STUDIES IN STREAM LIFE IN TRIBUTARIES OF THE WELSH DEE

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(With 1 Figure in the Text)

CONTENTS

1. INTRODUCTION

This study attempts to investigate the fauna of some streams of the Dee river system in Wales, with reference to seasonal variation, food cycles and the available food for the fish population. The field work, apart from preliminary summer samples, extended from September 1946 to July 1947, and involved quantitative studies of the lithophilic fauna in two streams, the Ceirw and the Merddwr, amplified by general collections from various habitats. The gut contents of many forms were investigated and considered in relation to mode of feeding and the constitution of the microscopic planktonic and benthic fauna and flora.

Many of the earlier investigations on the benthic fauna of running waters, both continental and American, are cited by Carpenter (1928) and by Welch (1935). In Britain, the main general surveys of unpolluted waters are those of Carpenter (1927), Percival & Whitehead (1929, 1930), Butcher, Longwell & Pentelow (1937) and Jones (1941, 1943, 1948). Edmonds (1939, unpublished) made an extensive study of the plankton of the Dee, and some observations on the benthos. The chief seasonal quantitative surveys deal with the fauna of a chalk stream (Whitehead, 1935), and of submerged mosses (Frost, 1942). Neill (1938) discusses the fauna of the Scottish Don quantitatively in relation to the food of brown trout. The food of salmon parr has been considered in relation to available fauna of the Eden and Thürso (Allen, 1941) and the Welsh Dee (Carpenter, 1940).

2. METHODS

The three main sampling sites were at Dinmael, a hamlet situated at the confluence of the Merddwr and Ceirw, 5 miles west of Corwen (Fig. 1). The two Ceirw stations (A and B) were below the confluence. Successive samples were collected just upstream (Merddwr A, Ceirw A) or downstream (Ceirw B) from the previous sites and were taken at fortnightly or monthly intervals except when the streams were frozen or too heavily in spate.

Each quantitative sample consisted of the fauna from 2500 sq.cm. of stream bed. Sampling methods which involved removal of large amounts of gravel were not possible owing to transport difficulties. The measured area was marked out with a square frame below which a fine tow-net (129 strands per inch) with an attached jar was placed. Stones were carefully lifted, held in the mouth of the net and rubbed clean. Some organisms were bound to escape because of the swirl, especially during spates. In a few summer samples, this loss was investigated by trapping escaping organisms in an outer cone of mosquito netting with the rim bent so that it formed lateral flaps extending beyond the mouth of the enclosed tow-net (see p. 197). Small forms (below about 3 mm.) were only occasionally retained in either net.

The contents of the nets were washed down into the attached jars, and either preserved in formalin in the field or taken back alive to the laboratory for sorting. All the organisms detected by the naked eye were picked out, sieves (ranging down to 0·5 mm.)

being used when the sample contained much gravel and silt. The animals were identified and counted.

From April onwards, in order to minimize errors due to local distribution, two half samples (each 50 × 25 cm.) were taken at a little distance apart and combined, a procedure discussed by Prebble (1943) for studies of saw-fly populations.

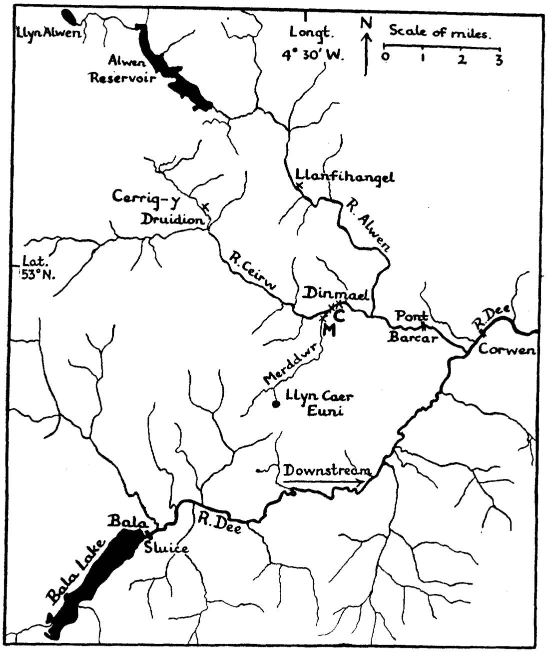

Fig. 1. The upper reaches of the Dee, west of Corwen. C = Ceirw stations A and B. M = Merddwr station A.

Simple physical data obtained at the times of sampling included air and water temperatures, depth of water in the measured area and its average surface velocity, estimated by timing a twig as it floated 20 ft. downstream. The oxygen content of the water was determined by the Winkler method and bromothymol blue was used to indicate the pH.

3. ENVIRONMENTAL CONDITIONS

The Welsh Dee and the tributaries of its upper reaches rise in the hills of Merionethshire and Denbighshire among rocks which are chiefly Ordovician (Bala series, etc.) and Silurian (Caradoc sandstone, Wenlock shales and slates); there are superficial deposits of peat and boulder clay in many places. The sources of the Merddwr, Ceirw and Alwen are in moorland or rough pasture, often boggy, while lower down, these brooks flow through arable or pasture land, partly wooded. There is a small outcrop of Silurian limestone just west of Corwen and a Carboniferous limestone escarpment towers above the Dee at Llangollen, but water of the higher reaches of the Dee and most of its upper tributaries is soft (e.g. Ca as $CaCO_3$—20 mg./l.—Suckling, 1944). The physical history of the valley is discussed by Ramsay (1876).

At Dinmael (550 ft. = 169 m.) the Merddwr is about 4 m. wide and the Ceirw about 7; the beds are mostly stony and unstable, with little vegetation other than mosses on scattered fixed stones. The measured areas were chosen so as to avoid moss. The station Ceirw A was slightly quieter than Ceirw B where the incline was steeper and there were more ripples. Recorded average velocities for Ceirw A range from 30 to 110, for Ceirw B from 45 to 175 and for Merddwr A from 30 to 90 cm./sec. At the nearest meteorological station, Wrexham, the lowest monthly rainfall between September 1946, and July 1947 was 41 mm. (October); peaks were 120 mm. (November) and 160 mm. (March). Depth of water over the various measured areas ranged from 9 to 41 cm. Recorded water temperatures at Dinmael ranged from 0 to 16° C., usually with little difference between the two streams. Ceirw pH values, estimated from water samples collected about noon or in early afternoon, were 7·2 or 7·3 and a single record for the Merddwr was 7·1.

Determinations of dissolved oxygen content of Ceirw water ranged from 9·55 to 16·1 mg./l. at N.T.P., i.e. 87% (at 12·2° C.) to 151% (at 12·8° C.) saturation. Supersaturation was only found on sunny days during the abundance of green algae.

4. THE LARGER BENTHIC FAUNA

(a) *Composition of the quantitative samples*

I am indebted to Mr S. T. Burfield and Dr H. B. N. Hynes for checking my identifications of mites and stone-fly nymphs respectively, and to Mr D. E. Kimmins for identifying caddis imagines. I am responsible for other identifications.

Table 1 summarizes the fauna collected in each sample. The population from the stony bed of both streams consisted mainly of insect nymphs and larvae, and is typical of this habitat. Other groups were present in relatively small numbers.

The detailed occurrences of some species of stonefly nymphs are shown in the table; the genus *Leuctra* included *L. fusciventris* Stephens, *L. geniculata* Stephens, *L. hippopus* Kempny and *L. inermis* Kempny. 'Other Plecoptera' comprises infrequent forms such as *Isoperla grammatica* (Poda), *Perlodes mortoni* (Klapálek), *Brachyptera risi* (Morton) and *Protonemura meyeri* (Pictet).

