OBSERVATIONS ON THE FOOD OF EELS (*ANGUILLA ANGUILLA*) FROM THE WINDERMERE CATCHMENT AREA

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1. INTRODUCTION

Some investigation of the food of the eel (*Anguilla anguilla* (L.)) in fresh water has been carried out on the Continent, but no such study, apart from that based on 27 eels from East Anglia (Hartley, 1940) appears to have been made for British waters. The following account, although based on limited observations, provides some information on the subject. The eels examined were collected, over a number of years, from the Windermere catchment area. They formed part of the material obtained for a study primarily of age and growth (Frost, 1945*a*, *b*), thus the collection of data on food was subordinate and the information obtained from them will not give a comprehensive picture of the food of eels in this district. The eels came from three places in the catchment region, namely, Windermere, the Cunsey Beck which flows out of Esthwaite Water into Windermere, and the River Leven, the outflow of Windermere (see Frost, 1945*a*, Fig. 1). Yellow eels were examined from all three stations, including small individuals that is those under 35 cm. (but not including elvers) locally called 'snigs', and in addition an examination was made of migrating (silver) eels that came from the Cunsey Beck.

2. MATERIAL AND METHODS

The material obtained at each of the three stations and the method of collecting it will be described under the appropriate heading when the results from each station are given. The food organisms in the stomach, which in the eel consists of a blind sac and a relatively much smaller pylorus, were little digested and thus were recognizable and could be counted; in some cases this was also true of the contents of the intestine, but in others it was not so. In view of this the results are based on the contents of the stomach and not of the alimentary canal. The food organisms were counted individually (except in the case of silver eels, Table 5) and the number of fish containing any organism was noted. In the table the number of individual organisms of any one type is given and expressed as a percentage of the total number of organisms eaten; the number of fish containing each type of food organism is shown, this number also being expressed as a percentage of the total number of fish examined.

The food organisms have been determined to the species or to groups. I wish to acknowledge the help of Mr J. R. Le Brockton Tomlin in connexion with the identification of the Mollusca and of Dr N. E. Hickin for his examination of the Polycentropid larva from Cunsey Beck which he finds to resemble that of *Polycentropus flavomaculatus* Pict. The following notes are given on the organisms recorded from the stomachs.

Fish. The fish were the minnow (*Phoxinus phoxinus* (L.)), the perch (*Perca fluviatilis* L.) and one specimen which was probably a small brown trout (*Salmo trutta* L.).

Mollusca. In the Windermere eels *Limnaea pereger* (Müll.), *Valvata piscinalis* (Müll.), *Ancylastrum fluviatile* (Müll.), *Sphaerium corneum* (L.), *Pisidium* sp. and *Planorbis* sp. were found. *Limnaea*, *Planorbis*, *Pisidium* and *Sphaerium* were found in the silver eels taken at Cunsey Beck, and *Limnaea* was the mollusc identified from the yellow eels taken at this station. It was not always possible to distinguish *Pisidium* and *Sphaerium* from each other and therefore they have been considered together.

Trichoptera. These were all, save one adult and two pupae, larval forms. In the lake eels a Leptocerid most probably *Leptocerus* sp., a Polycentropid and *Phryganea* sp. were identified and in the beck and river eels *Rhyacophila* sp., *Hydropsyche* sp., *Hydroptila* sp. and a Polycentropid. The latter, which occurred in large numbers in the yellow eels of the Cunsey Beck, was, as noted above, most probably *Polycentropus flavomaculatus* Pict.

Ephemeroptera. All but one specimen were nymphal forms. In the Windermere eels *Ephemera danica* Müll., *Leptophlebia* sp. and an Ecdyonurid, were taken and from those of the Cunsey and Leven *Baëtis* sp. and *Ephemerella ignita* (Poda). The one adult Ephemeropteran was a subimago, too much digested for identification, eaten by a silver eel.

Plecoptera nymphs, which occurred only in the River Leven fish, were *Amphinemura cinerea* (Oliv.).

