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The distribution, life cycle, and predators of Ephemerella ignita (Poda) in the River Endrick, Scotland

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Abstract

Ephemerella ignita (Poda) occurs in most parts of the River Endrick in Scotland except the extreme lower reaches. It is most abundant in the middle reaches, especially among weed and stones where the current is strong. The life cycle is an annual one, the eggs lying dormant over winter to hatch in April and May. The larvae develop rapidly thereafter to emerge and lay eggs in July and August. The principal predators of this species in the Endrick system include several fishes, notably Salmon *Salmo salar* L.

Резюме

Распространение, жизненный цикл и хищники Ephemerella ignita (Poda) В реке Индрик (Шотландия)

Ephemerella ignita (Poda) встречается почти на всем протяжении реки Индрик за исключением ее нижнего течения. Она наиболее многочисленна в среднем течении реки, особенно среди растительности и камней, где течение очень быстрое. Продолжительность жизненного цикла – один год. Яйца отлкадываются медленно, в течение зимы, вылупление личинок происходит в апреле мае. Личинки быстро развиваются и откладывают яйца в июле августе. Основными хищниками, уничтожающими этот вид в реке Индрик, являются некоторые рыбы, особенно семга – *Salmo salar* L.

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1. Introduction

Of the 47 species of Ephemeroptera known in Great Britain, 21 have recently been recorded from the River Endrick in Scotland (Maitland 1963). One of the commonest of these and in many parts of the river the most abundant is *Ephemerella ignita* (Poda). This is the most widespread of the two British species of *Ephemerella*, being found in suitable habitats in most parts of the country. The second species, *Ephemerella notata* Eaton, is much less common, and Macan (1961) indicates that it has not been recorded in Scotland – though Neill (1938) lists it from the River Don in Aberdeenshire. None were found in the River Endrick during the present study. The distribution maps given by Macan (1961) also indicate that *E. ignita* has not been recorded from either Dunbartonshire or Stirlingshire (through which counties the River Endrick flows), though Weerekoon (1956) noted it to be common in parts of Loch Lomond lying within Dunbartonshire. The present account deals with certain important features of the biology of *E. ignita* in the River Endrick, notably its distribution, life cycle and predators.

As a common member of the invertebrate fauna of streams and some lake shores in Great Britain, *E. ignita* is frequently mentioned casually in the literature on freshwater ecology in this country. Views on the biology of this species, especially with regard to its life cycle, were formerly somewhat conflicting (e.g. Whitehead 1935, Neill 1938), and though the position has recently been clarified by Macan (1957a) there still appear to be certain anomalies which are discussed further below. Data on the numbers and flight season of the adults of *E. ignita* have been published by Macan (1957a, 1961) and Gledhill (1960), whilst information on the larvae has been given in general papers on Ephemeroptera written by Macan (1957a, 1957b, 1961). Many scattered references to this species can be found in general ecological accounts of freshwaters in this country (e.g. Percival and Whitehead 1929, Badcock 1949, Weerekoon 1956, Hynes 1961, Maitland 1964 etc.) and of the food of freshwater fish (e.g. Neill 1938, Badcock 1949, Frost 1950, Mills 1964, Maitland 1965 etc.). Many general ecological accounts note simply *Ephemerella sp.* (e.g. Allen 1941, Frost 1945, Jones 1949a, Badcock 1953 etc.); it is probable that many of these refer to *E. ignita*.

2. Methods

Most of the field work for the present study was carried out between 1959 and 1962, whilst the author was engaged in an ecological survey of the River Endrick (Maitland 1963). All the general distribution data were obtained by taking comparable samples at each station with a handnet (diameter 40 centimetres, depth 60 centimetres, mesh 16 threads per centimetre) for a standard period of 10 minutes. Such semi-quantitative collections on a time basis have been shown to be very useful in connection with distribution studies of various species of invertebrates (e.g. Mann 1955, Macan 1957b, Reynoldson 1958). In the River Endrick, when different types of habitat were found to be present, several samples were taken at each station. Sampling was carried out at 12 stations on the main river, and also at 8 stations on selected tributaries; 3 series of samples were taken: in October, 1959, February, 1960, and June, 1961.

