v	.	v
Staurastrum spp.	.	.	.	.	.	.	r
Xanthidium armatum (Bréb.) Rab.	.	.	.	.	.	v	.
Hyalotheca dissiliens (Sm.) Bréb.	.	.	.	.	.	.	v
RHODOPHYCEAE							
Batrachospermum moniliforme Roth.	.	.	.	.	r	.	.
Lemanea mammillosa Kütz.	r	.	.	.	.	.	.
MYXOPHYCEAE							
Merismopedia sp.	.	.	.	v	.	.	.
Synechococcus sp.	r	.	.	.	.	.	v
Chamaesiphon sp.	.	r	r	.	r	r	.
Phormidium spp.	r	C	r	r	r	C	r
Nostoc sp. (young spherical colonies)	r	.	.	v	.	.	r
Tolypothrix sp.	r	v	.	.	.	.	.
Rivulariaceae sp.	.	.	.	.	.	r	.

Table 3. (*cont.*)

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April 27 Aug. 14 Sept. 10 Nov.	10 April 29 July 17 Aug. 14 Sept. 23 Sept. 28 Dec.	24 March 1 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov.	24 March 1 Aug. 14 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov. 28 Dec.	10 July 19 Aug. 6 Sept. 20 Sept.	24 Maıch 14 July 28 July 22 Aug. 16 Sept. 2 Oct. 10 Nov.	24 March 26 July 30 Aug. 9 Sept. 10 Nov.
BACILLARIAE							
Melosira varians Ag.	.	.	r	A	.	.	.
M. arenaria Moore	r	v	.	.	.	.	.
Cyclotella sp.	r	.	.	.	.	.	.
Tabellaria flocculosa (Roth.) Kütz.	r	r	r	r	C	C	C
T. fenestrata (Lyngb.) Kütz.	v	v	.	.	.	v	v
Diatomella Balfouriana Grev.	v	v	.	.	.	.	v
Meridion circulare Ag.	r	r	r	r	r	C	C
M. circulare var. constrictum (Ralfs) Van Heurck	v	r	.	.	.	.	v
Diatoma vulgare Bory	r	C	A	A	.	r	C
D. hiemale (Lyngb.) Heib.	.	r	r	.	.	C	.
D. hiemale var. mesodon (Ehr.) Grun.	r	r	r	r	.	A	r
Fragilaria capucina Desmaz. F. intermedia Grun	r	r	r	C	.	r	r
F. construens (Ehr.) Grun.	.	r	v	.	.	.	.
Synedra ulna (Nitzsch.) Ehr.	C	C	C	C	r	C	C
S. acus Kütz. ?	r	r	.	.	.	.	.
Ceratoneis arcus Kütz. C. arcus var. amphioxys (Rabh.)	A	A	A	A	r	C	C
Eunotia arcus Ehr. E. arcus var. fallax Hust.	A	r	r	r	r	C	C
E. pectinalis (Kütz.) Rabh. E. pectinalis var. minor (Kütz.) Rabh.	A	C	r	r	C	C	r
E. lunaris (Ehr.) Grun.	r	.	.	.	.	C	.
E. robusta Ralfs var. tetraodon (Ehr.)	.	.	.	.	v	.	.
E. tridentulata Ehr.	v	.	.	.	.	.	.
Achnanthes coarctata (Bréb.) Grun.	.	v	v	v	.	.	.
A. lanceolata Bréb. A. lanceolata var. elliptica Cleve	r	r	r	r	r	C	r
A. microcephala Kütz.	C	r	r	r	.	r	r
A. minutissima Kütz. A. minutissima var. cryptocephala Grun. A. linearis W. Smith	C	A	A	A	r	C	A
Rhoicosphenia curvata (Kütz.) Grun.	v	r	r	r	.	r	r
Cocconeis placentula Ehr.	r	C	C	A	r	C	A
C. pediculus Ehr.	.	.	r	C	.	.	.
Navicula rotaeana (Rabh.) Grun.	v	v	v	r	.	v	v
N. cryptocephala Kütz.	r	r	C	r	r	r	C
N. anglica Ralfs	.	v	v	r	.	r	v
N. gracilis Ehr.	v	v	C	r	.	.	.
N. rhyncocephala Kütz.	r	r	.	.	r	r	.
N. viridula Kütz.	1	A	A	A	v	r	A
N. dicephala (Ehr.) W. Smith	.	.	v	.	.	.	v
Pinnularia leptosoma Grun.	.	r	.	r	.	.	.
P. interrupta W. Smith	r	.	.	.	r	.	.
P. brebissonii (Kütz.) Cleve	v	.	v	.	.	r	.
P. major (Kütz.) Cleve	r	v	v	.	.	.	.
P. viridis (Nitzsch.) Ehr.	r	r	r	.	r	r	r
P. subcapitata Greg.	.	.	v	.	r	r	r

Table 3. (*cont.*)