Diptera larvae, which were present in fish from all stations, were almost all Chironomidae, these were not identified further than the group. Tipulid larvae occurred in the Cunsey and Leven eels and *Simulium* larvae in the Cunsey fish. Pupal Diptera were represented by the Chironomidae.

Other aquatic insect larvae found in the stomachs

were *Sialis* sp. and unidentified Odonata and Coleoptera, the first being taken in eels from Windermere and Cunsey Beck, the second from all three stations and the last from the Leven fish.

Aquatic Hemiptera were represented by one fragmentary specimen of *Sigara* sp. found in a Leven fish.

Winged insects were represented by one Trichopteran, one Ephemeropteran and two insects of terrestrial origin and all were found in eels caught in the Cunsey Beck.

Crustacea. Gammarus pulex De Geer was recorded from Windermere and Cunsey fish and *Asellus* sp. from the lake and Leven eels.

Oligochaeta were found in eels from all stations and although the size of their setae suggested earthworms the shape of these did not preclude the worms being Enchytraeids or Lumbriculids.

'*Others*' included creatures which had become accessible food by chance such as caterpillars, slugs, a woodlouse and a spider, and any unidentifiable debris.

3. RESULTS

The data obtained from the investigation of the stomach contents are considered under the following headings: (*a*) food of yellow eels in Windermere, (*b*) in the Cunsey Beck, (*c*) in the River Leven, and (*d*) food of migrating eels.

(*a*) *Food of yellow eels in Windermere*

Windermere has a length of 10·5 miles (17 km.), a mean breadth of 950 yd. (874 m.) and a mean depth of 75 ft. (24 m.); there is a narrow littoral zone. The water of the lake has a low nutrient salt content and is 'soft' in character. The 106 yellow eels upon which the following account is based were taken from various parts of the lake and from deep and shallow water. The fish were captured by seine (41), Dutch Fyke net (22) †, perch trap (20), long line (17) and rod and line (6), over a period of several years. Many other eels were examined but those caught in perch traps which had obviously been feeding on captive perch and those specimens taken on long lines which had clearly fed upon the bait could not be considered. The eels examined were captured in May (14), June (22), July (8), August (48), September (4), October (8) and December (2). They ranged in length from 35·5 to 60 cm., the mean being 45 cm. and the majority of the fish were between 40 and 50 cm. long. The age of these eels deduced from a previous study (Frost, 1945*b*) is probably of the following order: 33·5 cm. = 6, 60 cm. = 11, 45 cm. = 9, 40 cm. = 8 and 50 cm. = 10 years in fresh water.

Table 1. *Food of yellow eels in Windermere;* 106 *fish*

Food organism	No. of individual organisms	% of total organisms	No. of fish containing	% of fish containing
Limnaea pereger	361	18·0	21	19·8
Valvata piscinalis	604	30·1	31	29·3
Pisidium/Sphaerium	445	22·2	36	34·0
Planorbis spp.	20	1·0	9	8·5
Ancylastrum fluviatile	2	0·1	1	0·9
Mollusca indet.	72	3·6	22	20·7
Leptocerid larvae	191	9·5	18	17·0
Polycentropid larvae	4	0·2	2	1·9
Phryganea sp. larvae	5	0·2	3	2·8
Trichopt. l. indet.*	28	1·4	16	15·1
Sialis larvae	38	1·9	13	12·2
Ephemera danica nymphs	22	1·1	9	8·5
Leptophlebia sp. nymphs	8	0·4	2	1·9
Ecdyonurid nymphs	2	0·1	2	1·9
Odonata nymphs	3	0·1	2	1·9
Chironomid larvae	40	1·9	8	7·5
Gammarus pulex	147	7·3	21	19·8
Asellus	4	0·2	1	0·9
Oligochaeta	12	0·6	3	2·9
Perca	1	0·05	1	0·9
Others	2	0·1	2	1·9
Totals	2011	100·05		

* Contained two Trichoptera pupae.