Nymphs of *Baetis*, the commonest Ephemeropteran genus, were not identified specifically. The large nymphs in the winter samples were probably *B. rhodani* (Pictet), but this was not verified by breeding them out. At least two species were present in April,

Table 1. *Numbers of larger benthic organisms in each sample from 2500 sq.cm. of stony stream bed.*

Day and month	1946: 11. ix			27. ix			14. x			28. x			16. xii			1947: 24. i		15. iv			16. v		13. vi			24. vi			22. vii		
Station	CA	CB	M	CA	CB	M	CA	CB	M	CA	CB	M	CA	CB	M	CA	M	CA	CB	M	CB	M	CA	CB	M	CA	CB	M	CA	CB	M
PLATYHELMIA																															
Dendrocoelum lacteum (Müller)	2	—	—	—	—	—	1	7	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Polycelis cornuta (Johnson)	—	—	—	—	—	—	—	—	—	—	—	4	—	—	2	—	—	—	—	8	—	1	—	—	—	—	—	—	—	—	5
OLIGOCHAETA																															
Enchytraeidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	28	—	3	17	8	1	2	4	9	6	8	—
Lumbriculidae	—	—	—	—	—	—	—	—	1	—	—	—	2	—	—	—	—	—	1	10	—	1	3	1	—	1	1	3	—	1	—
Other Oligochaeta	2	—	—	—	—	1	—	1	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	3	—
HIRUDINEA	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MOLLUSCA																															
Ancylastrum fluviatile (Müller)	—	—	6	5	—	1	4	4	4	9	—	1	—	—	—	—	—	—	—	1	—	5	4	1	1	—	6	1	2	1	7
CRUSTACEA																															
Gammarus pulex (L.)	—	—	2	—	1	8	1	—	12	—	—	1	1	—	8	—	—	—	2	7	—	1	—	—	15	2	1	19	3	—	2
HYDRACARINA	—	—	—	—	—	—	6	4	8	3	4	1	—	—	—	—	—	5	14	45	—	—	4	4	1	—	3	2	1	—	4
PLECOPTERA																															
Perla carlukiana Klapálek nymphs	—	—	—	2	—	—	—	1	2	1	6	—	—	—	—	—	—	1	1	—	2	—	3	2	—	—	6	1	—	—	—
Chloroperla torrentium (Pictet) nymphs	1	—	—	—	—	1	15	12	7	1	3	1	7	3	6	1	—	4	7	8	10	5	6	1	2	—	11	1	—	—	—
Chloroperla tripunctata (Scopoli) nymphs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—	2	2	2
**Leuctra* spp. nymphs	—	—	6	—	—	—	—	—	—	—	—	—	7	—	—	—	—	4	7	3	12	4	76	82	6	8	124	51	13	35	16
Amphinemura cinerea (Olivier) nymphs	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	3	3	—	—	—	—	—	—	—	—	—	—	—	1
Other Plecoptera and young nymphs	1	2	—	—	—	—	—	1	—	1	—	1	1	2	—	2	—	2	1	4	—	1	1	28	—	1	32	—	2	—	—
EPHEMEROPTERA																															
**Baetis* spp. nymphs	9	2	1	1	2	8	27	46	18	17	1	40	18	7	16	12	5	5	24	67	8	15	12	6	2	1	23	43	4	22	57
Ephemerella ignita (Poda) nymphs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	14	5	5	9	17	16	1	2
Ecdyonurus nymphs	—	1	2	—	—	5	1	—	—	—	—	6	—	—	1	—	—	—	—	—	—	—	1	5	1	—	4	—	1	3	1
Rhithrogena semicolorata (Curtis) nymphs	1	—	—	12	1	2	14	2	1	5	3	1	5	6	2	4	—	9	28	14	11	10	5	—	—	—	1	—	1	—	—
Caenis nymphs	—	—	—	—	—	—	10	6	4	1	4	1	—	—	—	—	—	12	50	6	2	—	—	5	1	1	4	4	—	—	—
Young Ephemeropteran nymphs	—	—	—	—	—	1	—	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	2	—	4	—	—	—
TRICHOPTERA																															
Rhyacophila dorsalis (Curtis) larvae	1	—	2	1	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	3	—	—	9	7	1	4	4	9	—	—	16
Rhyacophila dorsalis (Curtis) pupae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1	—	—	—	—	—	—	—	—
Glossosoma boltoni Curtis larvae	—	—	2	—	—	1	3	—	—	3	5	1	1	—	—	2	—	1	5	7	3	2	5	1	—	—	24	6	9	16	8
Glossosoma pupae	—	—	—	1	—	1	—	—	—	6	1	—	—	—	—	—	1	—	—	—	2	—	4	—	—	1	3	—	1	—	1
Agapetus fuscipes Curtis larvae	—	—	2	—	—	3	1	—	—	—	—	6	—	—	—	—	—	—	—	1	—	19	—	—	17	—	—	1	—	—	—
**Agapetus* pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	5	57	—	—	15	—	—	15
Hydroptilid larvae	1	—	—	—	—	—	5	1	—	4	—	—	1	—	—	—	—	1	1	—	—	—	3	—	—	—	—	—	5	1	—
Chimarrha marginata (L.) larvae	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	7	—	—	—	5	—	—	3
Chimarrha marginata (L.) pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	—	2
Polycentropus flavomaculatus (Pictet) larvae	—	—	3	—	—	—	—	—	—	8	—	2	—	—	—	1	—	1	—	1	—	1	3	11	1	1	6	—	5	3	—
Hydropsychid larvae	—	—	1	—	—	1	—	2	—	1	—	3	1	—	—	—	—	—	3	3	—	—	6	1	1	—	8	4	7	8	5
Hydropsychid pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1	3	3	—	—	—
Limnophilid larvae	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	1	—	—	—	—	2	—	—	—	1	—	—
Goerinae larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	5	1	6	1	—	4	5	—	3	2	—	1
Silo pallipes (Fab.) pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	8	—	11	5	—	4	9	1	11
Lepidostoma hirtum (Fab.) larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	8	—	1	1	—	2	—	2
Sericostoma larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	5	6	—	—	—	1	—	—	1	6	4	—	—
Other caddis larvae	1	—	—	—	—	—	—	—	—	—	—	2	1	—	1	—	—	—	—	2	—	4	—	2	4	1	—	2	4	—	—
Other caddis pupae or indetermined	—	—	—	3	—	1	1	—	—	—	—	3	—	—	—	—	—	—	—	—	—	1	3	1	4	1	2	—	3	4	—
COLEOPTERA																															
Helmid (=elmid) larvae	—	—	2	—	1	—	—	5	—	2	1	—	1	—	—	—	—	8	6	8	—	2	4	1	3	1	17	5	17	13	8
Helmid (=elmid) and *Hydraena* imagines	—	—	—	—	—	—	—	2	1	—	2	—	2	1	3	—	—	14	16	9	3	3	6	11	—	3	8	5	1	—	1
Other beetle larvae	—	2	—	—	—	1	—	2	1	1	—	1	—	—	—	—	—	3	—	1	2	—	—	3	—	—	5	—	1	—	—
Other adult beetles	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DIPTERA																															
*Chironomid larvae	1	1	6	3	—	5	1	10	5	1	4	18	—	—	—	3	1	19	227	53	42	23	—	269	19	210	605	82	282	51	186
Simulium spp. larvae	1	1	2	9	5	4	—	10	—	3	—	—	14	—	—	2	—	1	4	11	—	—	—	—	1	—	16	20	—	—	9
Dicranota larvae	—	—	1	—	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	3	—	—	1	1	1	—	2	—
Atherix larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	1	2	—	—
Other dipteran larvae	2	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	2	1	1	—	—	1
Dipteran pupae	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1	5	—	—	—	—	—	4
MISCELLANEOUS	—	1	—	1	—	—	—	3	—	—	—	1	—	1	—	—	—	—	1	—	—	1	—	1	—	1	—	1	—	—	2
Total number of organisms per sample	24	10	40	39	11	45	95	122	71	67	35	94	65	21	42	29	10	102	408	315	101	114	214	506	166	263	924	329	409	175	372

CA = Ceirw station A, CB = Ceirw station B, M = Merddwr station A.

when imagines of *B. scambus* Eaton were recorded from the area. *Ecdyonurus* imagines captured were *E. venosus* (Fab.) and *E. insignis* (Eaton), but nymphs were mostly *E. venosus*.