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April 27 Aug. 14 Sept. 10 Nov.	10 April 29 July 17 Aug. 14 Sept. 23 Sept. 28 Dec.	24 March 1 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov.	24 March 1 Aug. 14 Aug. 22 Aug. 29 Sept. 2 Oct. 10 Nov. 28 Dec.	10 July 19 Aug. 6 Sept. 20 Sept.	24 March 14 July 28 July 22 Aug. 16 Sept. 2 Oct. 10 Nov.	24 March 26 July 30 Aug. 9 Sept. 10 Nov.
BACILLARIAE (*cont.*)							
P. gibba Ehr.	.	v	.	.	.	.	.
P. lata (Bréb.) W. Smith	.	v	.	.	.	.	.
Neidium iridis (Ehr.) Cleve	.	.	.	.	.	r	.
Diploneis elliptica (Kütz.) Cleve	v	v	.	.	r	v	.
Stauroneis phoenicenteron Ehr.	v	v	.	.	v	.	.
S. anceps Ehr.	.	v	v	.	.	v	.
Amphipleura pellucida Kütz.	v	r	.	.	v	r	r
Frustulia rhomboides (Ehr.) De Toni	.	v	.	.	.	v	.
F. vulgaris Thwaites	v	r	v	.	.	v	v
Gyrosigma Spenceri (Queckett) Cleve	.	v	.	.	.	.	.
Gomphonema acuminatum Ehr. (mainly var. coronatum (Ehr.) W. Smith)	r	r	r	r	C	r	r
G. constrictum Ehr.	r	.	r	.	.	.	r
G. parvulum (Kütz.) Grun.	r	r	.	r	r	C	r
G. angustatum (Kütz.) Rabh.	.	.	v	r	.	r	v
G. lanceolatum Ehr.	r	.	.	r	.	.	.
G. intricatum Kütz.	r	.	r	r	.	r	.
G. olivaceum (Lyngb.) Kütz.	r	C	C	C	.	C	C
Didymosphenia gemminata (Lyngb.) M. Schmidt	r	r	r	A	.	.	r
Cymbella cuspidata Kütz.	.	.	.	.	.	r	v
C. affinis Kütz.	v	.	v	r	.	r	.
C. sinuata Greg.	r	r	C	C	.	r	C
C. lanceolata (Ehr.) Van Heurck	v	.	v	.	.	v	v
C. cistula (Hempr.) Van Heurck	C	r	r	r	.	C	r
C. helvetica Kütz.	r	r	r	r	r	C	r
C. angustata (Kütz.) Cleve	.	.	.	.	.	.	v
C. ventricosa Kütz.	C	C	C	C	r	C	C
C. prostrata (Berk.) Cleve	.	v	v	r	.	v	.
C. delicatula Kütz.	r	v	v	.	.	C	.
Ampora ovalis Kütz.	.	v	.	v	v	.	.
Epithemia argus Kütz.	r	.	.	.	r	.	.
E. zebra (Ehr.) Kütz.	.	v	v	.	r	r	.
E. gibberula (Ehr.) Kütz.	.	.	.	.	.	r	.
Rhopalodia gibba (Ehr.) O. Müll.	r	.	.	.	.	v	.
Nitzschia linearis W. Smith	v	r	r	v	.	.	v
N. palea (Kütz.) W. Smith	.	r	r	C	.	.	r
N. dissipata (Kütz.) Grun.	.	.	r	A	.	.	.
N. sinuata (W. Smith) Grun.	v	.	v	.	.	.	.
N. acicularis W. Smith	.	.	v	v	.	.	.
Hantzschia amphioxys (Ehr.) Grun.	.	.	.	.	.	r	v
Denticula sp.	.	.	.	.	.	r	r
Cymatopleura solea (Bréb.) W. Smith	.	v	v	.	.	.	.
Surirella ovata Kütz.	v	r	r	r	.	.	.
S. robusta Ehr.	.	r	.	.	.	.	.

of the Tees, where *Diatoma vulgare*, *Achnanthes microcephala*, *Gomphonema olivaceum*, *Cocconeis placentula*, *Navicula viridula* and *Cymbella ventricosa* are common diatoms (Butcher *et al.* 1937, p. 69). *Cocconeis placentula*, *Achnanthes minutissima* and *Gomphonema olivaceum* are dominant diatoms in the unpolluted rivers Test and Itchen, which contain a plentiful supply of calcium and other mineral salts (Butcher, 1946, pp. 274, 283).

The only phanerogam seen in the Clydach is a species of *Potamogeton*, of which a little grows at one point in region E. No phanerogams occur in the main stream of the Sawdde. The only common bryophyte is the moss *Fontinalis antipyretica*, which is generally distributed throughout the Sawdde system, including all its main tributaries. The stability of the river bed probably accounts for the abundance of the moss, which grows most luxuriantly in the cascade section of the Clydach at region F.