Monthly quantitative samples of the invertebrate fauna on an area basis were taken for a period of 15 months at 2 stations on the main river – one in the lower reaches (Woodend), the other in the middle reaches (Drumtian). This sampling has been fully described elsewhere (Maitland 1964). *E. ignita* occurred regularly only at Drumtian, where the samples were taken with a modified shovel sampler. On one of the most important tributary streams in the Endrick system – the Altquhur Burn – in connection with a study

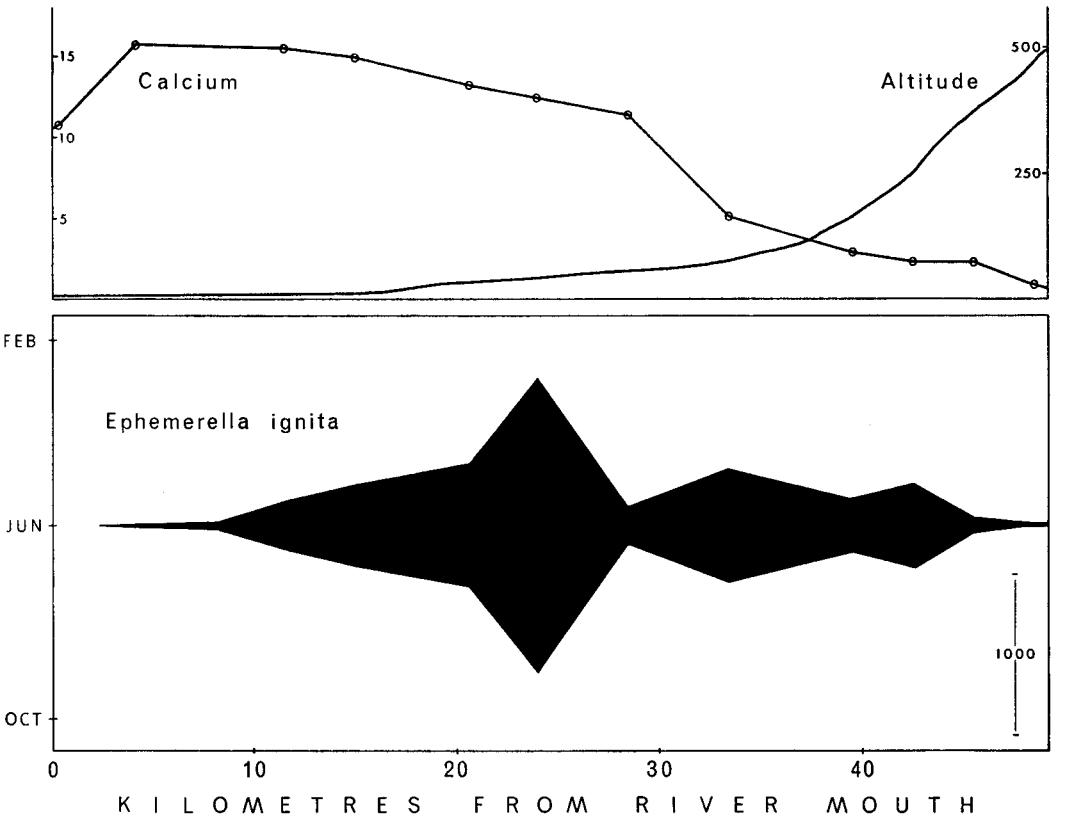

Fig. 1. The altitude in metres above sea level and the average calcium content in milligrams per litre of the River Endrick (above); and the numbers of *Ephemerella ignita* collected in 10 minutes at 12 stations during February, June and October.

of the feeding habits of certain fish (Maitland 1965), monthly samples of invertebrate fauna were collected by means of a handnet (mouth 23×23 centimetres, depth 110 centimetres, mesh 65 threads per centimetre) used for a standard period of 10 minutes.

Less regular samples were taken in other parts of the River Endrick. Many of these were used in connection with pollution studies (Maitland 1962), and sampling was carried out with both handnet and shovel sampler. Collections of adult Ephemeroptera were also made at irregular intervals at various stations on the river.