The commonest caddis are enumerated specifically in Table 1. No one species was outstandingly abundant. The majority of the Hydropsychidae were *Hydropsyche angustipennis* (Curtis) and *H. instabilis* (Curtis), but larvae and pupae of *Diplectrona felix* McLachlan were recorded in July. Hydroptilids were mainly *Hydroptila* sp. Limnophilids were represented by *Stenophyllax stellatus* (Curtis), *Halesus* and *Apatania*; and Goerinae by *Silo pallipes* (Fab.) and *Goera pilosa* (Fab.) The term 'other caddis larvae' in Table 1 includes the following less frequent forms: *Glossosoma vernale* (Pictet), *Agapetus comatus* (Pictet), *Odontocerum albicorne* (Scopoli), *Notidobia*, *Leptocerus* and *Plectrocnemia*. 'Other caddis pupae' includes *Polycentropus*, *Odontocerum albicorne*, *Lepidostoma hirtum* (Fab.), *Leptocerus* and limnophilids.

The prevalent adult beetles were the helmids [=elmids]: *Esolus parallelopipedus* (Mueller), *Latelmis volkmari* (Panzer) and *Limnius tuberculatus* (Mueller), and the hydrophilid, *Hydraena gracilis* Germar. The helmid larvae included both flattened forms with marginal hairs and cylindrical forms. 'Other beetle larvae' included gyrinids and four rarer types not correlated with their adults.

The Chironomidae included representatives of the Tanypodinae (*Pentaneura* spp.), Chironominae (*Endochironomus* and *Tanytarsus* groups), Diamesinae, Orthocladiinae and an occasional ceratopogonid. Specific identification of *Simulium* larvae was uncertain in preserved material, when the colour pattern on the head is not reliable. *S. tuberosum* Lundstroem larvae and flies were prevalent in June and July, and it is thought that December larvae were this species. *Dicranota* was the commonest tipulid, but *Pedicia* (included under 'other dipteran larvae') occurred sporadically, and so did the leptid *Atherix*. Other larvae were rare.

The few leeches found were *Glossosiphonia complanata* (L.) and *Herpobdella octoculata* (L.). Hydracarines identified were *Atractides anomolus* Koch, *Hygrobates longipalpis* (Hermann), *Lebertia stigmatifera* Thor, and *Pseudosperchon verrucosus* (Protz). The term 'Miscellaneous' includes adventitious and very rare forms.

(*b*) *Distribution as indicated by quantitative samples and general collections*

Polycelis cornuta was the predominant Triclad in the smaller stream, the Merddwr, and *Dendrocoelum lacteum* in the Ceirw, but *D. lacteum* also occurred in the Merddwr. Oligochaetes were apparently very scarce, except for Lumbriculidae and Enchytraeidae, which tend to be associated with stones. Some forms may have escaped by burrowing in the gravel, but the absence of very close moss clogged with detritus and silt probably accounts for the rarity of Naididae. Soft water, dearth of aquatic phanerogams and molar action in floods may account for the paucity of molluscs. *Ancylastrum fluviatile* can tolerate a low calcium content (Boycott, 1936), but it was not very common even on clean stones and was absent where a muddy crust on the stones would prevent adhesion and block the mantle cavity.

Gammarus pulex reproduces at all seasons, but young stages are especially prevalent in summer. Some individuals were infested internally with the orange larva of the acanthocephalan *Polymorphus minutus* Goeze. *Gammarus* and water mites were most numerous in sheltered niches with silt or in moss.

The predominantly carnivorous perlid and perlodid nymphs were not very numerous. *Perla cephalotes* Curtis was very rare compared with *P. carlukiana*—the former is associated with a stable and the latter with an unstable substratum (Hynes, 1941). *Chloroperla torrentium* was relatively common; it eats smaller animals and more detritus (Hynes, 1941). *Leuctra* nymphs, especially *L. fusciventris*, were very abundant during late spring and summer. A few young nymphs (under 3 mm.) of this species were found in April and May; in June, nymphs 4 mm. long were retained in numbers. Numbers decreased by the end of July, probably due to emergence, and only a few fully grown nymphs were found in September. *L. geniculata* nymphs (3–5 mm.) were first recorded in mid-June, there were more at the end of the month, mostly about 5 mm. long and they were common in July. The tendency of *L. geniculata* nymphs to dwell under boulders (avoided in selection of sampling sites) and in deeper water than *L. fusciventris* (Hynes, 1941) would influence the relative abundance in the samples. The prevalent species between December and May was *L. hippopus*. *L. nigra* (Olivier) was found in sheltered situations. *L. inermis*, *Brachyptera risi* and *Isoperla grammatica* were more frequent in the higher reaches of the Merddwr than at Dinmael. *Protonemura meyeri* was only numerous in moss.

Baetis nymphs (not specifically identified) were very common at Dinmael, and dispersal of young nymphs in the plankton is frequent, especially in spring. Nymphs of *Ephemerella ignita*, only recorded in June and July samples, constituted the greater part of the well-developed ephemeropteran nymphs when the baetids were emerging and the new generations hatching, but *Ephemerella* never reached the peak figure for *Baetis*. Its absence from samples before June agrees with observations that *Ephemerella ignita* has a long incubation period (Percival & Whitehead, 1928), and that from November to May the population consists chiefly of small nymphs (1–3 mm.) (Frost, 1942). *Ecdyonurus* nymphs were less frequent than those of *Rhithrogena semicolorata* in Dinmael samples, especially during winter when they were rarely recorded in the Ceirw, which is liable to spates. Young *Ecdyonurus* nymphs still with strap-like gills were recorded in October and June, which agrees with Rawlinson's (1939) demonstration of two broods a year. The small, rather delicate *Caenis* nymphs were not very numerous amongst stones and gravel except in April, when many small nymphs (1–2 mm.) occurred in the samples.

Agapetus fuscipes, a caddis typical of the quieter niches of stony streams, was much commoner in the Merddwr than in the frequently swifter Ceirw. October larvae were all young, sizes varied in May and June, when pupae were also found. This species is probably univoltine (Whitehead, 1935). *Glossosoma boltoni*, with its larger, more robust case, frequents stones in both streams and overwinters both as immature larvae and pupae. No account of its life history or of that of *Rhyacophila dorsalis* has been seen. Pupae of *R. dorsalis* were collected between April and September, and larvae of varying sizes at all seasons. These caseless larvae, using their stout grappling claws for anchorage, creep about the stony stream bed in the current or cling to moss. In the laboratory, they have been observed swimming with an undulating movement.

Dense populations of the larvae of *Polycentropus flavomaculatus* are associated with gently flowing waters, and amongst stones the rather fragile nets are most numerous where there is a slight deposition of silt indicating quiet conditions, such as are often correlated with lake outflows. These larvae also frequent the stony but slightly silted shores of lakes where there is little wave action but sufficient aeration. At Dinmael *Polycentropus flavomaculatus*, *Hydropsyche angustipennis* and *H. instabilis* spin their nets underneath stones. The life histories are incompletely known and are being studied for a further paper on the biology and ecology of net spinning and caseless caddis.

Notidobia larvae dwelt amongst stones in the Ceirw, Merddwr and Alwen, especially in quiet regions with slight silting, and amongst water weeds.

The philodinid rotifer, *Embarta laticornis* (Murray), was epizoic on larvae of *Halesus digitatus* (Shrank) among *Myriophyllum* and dwelt in the cases (made of fragments of the weed) of very young limnophilid larvae. As it was not found free in samples of the weed, a definite association of this rotifer with the caddis can be established. Murray (1905), who found it among mosses, considered that its form suggested a parasitic habit, but had not then discovered it attached to any host. Mr A. L. Galliford, who kindly identified this rotifer for me, says he has since found it on caddis from Hatchmere, Cheshire, and Dr Slack tells me that *Halesus* and *Silo* larvae from the River Test, Hampshire, sometimes had a philodinid rotifer associated with them.

Beetles were never abundant in the quantitative samples; they are commoner in sheltered moss than among stones (Percival & Whitehead, 1929). Only imagines and larvae were recorded, the pupae are terrestrial.

The numbers of chironomid larvae varied greatly in different samples, and are discussed below. *Simulium* larvae clustered on some boulders in ripples, but were not numerous in the quantitative samples.