It would appear from this examination of the flora of the Clydach and the Sawdde that the chief plants available as food for the fauna are *Fontinalis*, *Ulothrix* and a considerable variety of diatoms. Less abundant and more irregularly distributed plants are the liverwort, *Aplozia*, the green algae *Zygnaema*, *Microspora*, *Mougeotia*, *Cladophora* and *Stigeoclonium*, and the blue-green alga *Phormidium*. In addition to plant material actually growing in the water there is a plentiful supply of leaves from the trees and other plants on the banks, for the Sawdde valley is well wooded with coniferous and deciduous trees. The extent to which the plant food supply is utilized by some of the chief insect species is discussed in the next section.

4. THE FOOD OF THE DOMINANT INSECT SPECIES

(a) *Literature*

Throughout zoological literature there is scattered a great deal of information regarding the feeding habits of aquatic insects. Not all this information is accurate, some of it is largely conjecture, and it would appear that observations on the feeding habits of particular species have led to general statements recklessly applied to related species and genera, and even all insects of the same order. Thus Rousseau (1921, p. 279) and more recently Mellanby (1942, p. 128) have stated that all stonefly nymphs are carnivorous, a generalization which is far from correct.

Most investigators have confined their attention to particular genera, families or orders. Rawlinson (1939, p. 405) has dealt with the method of feeding in *Ecdyonurus*, and has reviewed earlier literature dealing with the feeding habits of mayfly nymphs; Needham, Traver & Hsu (1935, p. 224) have supplied some information regarding the nymphs of North American Ephemeroptera. Frison (1929, p. 365) has reviewed the literature on the feeding habits of Plecopteran nymphs, and Hynes (1941, p. 529) has studied all the British species of this order. Tillyard (1917, p. 329) makes some general observations on the food of the naiads of the Odonata. Lloyd (1921) and Ross (1944, p. 4) have described the food of North American trichopteran larvae; Slack (1936) has studied a number of British species, mainly of the case-carrying type, and Nielsen (1948, p. 163) describes the mode of feeding of the Hydroptilidae.

In regard to the Coleoptera it appears to be generally accepted that the Gyrinidae and Dytiscidae are carnivorous and the Hydrophilidae and Haliplidae phytophagous (Ward & Whipple, 1918, pp. 907–8; Miall, 1903, pp. 33–89), but little detailed investigation of the food and feeding habits of the water beetles appears to have been made except in the case of *Dytiscus* and a few other genera. Alexander (1920, p. 717) has discussed the feeding habits of the larvae of the Tipulidae. Smart (1944, p. 20) and Puri (1925, p. 298) deal with the food of *Simulium*, and Goeghtgebuer (1927, 1928, 1932) supplies information regarding the food of some genera of the Chironomidae.

The food of aquatic insects is determined to a considerable extent by the environment in which they live; thus *Polycentropus flavomaculatus* in Lake Windermere feeds upon small Crustacea (Moon, 1934), in the river Amman on chironomid larvae (Jones, 1948); and in the river Rheidol I have found that it feeds mainly upon *Rhithrogena* and *Baetis*; nymphs of *Nemoura vallicularia* under natural conditions will eat decaying leaves and a great variety of desmids, diatoms and other unicellular algae, but in captivity they will live entirely upon elm leaves (Wu, 1923, p. 39). Puri (1925, p. 298), reviewing the literature relating to the food of *Simulium*, remarks that larvae of different species collected from the same locality always show more or less the same type of gut contents, and that the wide divergencies in the accounts given by different investigators of the food of *Simulium* larvae can be attributed to the insects they examined having come from different localities. The very abundance of a plant may force phytophagous insects to eat it; thus Needham *et al.* (1935, p. 225) describe a stream in which the diatom *Meridion* may appear in such profusion as to cover every available object; mayfly nymphs collected have their stomachs full of this diatom and little else.

In this study the writer has attempted to gather some information on the feeding habits of the dominant insect species of the Clydach-Sawdde stream system, taking into account, as far as possible, the type of fauna present, the flora and the general nature of the environment. During July and August 1948 about 600 specimens were examined for gut contents, and an attempt was made to identify as accurately as possible the nature of the food, whether plant or animal.