Only a short account of the River Endrick is given here as it has been described more fully elsewhere (Maitland 1963). Rising at a height of just under 500 metres above sea level in the Gargunnock Hills in Stirlingshire, it flows mostly westward through a distance of 49 kilometres to enter Loch Lomond (of which it is the major tributary) in its south-east corner, at a height less than 10 metres above sea level. The catchment area of the River Endrick is approximately 26700 hectares and its profile is a relatively simple one (Fig. 1). Most of the Endrick basin is underlain by Old Red Sandstone, which in places gives way to a calciferous sandstone, whilst the chief hills of the region are formed from basaltic lavas overlying these. The region is relatively sparsely populated, and much of the land of the river valley is used for agricultural purposes.

Table 1. The numbers of *Ephemerella ignita* collected in 10 minutes from 3 different substrates at 5 stations on the River Endrick in June 1961.

Stations	Drymen	Dalnair	Culcreuch	Fintry	Burnfoot
Kilometres from river mouth.....	12	15	33	39	45
Metres above sea level	13	15	80	180	340
Milligrams of calcium per litre	16	15	5	3	2
Weed in current.....	183	496	830	423	19
Stones in current.....	617	551	197	84	99
Stones in pools.....	12	69	37	10	16

3. Distribution

The results of standard collections taken at 12 stations on the main river are shown in Fig. 1; these stations have been described elsewhere (Maitland 1963). No *E. ignita* were found during February at any of these stations. In June, the species was absent from the extreme lower reaches of the River Endrick, but occurred in all stretches above this – being most common at places between 10 and 45 kilometres from the river mouth. In some places it was extremely abundant at this time. 4 specimens only were found during October, all of them mature larvae, and all occurring in the lower half of the river. This great variation in the numbers found at different times of the year is in agreement with the observations on the life cycle of this species which are described below.

Results from collections made in tributary streams give a similar picture – *E. ignita* was uncommon or absent in February and October but was common in most places during June. The species is clearly commoner in some habitats than in others: Table 1 gives the results of 15 standard collections taken in June 1961 from 3 different habitats (weed in current, stones in current and stones in pools) at 5 stations on the main river. At all these stations *E. ignita* is obviously commoner on weed and stones in current than on stones in pools where the current is weak.

The greatest numbers of *E. ignita* collected in any one habitat in the River Endrick were found among loose moss – *Fontinalis antipyretica* L. at Fintry, but the species is also very common among other vegetation (e.g. *Myriophyllum alterniflorum* D.C. and *Potamogeton crispus* L.), and also, as noted above, on stones where the current is strong. Percival and Whitehead (1929) found that the greatest numbers of *E. ignita* in the rivers which they studied were among loose moss; they found that *Cladophora* and thick moss had about the same average number present but this was always less than that from loose moss.

The species undoubtedly appears to be rheophilic; this would account for its absence in the extreme lower reaches of the River Endrick, where the current is very slow indeed (Maitland 1964). Ambühl (1959) has shown experimentally that the optimum current for *E. ignita* lies between 10 and 30 centimetres per second, and that above and below this the numbers found will decline. Macan (1957b) postulates the distribution of *E. ignita* (and other Ephemeroptera) in an imaginary river which rises in poor mountainous country and finishes by flowing through rich low-lying countryside – a river essentially similar to the River Endrick in fact. In such a river it is suggested that *E. ignita* would be absent near the source, but then appear further downstream, gradually becoming more and more abundant all the way to the mouth. In the River Endrick the distribution essentially follows this pattern, except that in the extreme lower reaches, the current is so slow that the species disappears instead of becoming more abundant, as postulated by Macan.

As noted above, the River Endrick is the major tributary supplying Loch Lomond, where *E. ignita* is common during summer on stony shores – nowhere, however, reaching the abundance found in the middle reaches

of the River Endrick. Weerekoon (1956) notes that *E. ignita* is the most common Ephemeroptera larva on stones and boulders along the margin of Loch Lomond, and that it also occurs on swards of *Littorella uniflora* (L.) in shallow water there. He points out that where the stones are exposed to severe wave action, however, this species is replaced by *Ecdyonurus dispar* (Curtis), a species better adapted to these more rigorous conditions.