(c) *Discussion*

The quantitative samples were from one major type of botton habitat—the loose stones devoid of larger vegetation—which is poor in numbers of individuals compared with moss (Percival & Whitehead, 1929), but supports forms—such as *Baetis*, *Ecdyonurus*, *Ephemerella*, many stone-fly nymphs, *Simulium* and chironomid larvae and *Ancylastrum*—which are readily eaten by salmon parr (Carpenter, 1940, Allen, 1941). Much of the fauna living within the gravel was not taken, but it is of little importance as food for salmonids.

The crude sampling method could not be expected to collect the whole bottom population of the measured area, even exclusive of the forms which readily burrow; escape of animals was bound to occur because of the swirl at the mouth of the net. The loss was greatest in floods, and in November the swirl was so strong that practically all the organisms were lost and sampling had to be abandoned.

A typical result obtained during summer for the inner net (the contents of which alone were considered in the quantitative result) and the larger outer net of mosquito netting used to estimate the loss is shown in Table 2. When for each of five samples, the numbers in the outer net were expressed as percentages of the total for both nets it was found that the loss, as estimated by the outer cone, ranged from 4 to 20%. Analysis shows that a wide range of organisms is lost and not merely the smaller forms, some of which might pass through the outer net. Even considering only the variability of total loss, it is apparent that only the most general conclusions may be drawn from a study of the numbers of organisms in the quantitative samples (Table 1).

Any examination of the lithophilic animal population reveals that its distribution is very irregular. Table 1 shows this clearly, especially if the figures are compared for Ceirw A and Ceirw B, stations which are close together and very similar. Hence the necessity for caution in deriving any conclusions from the figures themselves, a point also emphasized by the work of Mottley, Rayner & Rainwater (1938). Leonard (1939) likewise showed the great variation in the composition of the fauna, although the total volume of organisms present in a given area was more consistent. As an animal population is so variable both seasonally and in its spatial distribution, especially in such a very diversified environment as the bed of a stony stream, only very large numbers of simultaneous samples could be expected to give adequate statistics on the general density of population at one time and place. Also sampling, except at very short intervals of time, could not reflect any but the grossest seasonal changes in the population.

Table 2. *Quantitative yield of sample from Ceirw B on 24 June 1947*

	Inner net	Outer net
Enchytraeid Oligochaetes	4	4
Lumbriculid Oligochaetes	1	2
Ancylastrum fluviatale	6	—
Gammarus pulex	1	—
Hydracarines	3	—
Perla Carlukiana nymphs	6	1
Chloroperla torrentium nymphs	11	1
Leuctra nymphs (*L. fusciventris*, *L. geniculata*)	124	4
Various young Plecopteran nymphs	32	—
Ecdyonurus nymphs	4	—
Rhithrogena semicolorata nymphs	1	—
Caenis nymphs	4	2
Ephemerella ignita nymphs	9	4
Baetis nymphs	23	2
Rhyacophila dorsalis larvae	4	—
Glossosoma boltoni larvae	24	3
Polycentropus flavomaculatus larvae	6	—
Hydropsyche angustipennis larvae	8	—
Silo pallipes larva	—	1
Lepidostoma hirtum larva	1	—
Sericostoma larva	—	1
Caddis larvule (undetermined)	1	—
Glossosoma pupa	3	1
Hydropsychid pupae	3	—
Goera pilosa pupa	1	—
Odontocerum albicorne pupa	1	—
Esolus parallelopipedus imagines	6	—
Latelmis volkmari	—	1
Oreodytes rivalis Gyllenhal	—	1
Other adult beetles	2	—
Helmid larvae	7	—
Dryopid larvae	5	—
Simulium larvae	16	—
Chironomid larvae	605	3
Chironomid pupa	—	1
Dicranota larva	1	—
Pedicia larva	1	—
Adult Diptera	—	2
	924	34

Loss = 4 % of total

Most of the categories of organisms are not represented in any of the samples (except perhaps one) by numbers greater than 25. Those forms which are represented by a greater density of population (starred in Table 1) are *Leuctra* spp., *Baetis* spp. and the Chironomidae. Most of the unstarred forms in Table 1 are represented by numbers much lower than the arbitrarily chosen figure of 'over 25 individuals per 2500 sq.cm.' The list of abundant forms would not have been greatly increased had the chosen number been 'over 15'. Organisms falling into this intermediate group are: Enchytraeidae, *Ephemerella ignita*, *Glossosoma boltoni*, *Agapetus fuscipes* and *Simulium*. Other forms are less numerous.

Two generalizations may be made from analysis of the actual figures in Table 1, namely that the density of population of other forms is markedly lower than that of the starred categories and obviously that their range of variation is much more restricted (0–25). The figures for some of these forms may indicate a seasonal distribution, but the number of samples is too few to establish this for any form, and loss of the smaller individuals from the sampling apparatus leaves open the question of whether seasonal absence from the samples is due to size or to actual absence from the site.

Although the numbers of individuals of a given species may be low, if those of all the members of a higher category, say an order, are added up the importance of some groups becomes obvious. On expressing various groups of animals as percentages of the total population collected quantitatively between September 1946 and July 1947 inclusive, over three-quarters of the population in the Ceirw and Merddwr is seen to be composed of the same four groups (Table 3).

Table 3

	Percentage of total population: Ceirw A and B	Merddwr A
Chironomid larvae	48	25
Ephemeropteran nymphs	15	23
Trichopteran larvae and pupae	10	21
Plecopteran nymphs	16	8
Sum of the four groups	89	77

Other groups constitute but a small proportion of the total fauna, each less than 5 % and only very broad generalizations from such figures are considered valid.

From September to January inclusive, the measured area apparently supports a population ranging between 10 and 122 individuals (17 samples); in contrast, the April to July totals lie between 100 and 924 (14 samples). If the chironomid larvae, *Leuctra* and *Baetis* nymphs are deducted, the September to

January range becomes 7 to 66 and that for April to July becomes 39 to 172. The summer increase is due mainly to young insects and especially to the starred categories, the numbers of which vary considerably in different samples, hence actual numbers for seasonal averages (Table 4) are considered to have little value and statistical methods not applicable to the totals. The only statistically significant difference is that between the average total population for summer and winter.

Table 4. *Seasonal averages for total number of organisms per 2500 sq.cm. sample of stony stream bed*

Period	Average	No. of samples and site
Autumn 1946 (Sept. and Oct.)	54	Average of 12 samples— 8 Ceirw and 4 Merddwr
Winter 1946–7 (Dec. and Jan.)	33	Average of 5 samples— 3 Ceirw and 2 Merddwr
Spring 1947 (Apr. and May)	208	Average of 5 samples— 3 Ceirw and 2 Merddwr
Summer 1947 (June and July)	373	Average of 9 samples— 6 Ceirw and 3 Merddwr

The same trend—a fall during winter months and a rise during spring and summer—was found at each of the three stations. In interpreting the winter minimum, the slow growth, small size and hence potential escape of many nymphs and larvae at this season must be remembered; there is also the possibility of their absence not only from the particular measured area but from the stony substratum of all but the most sheltered parts of the stream. This suggestion is supported by the data of Whitehead (1935) correlating a decrease in the lithophilic fauna of a stream with a rise in the population of water weeds at the coming of autumn floods and by the studies of Moon (1934, 1935) and of Berg (1938) showing the considerable movement of the littoral benthic fauna of Windermere and Esrom lakes respectively. The negligible number of chironomid larvae in the Dinmael winter samples is particularly suggestive. The Chironomidae are a very diverse group, but in general they overwinter as larvae, and Frost (1942) found that there was normally a peak (although less than the summer one) of these larvae in moss during winter in the streams investigated by her. Butcher, Longwell & Pentelow (1937) give tables of the fauna from the stony substratum of the Tees which show absence or very low numbers of chironomid larvae in winter. It is unlikely that the April increase at Dinmael was due to growth of new broods, since there was insufficient time for emergence, hatching and growth between the late thaw in April after the exceptionally cold winter of 1946–7 (snow persisted from January to April) and the collection of samples; also, emergence had not been observed. Humphries (1938) showed that in the Grosser Plöner See emergence of chironomids was correlated with temperature, and that the earliest to emerge were some members of the Orthocladiinae at the end of March, when the average temperatures were 7·0° C. (air) and 3·5° C. (lake surface). She cites Lenz as stating that a species of *Paratendipes* is the only form found emerging in winter and then but rarely. Mr P. Freeman tells me that he does not know of any British chironomids which emerge in cold, snowy weather. Thus possibly in a stream which, like the Ceirw, is liable to spates, much of the lithophilic fauna, if not actually destroyed by molar action, is washed or migrates into sheltered habitats such as moss which act as nurseries from which the bare stony substratum is recolonized in spring. Detailed quantitative studies of moss and stone fauna in the same area would be interesting.