(*b*) *Methods*

In the case of large, carnivorous insects such as *Perla*, *Dinocras* and *Plectrocnemia* the specimens were dropped into 70% alcohol at the collecting station and could be examined, if necessary, 2 or 3 days later, though removal of the gut is facilitated by prompt examination, and vegetable food, if present, can be more easily recognized. The head of the insect is cut off, the end of the abdomen is cut off to free the hind-gut, the alimentary canal is pulled out and placed on a microscope slide. Using a low-power binocular the anterior portion of the gut is slit open with a cutting needle, the contents removed, spread on the slide and covered with a drop of dilute glycerine and a cover-slip for examination with the microscope. Considerable care is necessary in removing animals from the gut in order that the food of the prey is not mistaken for food eaten by the predator; here, knowledge of the food of the prey is very helpful in preventing mistakes. With trichopteran larvae an alternative method of removing the gut was found very successful; the larva, killed with 70% alcohol, is placed on its side on the microscope slide, the head is held with one pair of forceps, and with another pair the base of one front leg is gripped and pulled backwards so that the body wall is torn down the side of the thorax and abdomen. It is then a very simple matter to extract the gut. The gut contents in a large trichopteran larva may be very bulky, and five or six preparations may have to be made in order to examine it all. In the case of the smaller insects studied, particularly omnivorous and phytophagous types, it was found that the examination of specimens placed in alcohol was not very satisfactory, as the removal of the gut and its contents might be very difficult. Here the procedure adopted was to collect the specimens, transport them to the laboratory as quickly as possible, and begin the examination of the gut contents at once. The live insect is placed on the microscope slide, quickly decapitated with a cutting needle, the end of the abdomen is cut off; usually the longitudinal muscles of the body contract so that the gut protrudes from the prothorax and is readily extracted. Usually it was possible to make successful determinations of the food up to about 2 hr. after capture.

In the case of adult Dytiscidae and Gyrinidae the removal of the fore-gut is very simple; the beetle is killed with 70% alcohol, or with chloroform water, the thorax is gripped with one pair of forceps, and another is used to pull the head away from the body; the alimentary canal breaks at the anterior end of the mesenteron, and gizzard and crop come away with the head.

The part of the alimentary canal where recently eaten and recognizable food was found varied in the different species studied. In *Perla* and *Dinocras* and the Coleoptera identifiable material is generally found in the fore-gut only; in *Leuctra*, the Ephemeroptera and the Trichoptera the whole of the mid-gut may contain materials that can be recognized. The larger stoneflies swallow their prey entire, so that its identification is easy; in the case of insects which bite their prey into pieces the food organism can usually be recognized by some characteristic feature; thus ecdyonurid nymphs can be identified by their brush-bearing mouthparts even if extensively fragmented, *Simulium* larvae by their feeding brushes and anal hook circles, small Plecoptera by the form of the tarsus, and the Tanypodinae by the lingua. When many much-fragmented prey organisms of the same kind occurred in one gut, the number eaten was estimated by counting the number of heads present.

The results are summarized in Table 4. 'Gut contents digested' means that the anterior part of the gut contained a soupy mass of food in which nothing could be recognized. 'Detritus' means amorphous vegetable matter mixed with fine grit and occasionally with a few empty algal cells. The presence of algae is indicated only when the cells contained chloroplasts, showing that the insect had swallowed the living plant, odd empty cells were ignored. Diatoms are indicated as present only when the gut contained what appeared to be a significant number; a few diatoms, mainly empty frustules, were always present when the gut contained detritus.

The unbracketed numbers opposite the list of 'foods' signify the number of specimens in which this food was found. The bracketed numbers inserted in the case of some of the predatory species indicate the numbers of prey organisms found in the total number of specimens examined. Thus in the case of *Perla carlukiana* 14 of the specimens examined had *Simulium* larvae in the gut; the total number of *Simulium* larvae seen in the 75 *Perla* nymphs examined was 31.

(*c*) *Plecoptera*

Perla and *Dinocras* appear to be the dominant predatory insects, feeding on a wide range of food organisms, particularly *Baetis*, *Ephemerella*, chironomid larvae and *Simulium*. The chironomid larvae were mainly Orthocladiinae. It was found that *Baetis* and *Ephemerella* nymphs present in the gut contents could seldom be distinguished with certainty, though both genera could easily be distinguished from *Ecdyonurus* by the combs on the tarsal claws; hence the two former genera are grouped together in Table 4. One *Dinocras* nymph contained vegetable

Photo 4. The river Sawdde at Station D (Careg-Sawdde).

food only (*Fontinalis* and *Ulothrix*); one had several desmids in its crop together with insect food. None of the *Perla* nymphs appeared to have been feeding on plant food alone, but the crops of four contained green masses of *Ulothrix* as well as a variety of insect food.

Most of the insects eaten by these large stonefly nymphs appeared to have been swallowed entire. One *Perla* specimen contained 8 *Baetis* and one contained 12 chironomids and 3 *Protonemura* nymphs, but in most of the specimens the meal tended to consist of a small number of prey of moderate or large size rather than a large number of small animals. The trichopteran larvae eaten were of considerable size, one sufficing to fill the stomach of the predator. At other times of the year, of course, very small prey may form a greater proportion of the food. *Perla* appears to have a larger appetite than *Dinocras*; thus 46 *Dinocras* nymphs contained insect food totalling about 71 prey individuals, while the 40 *Perla* nymphs which contained recognizable food had eaten 191 insects.

In the streams of the Lake District *Perla carlukiana* appears to be more partial to vegetable food, for Hynes (1941, p. 530) found that 16 % of the specimens he examined contained vegetable food only, and only 50 % had fed exclusively on animal matter. The corresponding figures for *Dinocras* (*Perla cephalotes* in Hynes's Table) are 4 and 64 %.