The maximum numbers of *E. ignita* found at Drumtian in the middle reaches of the River Endrick occurred during May when, in 1960, the density reached 7163 individuals per square metre. This is considerably higher than the maximum densities of 1960 per square metre found in the River Wharfe by Percival and Whitehead (1930), of 690 found in the River Don (Aberdeenshire) by Neill (1938), of 68 per square metre found in the River Dee (Wales) by Badcock (1949), and of 20 per square metre found by Weerekoon (1956) in Loch Lomond. In part at least, the lower numbers found by these workers may have been due to the fact that coarser nets were used by them thus allowing many of the smaller larvae to pass through (Jonasson 1955) – see Table 3. Thus the greatest numbers of larvae found in the Altquhur occurred in July and here numbered about 800 individuals per square metre. As noted below, this figure represents only those animals retained by a sieve of 16 meshes per centimetre (as compared to that of 65 meshes per centimetre used for the samples from Drumtian), and it is probable that the true densities are similar to those at Drumtian, with the maximum number of larvae being far greater than 800 per square metre and occurring much earlier (i.e. during May).

The general effect of sewage effluents on the invertebrate fauna of the River Endrick has been noted elsewhere (Maitland 1962). *E. ignita* was absent from all samples taken in February 1961 and extremely uncommon in those taken during October 1961. In June 1961, the species was abundant in collections taken 20 metres upstream from 2 different sewage effluents, uncommon in those taken 20 metres downstream from these effluents, but common again 200 metres below them (Table 2). These effluents were found to have a similar effect on many common stream invertebrates, namely reducing their numbers drastically immediately below the effluents, after which the populations gradually recovered. Macan (1962) suggests that very mild organic pollution was responsible for an increase in the numbers of *E. ignita* in a small stream in the Lake District in England.

The food of *E. ignita* was found by Percival and Whitehead (1929) to consist mainly of moss, some unicellular and filamentous algae, detritus and occasionally other invertebrates. Jones (1949b) found that *E. notata* has a similar diet. Badcock (1953) noted that *Ephemerella* was commoner in the Swedish streams which she studied than in the Welsh ones – she attributed this to the larger amounts of *Cladophora* occurring in the former; earlier in the same paper the amount of *Cladophora* was noted to increase with an increase in dissolved salts. A similar situation might be postulated for the River Endrick where the increasing numbers of *E. ignita* found downstream from the source on stones coincide with an increase in the amount of dissolved salts present in the river water (e.g. calcium). Hynes (1961) also found a gradual increase in the numbers of *E. ignita* for some distance downstream from the source in the Afon Hirnant in Wales.

Table 2. The numbers of *Ephemerella ignita* collected in 10 minutes from stations (a) 20 metres above, (b) 20 metres below, and (c) 200 metres below the sewage effluent discharges from the villages of Balfron and Blanefield into the River Endrick in June, 1961.

Stations	(a)	(b)	(c)
Balfron.....	913	3	637
Blanefield.....	533	90	267

Table 3. The numbers of *Ephemerella ignita* in each millimetre length class retained when sieving a single 10-minute sample through meshes of 4, 8 and 16 threads per centimetre.

Mesh	Millimetre length classes									
	1	2	3	4	5	6	7	8	9	10
4	–	3	9	40	92	93	34	9	–	
8	7	62	88	241	177	106	40	9	–	
16	80	228	103	241	177	106	40	9	–	

4. Life cycle

As noted above, monthly samples were taken at 2 stations in the Endrick system, and these were used to analyse the life cycle of *E. ignita* in the area. The station at Drumtian in the middle reaches of the river, which was sampled each month in 1960, has been described fully elsewhere (Maitland 1964); the substrate here consisted of small stones and gravel, and though occasional clumps of *Fontinalis antipyretica* were present, none were included in the samples. The station on the Altquhur Burn, an important tributary flowing into the middle reaches of the River Endrick, was sampled every month in 1961, and has also been described fully elsewhere (Maitland 1965). The substrate here consisted of small stones and gravel, as well as large clumps of *Myriophyllum alterniflorum*, which was always included in the samples. The collections from Drumtian include all animals retained by a mesh of 65 threads per centimetre, whilst those from Altquhur include only those retained by a mesh of 16 threads per centimetre. The effect of this difference on the samples has already been alluded to and will be further discussed below (see Table 3).