The fecundity of an organism and its feeding habits effect its population density. The food chain is considered below. Little is known about the fecundity of many stream forms.

The general collections from various habitats in the Ceirw and Merddwr at Dinmael showed that the quantitative samples gave a representative picture of the population of these streams. Only a few forms were found which were not recorded in the samples. They were:

Ephemera danica Müller nymphs—burrowing in muddy gravel in sheltered situations near the banks.

Leuctra nigra (Olivier) nymphs.

Micronecta poweri (Douglas & Scott)—in shallow silted eddies, nymphs often very abundant.

Velia currens (Fab.)—skating on the surface of eddies.

Calliophrys (Muscidae) larvae—rare and only found in moss.

The fauna at Dinmael is typical of much of the Merddwr, with certain variations. The short narrow outflow gully just below Llyn Caer Euni, the tarn forming the source, is characterized by numerous *Polycentropus flavomaculatus* and *Hydropsyche instabilis*, quantities of *Spongilla lacustris* (L.) and the lacustrine *Leptophlebia vespertina* (L.) instead of *Baetis*. Bivalves, *Pisidium* and *Sphaerium*, rarer downstream, frequented the mud here. *Isoperla grammatica* and *Perlodes mortoni* were more numerous in the upper reaches than at Dinmael, while *Perla* and *Chloroperla* appeared to be absent. On the vertical faces of the rocks of the ensuing waterfall, the fauna is confined to tufts of moss; among bare stones in pools at the base of the falls *Simulium* spp. (including *S. tuberosum* and *S. angustitarsis* Lundström) and *Hydropsyche instabilis* predominated. In the slower middle reaches, the muddy gravel and the weeds *Callitriche*, water crowfoot (*Ranunculus* sp.) and *Myriophyllum* shelter many *Gammarus pulex*, leeches such as *Herpobdella octoculata* and *Helobdella stagnalis* (L.) and numerous limnophilid caddis larvae. The caddis characteristic of the cleaner, faster reaches were rare, most non-burrowing Ephemeropteran and Plecopteran nymphs were infrequent and mud dwellers such as *Sialis* prevailed. There are areas with a stony substratum, mostly stable, considerable moss* (*Fontinalis antipyretica*, *F. squamosa* and *Hypnum* sp.) and the umbellifer *Oenanthe crocata*, but the greater part of the Merddwr has a looser stony bed and less moss (mostly *Hypnum*) as at Dinmael, and the fauna is very similar to that station.

Incidental collections in the Ceirw above and below Dinmael also revealed a fauna resembling the Dinmael assemblage. More weed occurs in places, also pools which would affect the density of the fauna.

In the upper reaches of the Alwen, immediately below the reservoir and water works' filters, the stones have a flocculent muddy crust. *Hydropsyche* and *Polycentropus* were common, *Dendrocoelum lacteum*, tubificid worms, *Herpobdella* and limnophilid, culicid and chironomid larvae occurred, but Plecoptera and Ephemeroptera were not found. The mucilaginous alga *Palmodictyon*, an occupant of stagnant pools and peaty ditches, was recorded. Above Llanfihangel *Ecdyonurus* and *Isoperla grammatica* occurred, but below it, where the muddy crust was thicker, 'blood worms' predominated, and there was a dearth of larger organisms except for some Limnophilidae and *Polycentropus*. In 1947 the fauna here was not typical of a clean, unpolluted river. Lower down, at Pont Barcar, the fauna was rich and varied as in the Ceirw.

The composition of the fauna at the Dinmael stations seems fairly representative of the clean stony streams of the area and the quantitative studies stress the dominant forms. Only the broadest generalizations can be made from the numbers, and in attempting comparisons with other regions, season and habitats must be carefully considered. Hence detailed comparisons cannot be made with surveys such as those of Jones (1941, 1943, 1948), where collections from many habitats at various times are all added together in presenting the data. As bare, loose stones have been shown by other workers to be much less productive than vegetation, the figures obtained in the present survey probably represent the minimum resources of the Ceirw and Merddwr as food for fish.

5. MICROSCOPIC ORGANISMS

(*a*) *Composition of the flora and fauna*

The only survey of the 'plankton' of the River Dee is that of Edmonds (1939, unpublished) in 1937–8. Studies of river 'plankton' in Britain are not numerous and mostly deal only with phytoplankton. All show its adventitious nature and that much is derived from the benthos. Investigations of the benthic microscopic organisms have also been mainly confined to the algae, microfauna being largely an untouched field, although Picken (1937) discusses communities of ciliate Protozoa in the River Cam.

In the present study, five types of habitat were investigated in varying detail. They were the stones, mud, gravel, moss of the stream and river bed, and the 'plankton'.

Most of the observations were made at Dinmael, and as results in the Ceirw and Merddwr were essentially similar, these stations are considered together. A few additional samples were taken in the Alwen and Dee for comparison. The main difference was in the plankton.

Mr A. L. Galliford kindly identified some of the rotifers.

(1) *Benthos*

In the benthos, especially on stones, diatoms predominated; the genera—with *Cocconeis* frequently the most abundant—resemble those listed by Butcher (1932, 1946) and Butcher *et al.* (1937) and probably represent a typical climax diatom community in such rivers.

Forms recorded were:

Achnanthes
Amphora ovalis Kutzing
Cocconeis spp.
Cymbella spp.
Eunotia
Fragillaria
Gomphonema
Melosira
Meridion circulare (Greville)
Navicula spp.
Nitchia spp.
Stauroneis
Surirella
Synedra spp.
Tabellaria flocculosa (Roth)

The commonest desmids were *Closterium*, *Cosmarium* and *Ankistrodesmus*. Encrusting Chlorophyceae such as *Sphaerocystis*, *Botryococcus*, pleurococcoid forms and *Gongrosira* were characteristic of the stones and particularly abundant in spring. Filamentous Chlorophyceae, clustering in sheltered positions during summer, were represented mainly by *Ulothrix*, but also by *Chaetophora*, *Stigeoclonium*, *Mougeotia*, *Zygnema*, *Oedogonium* and *Spirogyra*. Common blue-green algae were *Nostoc* and the tangled filaments of *Oscillatoria*, which entrapped silt, so forming a muddy crust on stones in quiet regions during the spring abundance. *Chantransia* was the prevalent red alga, but *Hildenbrantia** imparted a dark olive-green slime to some stones and the tough, greenish filaments of *Lemanea** also occurred.

* Kindly identified by Dr E. M. Burrows.

The microscopic fauna dwelling on stones devoid of algal filaments or moss was scanty. The scrapings were either examined on a slide in the field or stored in tubes. Protozoa consisted mainly of occasional representatives of forms more numerous in other habitats. The small oligochaete, *Aelosoma hemprichii* Ehrenberg, and the rotifers, *Philodina roseola* Ehrenberg, *Cephalodella* and *Euchlanis*, occurred on some stones.

In the mud samples examined, diatoms were very numerous and were sometimes mixed with fragments of filamentous algae. Minute green flagellates were the commonest Protozoa, but colourless forms and various hypotrichous ciliates were present. *Difflugia*, diaschizid rotifers and *Pleurotrocha* occurred.

In studying the microscopic organisms of gravel, the most successful method was sucking up a little liquid using a douche syringe with the nozzle pressed well down among the gravel. The material was examined in the field immediately on collection and also after culture. Diatoms loose in the gravel were less numerous than in scrapings from stones but the forms were similar except that the encrusting *Cocconeis* was rarer. Desmids and fragments of algal filaments were present. The protozoan fauna was richer than that obtained from stones. Records included:

Sarcodina
- Actinophrys
- Actinosphaerium
- Arcella
- Difflugia

Mastigophora
- Chrysomonads
- Heteromita ovata Dujardin
- Minute colourless forms

Ciliophora
- Colpidium
- Colpoda
- Euplotes
- Glaucoma
- Holophyra
- Leucophrys patula Ehrenberg
- Liotonopsis
- Oxytricha
- Uroleptus musculus O. F. Müller
- Vorticella

The rotifers *Cephalodella*, *Lepadella*, *Monostyla* and philodinids were found. Gastrotricha were rare in this habitat, but *Chaetonotus* was recorded, so were free-living nematodes.