Leuctra fusciventris is herbivorous—detritus, leaf fragments, green algae and diatoms being its chief foods. The diatom feeders were among those captured at station D, and the chief genera of diatoms present were *Achnanthes*, *Cocconeis*, *Cymbella* and *Gomphonema*. *Leuctra geniculata* appears to feed mainly on detritus, though many specimens contained leaf fragments or green algae; the relative amount of these food substances present was very small. If detritus is the favourite food of *L. geniculata*, this would explain its occurrence at station D, where much detritus appears to be deposited in the stony shallows. Lestage (1920) has suggested that the peculiar processes on the antennae, which distinguish nymphs of this species from others of the genus, are an adaptation for burrowing.

Protonemura meyeri is common in the Sawdde at station A, but the specimens taken during the summer were too small for satisfactory examination. Hynes's data (1941, p. 530) show that it feeds mainly on 'higher plant and moss tissue'.

(*d*) *Ephemeroptera*

Of the dominant mayfly species in the stream system studied *Baetis rhodani* and *Ephemerella notata* are generally distributed. *Ecdyonurus venosus* is common at stations A, B, F and G. In the summer of 1948 *Siphlonurus lacustris* occurred only at station E in shallow pools with silt-sand bottom and fringed with grasses. Table 4 shows that these insects subsist on vegetable matter and detritus, but there are definite differences in the diets of the four species. *Ecdyonurus* is the chief detritus feeder, the gut being usually full of soft, amorphous matter mixed with much fine grit and sometimes very small fragments of moss. In some of the specimens diatoms were abundant; *Cocconeis*, *Achnanthes*, *Tabellaria*, *Ceratoneis* and *Synedra* were the main genera represented. Whether these diatoms were alive when eaten or were dead frustules forming part of the detritus was not clear. *Baetis* appeared to eat moss, detritus, green algae and diatoms in various proportions at the different stations. The main food of *Siphlonurus* appears to be detritus and leaf fragments, and *Ephemerella* seems to subsist chiefly on *Fontinalis* and *Ulothrix*. On 14 July 1948, 14 specimens of *Ephemerella* from station F were examined, and in these the moss was the main food; 6 specimens contained little else. On this date there was very little *Ulothrix* growing on the stream bed. A fortnight later an abundant growth of *Ulothrix* had appeared at this station. A further batch of *Ephemerella* was then examined, and in these the green alga was the main food present.

(*e*) *Trichoptera*

Six species of Trichoptera were studied. *Plectrocnemia* and *Rhyacophila* appear to be entirely carnivorous, the prey of the former displaying considerable variety. One *Rhyacophila* larva contained about 10 chironomid larvae, but 3–5 was usually the number of prey insects present. Ross (1944, p. 4) states that he has seen larvae of this genus with 40–60 chironomids in the gut. *Hydropsyche* appeared to be omnivorous but with a decided preference for animal food, for all those examined which had recognizable material in the gut had eaten animal food and 7 had eaten animal food only. *Hydropsyche* larvae are said to catch their prey in the net-traps; they spin amidst weeds and stones, but whether they obtain all their food in this way is not clear.

Philopotamus is mainly a diatom feeder; the gut often contained some gritty detritus and a few small fragments of moss, but in a typical case its main contents is a smooth mass of millions of diatoms in which a considerable variety of species are represented. Lloyd (1921, p. 109) states that the larvae of the Philopotamidae collect masses of diatomaceous ooze with the nets they spin. The *Hydropsyche* larvae examined had fed mainly upon small insects; only 3 specimens had any significant number of diatoms in the gut, and if it is correct that *Hydropsyche* and *Philopotamus* collect most of their food with nets some explanation is necessary for the difference in their diets. Perhaps the nets spun by the latter have a much closer mesh, and it may be that the former

Table 4. *Summary of observations on the gut contents of some of the dominant insect species*

(Explanation in the text, § 4 (*b*)).

	Plecoptera				Ephemeroptera				Trichoptera						Coleoptera	
Collecting station ...	A, F	A, B, D, G	D, F	D	B, F	D, F	D, F	E	A, B, D, G	G	D, E	F	B	B	F	D
Species ...	*Dinocras cephalotes*	*Perla carlukiana*	*Leuctra fusciventris*	*Leuctra geniculata*	*Ecdyonurus venosus*	*Baetis rhodani*	*Ephemerella notata*	*Siphlonurus lacustris*	*Rhyacophila obliterata*	*Hydropsyche instabilis*	*Plectrocnemia conspersa*	*Philopotamus montanus*	*Sericostoma personatum*	*Odontocerum albicorne*	*Oreodytes rivalis*	*Oreodytes septentrionalis*
No. of specimens examined	70	75	30	25	27	33	49	38	43	25	29	24	22	12	36	41
No. with the anterior part of the gut empty	16	25	3	1	2	1	3	—	5	1	8	6	—	—	11	16
No. with the gut contents digested	7	10	1	6	2	1	4	—	9	1	3	3	3	4	3	3
Gut contents:																
Detritus	—	—	17	16	22	25	11	38	—	—	—	9	6	6	—	—
Leaf fragments (*Fontinalis*)	1	—	15	14	6	—	21	—	—	9	—	2	—	—	1	—
Leaf fragments (various other plants)	—	—	—	—	—	—	—	35	—	—	—	—	18	2	—	—
Algae:																
Ulothrix	1	4	3	3	1	13	31	6	—	12	—	1	4	8	—	—
Microspora	—	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—
Stigeoclonium	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Cladophora	—	—	—	3	—	—	1	—	—	—	—	—	4	—	—	—
Cosmarium	1	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—
Other green algae	—	—	5	7	—	6	—	—	—	12	—	1	4	8	—	—
Batrachospermum	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Phormidium	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Diatoms	—	—	6	—	10	7	7	6	—	3	—	15	5	1	1	—
Crustacea:																
Copepoda	—	—	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	1
Gammarus pulex	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—