Each animal in these samples was measured for length from the anterior part of the head to the base of the caudal cerci; the length/frequency results from both stations were plotted as histograms and are shown in Figure 2. It can be seen that the life cycle at both stations was similar. No larvae were found in the first three months of either year, but in April a few small individuals appeared. By May there were large numbers of small individuals, whilst during June and July there were reasonable numbers of larvae of all sizes – especially medium-sized specimens. In August, fewer larvae were present – many of these being large individuals, whilst in September only occasional large specimens were found. None were collected at either station in the last three months of the years concerned. In collections of adult Ephemeroptera which were made during 1960 and 1961, *E. ignita* was found only during July and August.

The life cycle of this species, therefore, in the River Endrick, is an annual one. The eggs appear to hatch mainly in late April, and larvae from these grow rapidly during May, June and July. Adults emerging in July and August lay eggs which probably lie dormant in the stream bed until the following year.

The data obtained by Percival and Whitehead (1930) from the River Wharfe are rather different from the above. These authors noted that *E. ignita* presents quite definite indications of seasonal variation in numbers; in some places it could not be found in December and early January, but usually a few large larvae could be taken throughout the winter. Neill (1938) noted that larvae of *E. ignita* were first seen in the River Don in May and increased rapidly in number thereafter. He suggested that young individuals hatch immediately from the eggs and that they then find shelter at the roots of vegetation (thereby being missed during sampling); the great reduction in number of this species in autumn is said to be due to disturbance by floods. Neill notes that the suggestion previously made by Whitehead (1935) that the eggs of *E. ignita* have a long incubation period of about 6 months is improbable under natural conditions.

Macan (1957a) found that in a population of *E. ignita* in the English Lake District, the greater part of the year (9 to 10 months) was spent in the egg stage, larvae appearing at the