The microscopic fauna of moss was the richest of all the habitats examined. The forms identified are listed below:

Sarcodina
- Amoeba proteus Rose
- Arcella Ehr.
- Actinospaerium Stein
- Actinophrys Ehr.
- Difflugia Leclerc

Mastigophora
- Chlamydomonas Ehr.
- Euglena viridis Ehr.
- Heteromita ovata Dujardin
- Monas sp.
- Peranema Dujardin

Ciliata Holotricha
- Colpidium colpoda Ehr.
- Glaucoma sp. or near ally
- Lembadion bullinum Perty
- Holophyra Ehr.
- Lacrymaria Ehr.
- Lionotus wrzesniowskii Kent
- Liotonopsis Conn
- Loxophyllum Dujardin
- Trachelius ovum Ehr.

Ciliata Hypotricha
- Euplotes Ehr.
- Holosticha Wrzesniowski
- Oxytricha fallax Stein
- Ophrydium Ehr.
- Urostyla Ehr.
- Vorticella

Rotifera, especially bdelloid forms, are known to be numerous in moss and Mr A. L. Galliford identified the following species from the Merddwr:

- Cephalodella eva (Gosse)
- C. forficata (Ehr.)
- C. tenuior (Gosse)
- Lepadella acuminata (Ehr.)
- Philodina flaviceps Bryce
- Proales reinhardti (Ehr.)
- Proalinopsis sp.

Philodina roseola Ehr. also occurred in this habitat. Other organisms recorded were *Chaetonotus*, *Macrobiotus*, *Aelosoma hemprichii*, free-living Nematoda and larval Hydrachnidae. The diatoms and desmids were the same genera as in other benthic habitats.

(2) *Potamoplankton*

In collecting 'plankton' samples, a fine tow-net, weighted so that it was just below the surface of the water, was suspended in the river for 15 min. Hauls at Dinmael consisted largely of diatoms and plant debris. The diatoms were the typical benthic ones, except that *Cocconeis* was rare. Mingled with them were *Ankistrodesmus*, *Closterium* spp., *Cosmarium* and fragments of green forms which were especially frequent in the plankton in summer and after autumn floods. *Pandorina* and *Sphaerocystis* were recorded. Protozoa were represented mainly by a few individuals of some of the benthic forms. Rotifera were varied but not numerous; the following forms were identified by Mr A. L. Galliford:

- Cephalodella tenuior (Gosse)
- Dicranophorus
- Keratella cochlearis (Gosse)
- Lepadella acuminata (Ehr.)

L. triptera (Ehr.)
Microcodides chlaena (Gosse)
Monostyla lunaris (Ehr).
Notholca longispina Kellicott
Philodina sp.

Cephalodella tenuior and *Lepadella triptera* are characteristic bog forms which probably entered the plankton in the higher reaches of the Ceirw. Copepoda were rare, but species of *Cyclops* and *Canthocamptus* were found occasionally. Ostracoda were very rare. A considerable range of insect nymphs and larvae appeared in the 'plankton' at times, especially in spring, when juvenile forms were common. In summer there were larval mites also.

The few 'plankton' hauls taken in the Dee fall into the general pattern demonstrated by Edmonds during her continuous survey at the same collecting sites in 1937–8. These were Bala Sluice, Corwen Bridge and Farndon, named in order progressing downstream. The composition of the 'plankton' contrasted markedly with the tributary streams where it was characterized by its paucity, especially of zoöplankton and where seasonal variation, except in the Chlorophyceae was not very pronounced. As shown by Edmonds, the water flowing into the Dee from the Bala Sluice gate brings with it many forms from Bala Lake, including a very rich zoöplankton having definite seasonal variation, also lacustrine algae such as the abundant *Asterionella gracimilla* Heiberg and *Coelosphaerium naegelianum* Unger, in addition to forms from the river bed. Some forms were recorded at all Dee stations, the frequency of others such as *Ceratium hirudinella* Müller, *Keratella cochlearis*, *Notholca longispina*, *Filina longiseta* (Ehr.), *Daphnia longispina* (Müller), *Diaphanosoma brachyurum* (Lieven) decreased downstream, while others such as *Leptodora Kindti* (Focke) were recorded only at Bala. At Corwen Bridge, the 'plankton' was still very much richer and more varied than in the Ceirw and Alwen.

(*b*) *Discussion*

These observations illustrate the heterogeneous nature of stream and river 'plankton'—a feature noted by many workers, including Edmonds in her survey of the Dee—and especially the close interrelationship with the benthos. In the Ceirw and Merddwr, the chief difference between the planktonic and benthic microscopic organisms lies in the paucity in the 'plankton' of firmly attached, encrusting forms such as *Cocconeis* and *Gongrosira*. The predominance of diatoms is often characteristic of clean streams. It seems that microscopic organisms are the keystone of biological productivity, but that while in a lake the plankton may be of major importance, in a small stream its role may be played by the benthos. The importance of the age of the water

$$\left(\frac{\text{distance from source}}{\text{velocity}}\right)$$

in determining the nature and quantity of river plankton has been discussed by Kofoid (1903) and Eddy (1934). The influence of a lake on the amount of zoöplankton is obvious when the abundant 'plankton' of the Dee below Bala Lake is compared with the paucity of the tributaries.

Protozoa were investigated in the field whenever possible, immediately on return to the laboratory and in culture. Since forms from fast-flowing unpolluted streams are accustomed to highly oxygenated conditions, the most satisfactory culture method was to have just a little stream water in a large jar so that plenty of air was available and there was a large surface for gaseous exchange. Otherwise many forms disappeared, the culture quickly passing through a hypotrichous ciliate (e.g. *Uroleptus*) to a *Colpidium* association.

On stones, the protozoan fauna was sparse; that amongst gravel, especially under stones, was richer, but of the habitats examined the greatest variety and density was found sheltering in moss.

Picken (1937) correlated abundance of ciliates with plenty of interfaces enabling accumulation of food substances and providing a surface to which the Protozoa could become 'bound'. He found the densest ciliate populations associated with filamentous growths.

This preliminary survey of the microscopic organisms serves to give some indication of the range of forms available in the various habitats.

6. NOTES ON THE FOOD OF THE LARGER ORGANISMS

In order to study the inter-relationships of the fauna, the food of many animals found in the streams at Dinmael was studied and literature relating to such forms surveyed. The organisms were examined either immediately on collection or were preserved in the field. The results are summarized in Table 5.

(*a*) *Invertebrates*

Percival & Whitehead (1929) list the food of a wide range of benthic invertebrates from the Wharfe, and summarize the results in a general food chain. They note that while there is a definite association between *Glossosiphonia* and certain molluscs, *Herpobdella* is much more clearly associated with tubificids and chironomids and may be numerous where molluscs are absent (cf. Richardson, 1928). At Dinmael, *Herpobdella* fed chiefly on chironomid larvae which were often swallowed whole. Tubificids, rare in the