PLECOPTERA (nymphs):																
Perlidae	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chloroperla sp.	—	—	—	—	—	—	—	—	—	—	1 (2)	—	—	—	—	—
Leuctra sp.	2 (2)	1 (1)	—	—	—	—	—	—	—	1 (1)	1 (1)	—	—	—	—	—
Protonemura sp.	—	2 (4)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
EPHEMEROPTERA (nymphs):																
Baetis sp. } Ephemerella sp. }	20 (29)	32 (84)	1 (1)	—	—	—	—	—	9 (9)	16 (26)	5 (8)	—	—	4 (4)	7	6
Ecdyonurus sp.	2 (2)	—	—	—	—	—	—	—	2 (2)	—	1 (1)	—	—	—	—	—
TRICHOPTERA (larvae):																
Rhyacophila sp.	2 (2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hydropsyche sp.	1 (1)	1 (1)	—	—	—	—	—	—	1 (1)	—	1 (1)	—	—	2 (2)	—	—
Glossosoma sp.	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Philopotamus sp.	5 (7)	3 (3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA (imago):																
Sericostoma personatum	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COLEOPTERA:																
Haliplus sp. ? (imago)	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dytiscid larvae	1 (1)	—	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—
Helodid larvae	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DIPTERA (larvae):																
Pedicia sp. ?	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—	—	—
Dicranota sp.	—	—	—	—	—	—	—	—	2 (2)	—	—	—	—	—	—	—
Simulium spp.	2 (3)	14 (31)	—	—	—	—	—	—	11 (22)	4 (5)	6 (10)	—	—	—	—	1
Anatopynia sp.	1 (1)	1 (1)	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—
Pentaneura sp.	1 (1)	1 (1)	—	—	—	—	—	—	—	—	2 (4)	—	—	—	—	—
Cricotopus sp.	—	—	—	—	—	—	—	—	2 (6)	—	1 (1)	—	—	—	—	2
Tanytarsus sp.	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Other Chironomidae	8 (21)	17 (58)	—	—	—	—	—	—	13 (37)	13 (18)	3 (4)	—	—	—	11	14
DIPTERA (imagines):																
Species not identified	1 (1)	—	1 (1)	—	—	—	—	—	—	—	1 (1)	—	—	—	2	—
Animal remains not identified	5	3	1	—	—	—	—	—	5	6	5	—	—	3	3	4

supplements the net-caught food with prey caught in the normal way.

The chief case-carrying Trichoptera in this stream system are species with heavy cases made of gravel and small stones. Pupae of *Glossosoma boltoni* were abundant, but only 2 larvae were found, and in these the gut contained only green algae. The main food of the *Sericostoma* larvae appeared to be the dead leaves of deciduous trees, the stomach containing hundreds of small, square pieces. *Odontocerum* appears to be omnivorous, but only 12 specimens could be found Of these 8 contained recognizable food, including animal and plant material.

(*f*) *Coleoptera*

Oreodytes rivalis and *O. septentrionalis* are the common Dytiscidae. These little beetles appear to feed mainly on mayfly nymphs and chironomid larvae, but usually only isolated pieces of the prey are found in the crop, and it is rare to find an entire insect. Frequently the crop of the beetle contained only the tail end of one chironomid, or perhaps two heads with small portions of the thorax; sometimes only the legs of a mayfly nymph would be present. The crop of *Oreodytes* is very small and about three heads of small midge larvae are sufficient to fill it. Exactly how these small Dytiscidae feed is not clear; perhaps they kill the prey and swallow portions of it, perhaps they search for and eat pieces of insects killed by other predators or by movements of the stones on the stream bed. The high proportion of specimens with empty crops suggests that they feed at irregular intervals.

Seven specimens of *Orectochilus villosus* from station D were also examined; in each case the crop was full, but its contents was so fragmented that it could not be identified with certainty. The main prey present appeared to be *Velia currens*, which was common on the surface of the water where the beetles were swimming.