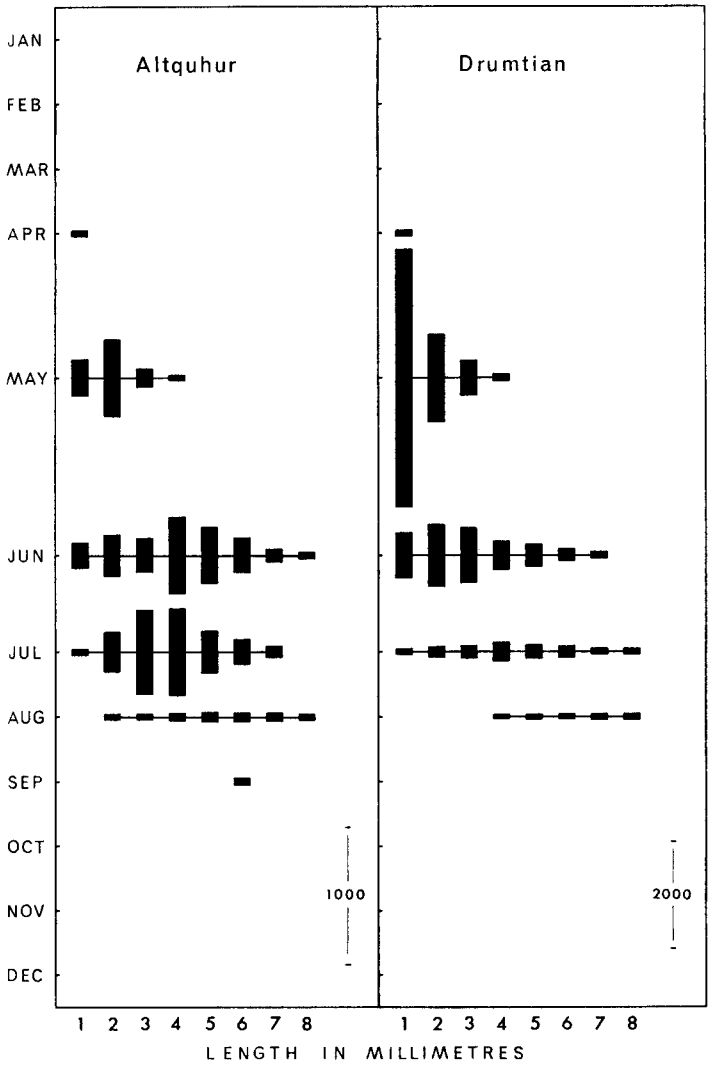

Fig. 2. The length/frequency diagrams of *Ephemerella ignita* from Drumtian in 1960 (numbers per square metre) and Altquhur in 1961 (numbers collected in 10 minutes).

beginning of June, growing rapidly and then disappearing at the end of August; a few larvae were sometimes to be found in late May and also in September. This life history for the species is again given in Macan (1957b, 1961). Hynes (1961) found that in a population in Wales the larvae started to hatch in late March, and thereafter growth was rapid until maturity was reached in August. A few specimens were found in September and October. Essentially similar data to these have been given by Badcock (1949) and Pleskot (1958) for populations in streams in Wales and Austria respectively.

Jensen (1956) noted that in Denmark, after a warm winter, young *E. ignita* were found in January, together with a few large nymphs from the previous year. Gledhill (1962) found

fully-grown larvae of this species in Dorset (England) both in April and in August. From all these results it would appear that whilst the type of life cycle found in the River Endrick is a typical one, *E. ignita* is capable of responding to the varying conditions of temperature (and possibly light – see Hynes 1961) which may occur both in time and space.

Hynes (1961) gives details of the life cycle of *E. notata* in Ireland. He says that the eggs hatch from August to February, and that by March most of the larvae are about 3 millimetres long. They grow rapidly thereafter to emerge in May and June. Hynes (1961) points out that *E. notata* and *E. ignita* form a pair of species which may occur together, but one of which is at all times ahead of the other in development.

A description of oviposition and the ova of *E. ignita* has been given by Percival and Whitehead (1928) who note that swarming for oviposition takes place in the evening starting in June and July. Adults of this species have been recorded from the Aberdeenshire Don in June and July by Neill (1938), from the Hampshire Avon in May and June by Macan and Macan (1940) and from the Lake District in August by Gledhill (1960). As noted already, the records from the River Endrick confirm that the normal flight period for *E. ignita* is during the summer months only.

5. Predators

During 1961 a study of the feeding habits of Salmon *Salmo salar* L., Trout *Salmo trutta* L., Minnows *Phoxinus phoxinus* (L.), Stone Loach *Nemacheilus barbatula* (L.), and Three-spined Stickleback *Gasterosteus aculeatus* L., in the River Endrick was carried out (Maitland 1965). These 5 species of fish are the common ones in those parts of the River Endrick where *E. ignita* is most abundant; all were found to eat large numbers of it. Most commonly, it was eaten by Salmon (and in spite of the fact that it was taken during 3 months of the year only – see below – it formed 6.4 per cent by bulk of the average annual food of this species in the Altquhur Burn), but also in appreciable numbers by the other species. These fish must clearly be of importance in controlling the populations of *E. ignita* in this area.

Other workers too have shown that *E. ignita* is commonly eaten by various species of fish: thus Neill (1938) found it to be an important part of the diet of Trout, Frost (1950) of the diet of Trout and Salmon, and