Table 5. *Gut contents of some of the organisms from the streams at Dinmael*

Organism	Months when examined	Number examined	Mineral particles	Diatoms and desmids	Other encrusting algae	Filamentous algae	Pulverized masses		Protozoa	Chironomid larvae	*Simulium* larvae	*Leuctra* nymphs	Indetermined Plecoptera	*Baetis* nymphs	Other Ephemeropteran nymphs	*Hydropsyche* larvae	*Rhyacophila* larvae	*Chimarrha* larvae	Adult Diptera	Entomostraca	Collembola	*Micronecta poweri*
			Gut contents																			
Herpobdella octoculata	viii, ix	10	·	·	·	·	·	·	·	O O	O	·	·	O	·	·	·	·	·	·	·	·
Ancylastrum fluviatile		5	O	O	O	·	·	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gammarus pulex	iv, v, viii	17	·	O	O	O	·	O O	·	O	·	·	·	·	O	·	·	·	·	·	·	·
Perla carlukiana nymphs	vii	5	·	·	·	O	·	·	·	O O	O	·	O	O	O	O	·	O	·	·	·	·
Baetis spp. nymphs	vii	12	·	O O	O	·	·	O O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ecdyonurus venosus nymphs	ii, v	5	O	O	O	O	·	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhithrogena semicolorata nymphs	ii, v	10	O	O	O	O	O	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ephemerella ignita nymphs	vii	5	·	·	O	O O	·	·	·	O	·	·	·	·	·	·	·	·	·	·	·	·
Micronecta poweri nymphs	xi	14	O	·	·	·	O O	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Glossosoma boltoni larvae	x, iv, vi	12	O	O O	·	·	O	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chimarrha marginata larvae	v	5	·	O	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Notidobia larvae	iv, v	5	·	·	·	O	·	O O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Stenophylax stellatus larvae	iv, vii	5	O	O O	·	O	·	·	·	O	·	·	·	·	·	·	·	·	·	·	·	·
Hydropsyche larvae	Various	18	O	O O	·	O O	·	O	O	O	·	·	·	O	·	·	·	·	·	·	·	·
Rhyacophila dorsalis larvae	iv, vii	10	·	·	·	·	·	·	·	O O	O	·	O	O O	·	O	·	·	·	·	·	·
Polycentropus flavomaculatus larvae	iv, vii	12	·	·	·	·	·	O	·	O O	O	·	·	O O	O O	·	O	·	·	·	·	·
Helmid larvae	vii	5	·	O	O	·	·	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chironomid larvae (excluding Tanypinae)	vii	12	·	O	·	O	·	O	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Simulium larvae	vii	12	·	O O	O	O	O	O O	·	O	O	·	·	·	·	·	·	·	·	·	·	·
Salmo salar fry (2·6–2·8 mm.)	iv–vi	23	·	O	·	O	·	·	O	O O	O	·	·	O	·	·	·	O	O	O	O	O
Phoxinus phoxinus (2·0–2·9 mm.)	v	15	·	O O	·	O O	·	O	O	O	·	·	·	O	·	·	·	O	O	O	O	·

O denotes presence, O O predominance.

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fauna, were not found in the guts of these leeches, but *Baetis* and *Leuctra* nymphs were sometimes eaten. *Ancylastrum fluviatile* had been scraping stones (see Boycott, 1936). The varied assortment of detritus which *Gammarus pulex* had eaten included bits of plant tissue, diatoms, other algal cells and also much mineral matter; insect remains, especially chironomid larvae, were sometimes found. These results agree with those of Percival & Whitehead and partly with the generalization of Embody (1911) that fresh-water gammarids eat both living and dead plants and animals. *Gammarus* is known to eat dead leaves (cf. Sexton & Matthews (1913) on *G. chevreuxi*), and in one of the *G. pulex* examined brown pieces of leaf were the only gut contents.

At Dinmael, the only Plecoptera examined for their gut contents were large *Perla carlukiana* nymphs and they had eaten a wide range of insect nymphs and larvae. Grau (1926) systematically studied the food of perlid stone-fly nymphs, showing that they ate animals and algae, Claassen (1931) and Küktreiber (1934) established the main differences between the carnivorous and phytophagous types of mouthparts, and Hynes (1941) studied the food of the two groups Setipalpia and Filipalpia.

Observations on *Ecdyonurus venosus* confirmed the range of herbivorous food described by Rawlinson (1939), while *Rhithrogena semicolorata*, with essentially similar mouthparts and mode of feeding, also brushed up encrusting algae, diatoms, morsels of plant tissue and, in summer, fragments of filamentous algae. It is not known whether the inclusion of filamentous algae is necessary for the growth of *Rhithrogena* as has been suggested in the case of *Caenis* (Moon, 1938). The form of the mouthparts and gut contents of *Baetis*, in which *Cocconeis* valves and plant tissue predominated, suggests that these nymphs both scrape and bite. The relatively large, powerful labrum with its considerable range of fore and after movement probably acts as a shovel, while the dissimilar mandibles each have well-developed 'canine' teeth and a ridged area for grinding; the maxillae with bristles and teeth may aid in brushing up and biting food. Even in those nymphs in which *Cocconeis* was most abundant in the fore-gut, it was rare or absent in the hind-gut, a feature which suggests regurgitation from the crop.

The amorphous mass in the crop of *Micronecta poweri* nymphs possibly represented the contents of algal filaments sucked out when these cells are pressed against the rostrum by the palea. There was no definite evidence of pharyngeal mastication as described by Walton (1938).

Several attempts have been made to correlate the food of Trichopteran larvae with anatomical characters of the head. Siltala (1907) concluded that those with brushes of setae on both mandibles were phytophagous, while those with brushes on the left mandible only might be phytophagous, omnivorous or carnivorous and those with no mandibular brushes were carnivorous or omnivorous. Wesenberd-Lund (1911) attempted to correlate the anterior or posterior position of the eyes and relative width of head with a carnivorous or phytophagous habit, a theory to which there are many exceptions as has been shown by Slack (1936). The generalization of Martynov (1930) that the Annulipalpia are mainly carnivorous and the Integripalpia phytophagous by preference is also too sweeping as has been shown by Ahmad (1936, unpublished) in his study of the mouthparts and alimentary canal of many caddis larvae in relation to feeding habits.

Observations of caddis larvae at Dinmael showed that *Glossosoma boltoni* ate diatoms and such other algae as may be included when it is brushing or scraping the surface of stones. The stout mandibles, devoid of teeth, each have a long brush of hairs and the eyes are posterior, so this larva resembles *Silo* in these features and fits into Wesenberg-Lund's theory. The coccoid algae and diatoms selected by *Chimarrha marginata* larvae also indicate a stone-scraping habit, agreeing with Noyes (1914) who found only vegetable food in this species, although the mandibles are strongly developed, have sharp teeth and lack the median tuft of hairs. In *Notidobia*, both mandibles are stout, have brushes of hairs and blunt teeth. Neatly cut-up pieces of fresh plant tissue predominated in their guts, but some algal filaments had been eaten. *Stenophylax stellatus* larvae were predominantly phytophagous.

It is generally agreed that *Hydropsyche* larvae are omnivorous and the predominant food evidently varies with availability and conditions, but the function of the net is controversial. Wesenberg-Lund (1911) considers that it catches food, and Richardson (1921) lists *Hydropsyche* among planktonic feeders in the Illinois. In contrast, Krawany (1929) concluded that in the brook at Lunz the larvae were plant eaters and did not use their nets to catch plankton in streams where moss and algae were prevalent. The presence in the guts of much *Cocconeis*, which was rare in the plankton, and the position of the dwellings under stones seems to indicate that in the Ceirw and Merddwr the food was brushed up from the bottom rather than netted. At Dinmael, the net and dwelling may be of greatest use for anchorage and perhaps protection.

Rhyacophila dorsalis larvae lived up to their 'typically carnivorous' reputation in devouring insect nymphs and larvae. *Polycentropus flavomaculatus* larvae were also carnivorous, demolishing a wide range of young insects and ignoring algae entangled in their nets.

Simulium larvae have been shown by Smart (1944) to catch particles in the passing current with their mouth brushes. Both he and Wu (1931) note that the larvae may pick up food from the substratum, but consider that this may be an adaptation to starvation conditions in the laboratory. Those studied at Dinmael were predominantly phytophagous, but occasionally ate their own species and chironomid larvae. The abundance of *Cocconeis* in the guts suggests that *Simulium* brush up their food from stones more commonly in nature than Smart and Wu supposed, especially in streams which are not rich in plankton.

While many chironomid larvae eat mainly plant detritus, the entire subfamily Tanypodinae are predacious, feeding especially on 'blood worms' and small crustaceans, although they may also eat the more rapidly moving diatoms (Leathers, 1921). A few observations at Dinmael served to confirm the generalization that forms other than Tanypodinae eat detritus and plant material and are more numerous than the carnivorous genera.