(*g*) *Diptera*

The gut contents of 24 *Simulium tuberosum* larvae from stations A and F were examined, and it was found possible to identify most of the food present in the alimentary canals of many *Simulium* found in the *Perla* specimens examined, but the species of these larvae could not be determined. The gut contents was much the same in all cases—a mixture of small fragments of moss and other leaves, short lengths of *Ulothrix* and other filamentous algae, diatoms and gritty detritus; two contained some *Ankistrodesmus* and one a little of the blue-green algae *Tolypothrix* and *Merismopedia*. No cases of cannibalism were seen, as reported by Smart (1944, p. 20). No attempt was made to study the gut contents of the chironomid larvae; in this group accurate identification is so difficult, particularly in the Orthocaldiinae, that specimens can be referred with certainty only to genera including a wide range of species, and it would appear that without accurate specific identification observations on the feeding habits of these larvae would not add to present knowledge.

(*h*) *General observations*

The foregoing results show that in this particular habitat *Baetis*, *Ephemerella*, *Simulium* and chironomid larvae are the most frequent prey of the carnivorous species. This is to be expected, for they are numerous, live in the swift current inhabited by the predators, and are not equipped with any form of protection. There are other common species which are not eaten to the same extent. *Ecdyonurus venosus*, though very common at most parts of the stream system, appears to escape the predatory Plecoptera and Ephemeroptera because it lives not in the swift current of mid-stream but in slack water near the banks, where the detritus on which it feeds accumulates, and it would appear that the flattened body shape of this species is not so much an adaptation for living in swift currents as one for creeping among tightly packed stones. *Glossosoma boltonii*, one of the most abundant insects in the Sawdde, is probably saved from being eaten by its massive, stony house. *Ancylastrum* is well protected by its smooth, conical shell. *Gammarus pulex* is plentiful in the upper part of the Clydach but is not preyed upon by any of the species studied; two *Oreodytes* had small pieces of *Gammarus* in their crops, but these contained no muscle and appeared to be moults. It may be that the large stoneflies, which like to swallow their prey entire, find the bristly Crustacean difficult to eat. The fishes are the chief enemies of *Gammarus pulex*; all the species recently studied by Hartley (1948) appeared to feed on it. The Hydracarina are another notable missing group in the list of food organisms in Table 4, and no Elminae seem to be eaten though, as a group, these beetles are not rare.

Of the different types of food material utilized by the phytophagous species the moss *Fontinalis* would appear to be that which varies least in amount; the amount of detritus available probably varies with the rainfall and the season, and the supply of green algae undergoes the most marked fluctuation. The quantitative data given for the Tees by Butcher *et al.* (1937, pp. 70–1) show the violent fluctuations that may take place in the amount of algal growth on the bed of a rapid, stony river; thus on 9 September 1931 no *Ulothrix* was recorded, on 28 September the growth amounted to 119 per sq.mm., on 7 October this had diminished to 1 per sq.mm., and these tables furnish many more such examples. Observations on the gut contents of *Ephemerella* described in § 4 (*d*) suggest that *Ephemerella* feeds on *Ulothrix* when this is plentiful and turns to *Fontinalis* when the *Ulothrix* is scarce, and it is possible that other species that feed on green algae have some standby to turn to when this is not available.

The role of the higher plants in the nutrition of fresh-water animals is discussed by Welch (1935, chap. 11). Shelford (1918, p. 47) considered that 'One could probably remove all the larger plants and substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations'. Welch regards this view as not well grounded, and points out that there is evidence that the larger plants serve as food for many invertebrate species; that they are eaten only to a very small extent by the fishes is probably correct.

The results of this investigation do not seem to suggest that the diatoms form a very important part