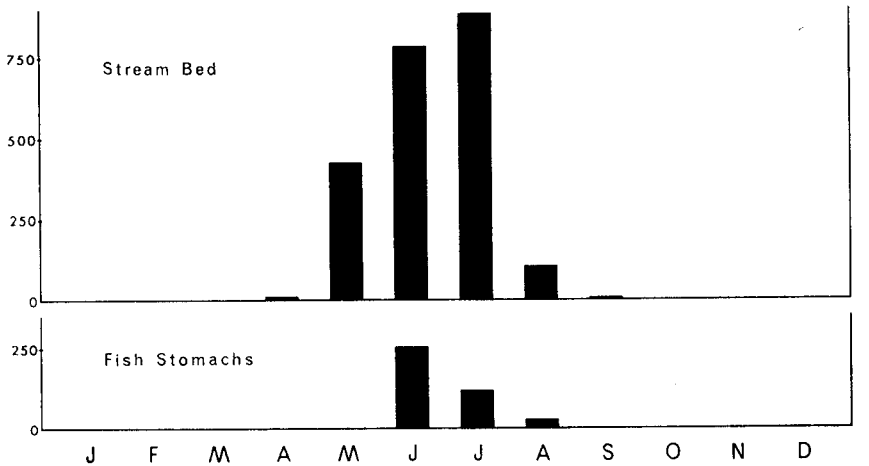

Fig. 3. The numbers of *Ephemerella ignita* collected in 10 minutes from the Altquhur Burn during each month in 1961, and the numbers found there at the same times in the stomachs of 100 fish (equal numbers of Salmon, Trout, Minnows and Stone Loach).

Table 4. The percentage composition of the millimetre length classes of *Ephemerella ignita* present (a) in standard 10-minute handnet collections and (b) in the stomachs of a random sample of four species of fish, all teken from the Altquhur Burn in 1961.

		Millimetre length classes									
		1	2	3	4	5	6	7	8	9	10
June	a	9.3	14.8	9.6	27.9	20.5	12.3	4.6	1.0	–	–
	b	–	–	6.6	21.2	21.2	27.0	18.3	5.7	–	–
July	a	0.7	13.9	28.8	30.1	14.6	8.3	3.6	–	–	–
	b	–	–	1.7	50.9	31.0	11.2	0.9	4.3	–	–
August	a	–	2.3	10.9	14.1	22.8	21.7	22.8	5.4	–	–
	b	–	–	4.2	25.0	25.0	4.2	25.0	12.5	4.1	–

Badcock (1949) and Mills (1964) of the diet of Salmon. It seems to be much more highly available to Salmon than to many other species of fish: the availability factors calculated for members of the fish community in the Altquhur Burn were 1.5 to Salmon, 0.4 to Trout, 0.3 to Minnows and 0.3 to Stone Loach. The reasons for such differences are still obscure, and could be due to one or more of a number of factors (Maitland 1965).

Though present in the Altquhur Burn for 6 months of the year (Fig. 2) larvae of *E. ignita* were eaten by the fish there only during 3 of these (Fig. 3). This species is a very good example of how the general availability of a single food item for a fish may fluctuate, this fluctuation depending almost entirely upon its life cycle. As noted above, the eggs of *E. ignita* appear to hatch in April and by May the larvae are common members of the bottom fauna of the Altquhur Burn. None are taken by the fish at this time, however, probably because they are still very small (Fig. 2) – i.e. their availability is low because of their size and not because of their numbers. During June and July there are large numbers of larvae of medium size and at this time they become important to the fish in the stream. It can be seen from Table 4 that there is a strong tendency on the part of these fish to eat the larger specimens only (cf. Table 3). In August the numbers of larvae are much lower (presumably due to predation and emergence) and in spite of the fact that their average size is much larger than in previous months fewer of them are eaten. By September there are only a few large larvae left in the bottom fauna and none have been found in the stomachs of fish at this time.

Several invertebrates are also known to feed on *E. ignita* – notably *Hydropsyche* (Percival and Whitehead 1929). Jones (1949b) also showed that *Hydropsyche* eat *Ephemerella* as do *Dinocras*, *Perla*, *Rhyacophila*, *Philopotamus* and *Oreodytes* – all of which occur commonly in the River Endrick. The situation is complicated by the fact that several of these carnivorous invertebrates are themselves eaten regularly by fish in the Endrick system (Maitland 1965). It appears probable that the major trend in the food web surrounding *E. ignita* in the River Endrick may be summarised thus: *Fontinalis antipyretica* L. → *Ephemerella ignita* (Poda) → *Hydropsyche instabilis* Curtis → *Salmo salar* L. → *Ardea cinerea* L.

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