(*b*) *Fish*

These Welsh streams are considered by anglers and the river bailiffs to be well stocked with brown trout (*Salmo trutta* L.), the natural population having been augmented with many 4–8 oz. fish. Planting out of salmon fry is also practised and there is quite a good natural population of salmon (*Salmo salar* L.). Minnows (*Phoxinus phoxinus* (L.)) are common and eels (*Anguilla anguilla* (L.)), loach (*Nemachilus barbatula* (L.)) and bullheads (*Cottus gobio* L.) are known to be present.

The food of older salmon and trout has often been studied, but fish under 1 year have received little attention, especially in Britain. Salmon fry (lengths 2·6–2·8 cm.) were obtained from the Pont Barcar hatchery tank which had a gravel bed and service pipe line from the river. It resembled a fairly natural lotic environment augmented by an occasional plankton haul from a neighbouring lake. While the intestine contained yolk, the fry mostly rested under stones unless disturbed and, although the mouth was open, the ones examined were not feeding. In later stages when the yolk was exhausted, the fish came out into the open and started devouring chironomid and *Simulium* larvae, also algae such as *Ulothrix* and *Stigeoclonium* filaments, *Synedra* and monads. Small flies, *Baetis* nymphs and collembolans were occasionally taken. Chydorids and *Canthocamptus* from lake plankton were acceptable and, in contrast to minnows, the salmon fry took nymphs of *Micronecta poweri* when these were offered. The diet of a couple of fry of this size caught in the Ceirw resembled that of the fish from the tank except for the absence of lacustrine organisms. Larger fry (4–5 cm.) from the stream had a wider range of diet, additions including *Leuctra* and *Ephemerella* nymphs and adult helmid beetles. This agrees with White (1936) in eastern Canada, who concluded that while smaller fry select smaller organisms such as chironomid larvae and minute pupae, probably the general character of the food is decided largely by its daily availability, a conclusion also arrived at by Carpenter (1940) for salmon parr, and Neill (1938) for trout. Salmon parr eat a variety of organisms (Carpenter, 1940; Frost & Went, 1940; Allen, 1941) and so do brown trout (Pentelow, 1932; Slack, 1934; Neill, 1938; Allen, 1945). As the fish grow larger, Ephemeropteran nymphs and chironomid larvae are eaten less, caddis larvae and molluscs become more accessible. A few observations on trout from the Alwen confirmed this wider range of diet in larger fish.

The food of the young minnows studied was varied (Table 5), and agreed with that found by Frost (1943) in the River Brathay except that diatoms were of more importance than in her fish of corresponding size. Frost points out, after considering all age groups of minnows, that in running waters the food requirements closely coincide with those of salmonids and that the possibility of serious competition is great. My observations on the food of salmon fry emphasize this similarity in the young stages. The eel is another potential competitor since it eats insect larvae (Frost, 1946) and may even prey on salmonids. Bullheads and loach devour some of the same organisms, as they feed on insects and Crustacea (Hartley, 1948).

7. FOOD-CHAINS AND THE STREAM COMMUNITY

This discussion should start at the level of water analyses, bacteria, microscopic flora and Protozoa. The nutrient and bacterial content of Ceirw and Merddwr waters were not analysed, but as they are well oxygenated and there are many young insects characteristic of unpolluted waters, the dissolved organic matter could not be very great. The mineral content was obviously adequate to support a varied algal flora and also the holophytic Protozoa. The food of Protozoa is reviewed by Sandon (1932), who stresses the importance of specific strains of bacteria, of various small algae including diatoms, and of other Protozoa and rotifers as food for free-living, holozoic forms. Picken (1937) illustrates this with diagrams of the food relationships within ciliate communities in the River Cam. He considers that Protozoa have few metazoan predators, their enemies being mostly other Protozoa. The food of rotifers (cited by Picken as bacteria) is very varied (Wesenberg-Lund, 1929); it consists of many small organisms, both plant and animal, including Protozoa. Owing to the rapidity with which delicate forms such as Protozoa would be digested, it is difficult to determine directly their importance as food for other organisms and the significance of diatoms with their indigestible tests may be over-stressed. Indeed, these may be swept into the gut together with the actual food, but may not always be utilized. Planktonic investigations which cast doubt on the complete dependence of marine copepods on diatoms are summarized by Clarke (1939), who stresses the need for considering the nannoplankton: this line of thought might well be pursued in fresh-water studies.

In the present survey, the presence of a varied protozoan fauna was demonstrated, especially in moss and amongst gravel, but these forms were rarely detected in the few guts examined. Apart from the impossibility of finding Protozoa in preserved material, it apparently made little difference whether the material was fresh or preserved. Rotifers were rare in the guts studied, except in limnophilid caddis which had evidently ingested their commensals, but they are recorded in the food of *Chloroperla* (Hynes, 1941). Table 5 indicates the apparent importance of algae and other plants as the basis of a food chain, and this emerges still more clearly if the larger members of the stream community are listed under their predominant feeding habits. An asterisk indicates forms for which the findings have been culled only from the literature and the authority is given in brackets.

Predominantly phytophagous forms	Omnivorous forms	Predominantly carnivorous forms
Ancylastrum fluviatile	*Hydropsyche* larvae	*Herpobdella octoculata*
Chironomid larvae excluding Tanypodinae	**Chloroperla* spp. (Hynes, 1941)	*Perla carlukiana* nymphs
Baetis spp. nymphs	*Phoxinus phoxinus*	*Polycentropus flavomaculatus* larvae
Ecdyonurus venosus nymphs	*Salmo salar* fry	*Rhyacophila dorsalis* larvae
Rhithrogena semicolorata nymphs	—	*Hydracarina (Mellanby, 1938)
Ephemerella ignita nymphs	—	**Dicranota* larvae (Miall, 1893)
Micronecta poweri nymphs	—	**Salmo salar* parr
Glossosoma boltoni larvae	—	**Salmo trutta*
Chimarrha marginata larvae	—	**Nemachilus barbatula* (Hartley, 1948)
Notidobia larvae	—	**Cottus gobio* (Hartley, 1948)
Stenophyllax stellatus larvae	—	—
Helmidae larvae	—	—
Simulium spp. larvae	—	—
**Silo* (Siltala, 1907)	—	—
*Enchytraeidae (Stephenson, 1930)	—	—
**Leuctra* spp. nymphs	—	—
**Amphinemura* nymphs (Hynes, 1941)	—	—
**Agapetus* spp. larvae (Percival & Whitehead, 1929)	—	—

The Chironomidae constitute a food chain among themselves, and as the proportions of Tanypodinae and other chironomid larvae were not determined, although it was apparent that the latter were considerably more numerous than the former, the figures in Table 1 cannot be used to demonstrate a pyramid of numbers in detail. It is evident, however, that the predominantly phytophagous species exceed the omnivorous and predominantly carnivorous ones and that all those stone dwellers with the greater population density, say 'over 15', in more than one 2500 sq.cm. sample (Chironomidae, *Baetis* spp., *Leuctra* spp., Enchytraeidae, *Ephemerella ignita*, *Glossosoma boltoni*, *Agapetus fuscipes* and *Simulium* spp.) are predominantly phytophagous.

Thus the invertebrate fauna of the Ceirw and Merddwr is varied and capable of supporting a good population of Salmonidae; with its numerous chironomid larvae and *Baetis* nymphs, it is especially suitable for the rearing of fry.

8. SUMMARY

1. Quantitative samples from the stony bed of some Welsh streams indicate the composition of the fauna and demonstrate the great variability in population density.

2. Immature insects, especially chironomid larvae, *Baetis* and *Leuctra* nymphs, predominate. The occurrence in the samples of various forms is considered in relation to their ecology and life histories.

3. The population of the stony substratum was least dense during winter.

4. A brief survey of the planktonic and benthic microscopic organisms in the streams, and a comparison with the plankton of the Dee itself, indicates the nature of the potential basic food supply. Zoöplankton is sparse in the streams, where the plankton consists chiefly of diatoms derived from the benthos. Moss has a richer microscopic fauna than gravel, mud or stones.

5. The gut contents of many organisms are considered. Forms feeding on algae and plant tissue (especially debris) predominate. Those animals

shown to be most numerous in the samples are detritus feeders or phytophagous. The invertebrate fauna is considered in relation to the fish population, the climax of the food chain in the stream.

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