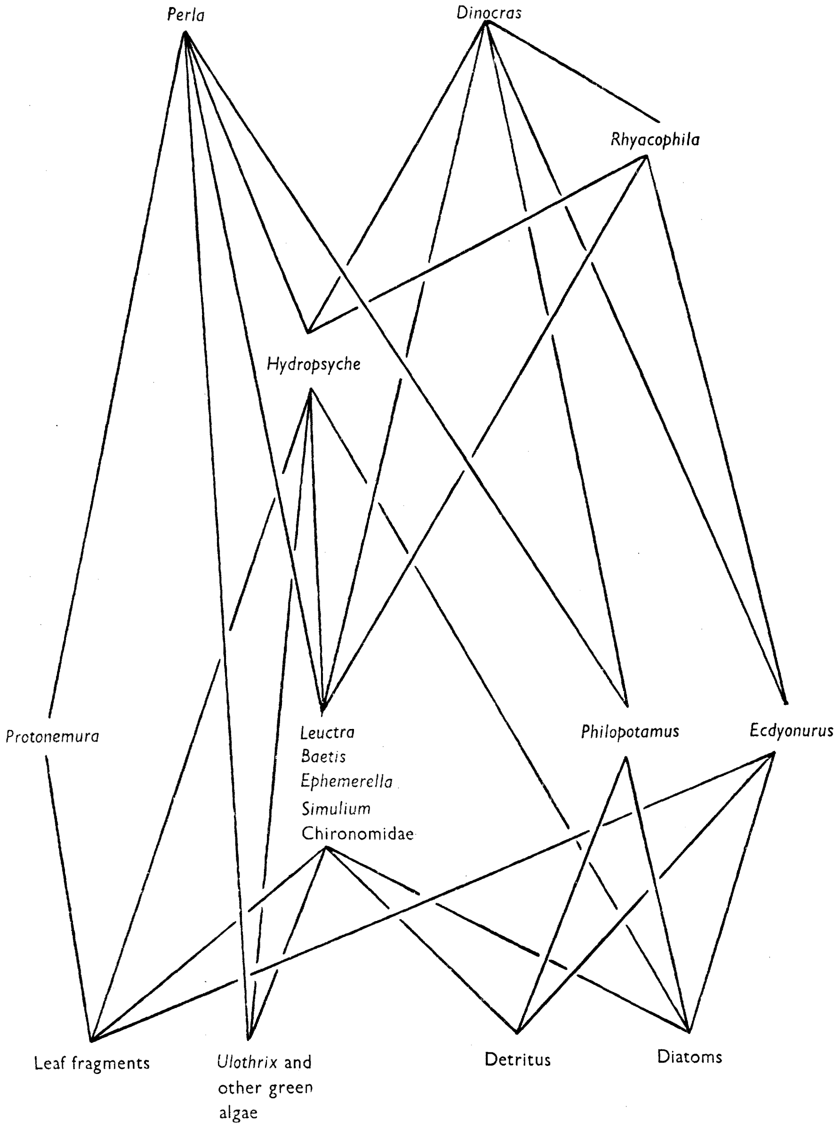

Fig. 2. The main features of the food chain in *Perla carlukiana*, *Dinocras cephalotes*, *Rhyacophila obliterata* and *Hydropsyche instabilis*. Based on Table 4 and, in the case of *Protonemura* and the Chironomidae, on the works cited in § 4 (*a*).

of the food of the fauna in spite of their abundance and variety. Of the species studied only *Philopotamus montanus* seems to be mainly dependent on them. However, it is possible that the very young stages of some species subsist to a considerable extent on diatoms. This, however, requires further investigation; in the case of the Plecoptera, Hynes (1941, p. 535) considers that the early stages feed mainly on detritus. Diatoms are probably an important food for the chironomid larvae; Needham & Lloyd (1916, p. 394) state that they are one of the chief foods of midge larvae, and it has been noted that the Chironomidae Orthocladiinae appear in the river Tees at the time of the spring diatom maximum (Butcher *et al.* 1937, p. 146).

From Table 4 it is possible to construct diagrams showing the food chain for the species investigated; Fig. 2 is an example summarizing the main features of the food chain in the case of *Perla*, *Dinocras*, *Rhyacophila* and *Hydropsyche*.

It would appear that further investigation on the lines of the present study should be of interest, and the writer hopes to carry out similar research on acid streams in the same area.

SUMMARY

1. This paper deals with the Sawdde and its tributary, the Clydach. These are swift, stony trout streams flowing on the northern side of a range of hills, and have cool, unpolluted, alkaline, moderately calcareous water, are very constant in flow and have a very stable bed.

2. The fauna of the Clydach has been described in a previous study. The fauna of the Sawdde, examined in July-September 1948, included about 75 species; dominant animals are *Atractides brevirostris*, *Perla carlukiana*, *Leuctra fusciventris*, *Ephemerella notata*, *Baetis rhodani*, *Glossosoma boltoni* and *Rhyacophila obliterata*.

3. The flora of the Sawdde and the Clydach is described. *Fontinalis antipyretica* is widely distributed and abundant at some points. *Ulothrix* is the dominant green alga. There is a rich diatom flora; characteristic species are *Diatoma vulgare*, *Ceratoneis arcus*, *Achnanthes* spp., *Cocconeis placentula* and *Navicula viridula*.

4. The food of the dominant insect species has been studied and about 600 specimens were examined for gut contents. *Perla carlukiana*, *Dinocras cephalotes*, *Rhyacophila obliterata* and *Plectrocnemia conspersa* are the chief predatory species; *Baetis*, *Ephemerella*, *Simulium* and chironomid larvae are their most frequent prey. The common mayflies are entirely herbivorous; *Baetis* feeds upon *Ulothrix* and other green algae, detritus and diatoms; *Ecdyonurus* mainly upon detritus; *Siphlonurus* upon the leaves of higher plants and detritus; *Ephemerella* upon *Ulothrix* and *Fontinalis*. *Ecdyonurus venosus* and certain other common animals in the stream system are apparently able to escape being eaten by the predatory Plecoptera and Trichoptera. Of the common, larger insects *Philopotamus montanus* is the only species mainly dependent on diatoms.

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