In Table 1 the results of the stomach analyses irrespective of the size of the fish or the month of its capture are given. It will be seen that molluscs, as indicated by the number consumed and the number of fish containing them, form much the greatest part of the diet, and of these *Valvata piscinalis* is the predominating species with *Limnaea* and *Pisidium/Sphaerium* next in importance. The

† A war-time fishery for perch in Windermere by means of unbaited wire traps lasts from mid-April to June and eels frequently enter these traps.

occurrence of 80 specimens of *Limnaea* in one fish and of 70 *Valvata* in another gives some idea of the quantities of these molluscs eaten. Of the remaining food organisms Trichoptera larvae and *Gammarus pulex* occur in a fair proportion of the fish, the former making up by number 11·5 % of the organisms eaten, a figure which is, however, affected by the fact that two fish contained 80 and 40 specimens, whereas the 87 cm., had been feeding on the trapped perch. The length of most of the individuals eaten was 10·0 cm., whereas the mean length of the captives is 13·5 cm. The consumption of the confined perch, which were also apparently selected for size, suggests that under natural conditions fish are not easily caught nor are those of suitable size encountered in the lake.

Table 1 gives the data obtained from the stomach

Table 2. *Food of yellow eels in Windermere in relation to size of the fish; number of fish given in brackets*

(*a*) Mean length of eels containing different foods

Food ...	Mollusca (91)	Aquatic insect larvae (52)	Chironomid larvae (8)	Crustacea (22)	Oligochaeta (3)	Fish (1)	Others (2)
Mean length in cm.	45·5	43·7	39·3	43·5	46·0	50·0	44·5

(*b*) Percentage composition of diet of three length groups

	Length groups in cm.					
	Less than 35 (6)		36–50 (79)		Over 50 (21)	
Food organisms	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing
Mollusca	84·1[1]	67·0	73·9	85·0	76·0	91·0
Aquatic insect larvae	9·1	50·0	17·5[2]	50·5	7·6	43·0
Chironomid larvae	1·1	16·7	2·6	8·7	—	—
Crustacea	5·7	33·4	5·4	21·5	15·2[3]	14·3
Oligochaeta	—	—	0·4	2·5	1·2	4·3
Fish	—	—	0·06	1·3	—	—
Others	—	—	0·1	2·5	—	—
Totals	99·9		99·96		100·0	

[1] 40, [2] 60, and [3] 80 specimens in one fish.

Table 3. *Seasonal food of yellow eels in Windermere; number of fish given in brackets*

	May (14)		June (22)		July (8)		August (48)		Sept.–Dec. (14)	
Food organisms	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing
Mollusca	43·0	78·5	55·8	82·0	59·0	75·0	88·7	96·0	87·3	64·0
Aquatic insect larvae	20·5	64·0*	40·3	68·0	28·0	50·0	4·5	46·0	1·3	14·3
Chironomid larvae	0·9	7·0	0·2	0·4	0·9	12·5	3·3	10·1	—	—
Crustacea	35·6†	28·5	3·7	27·3	9·6	37·5	3·5	14·8	4·7	14·3
Oligochaeta	—	—	—	—	1·7	12·5	—	—	6·7	14·3
Fish	—	—	—	—	—	—	0·09	2·1	—	—
Others	—	—	—	—	0·8	12·5	—	—	—	—
Totals	100·0		100·0		100·0		100·09		100·0	

* 80 and 40 Trichoptera larvae in two fish. † 60 *Gammarus* in one fish.

remaining 31 fish each contained less than 10. The predominant species of larval Caddis was a Leptocerid. The number of *Gammarus* is usually less than 12 per fish except in two cases when 30 and 60 were present. *Sialis* and Ephemeroptera occurred in several fish but they cannot be regarded as of importance. Chironomid larvae are negligible.

The virtual absence of fish in the diet is interesting since of 90 eels (excluding 20 noted above) examined from perch traps, 34, ranging in length from 42 to

analyses without any distinction as to the size or time of capture of the fish, Tables 2 and 3 present them with these factors taken into consideration. Table 2 shows (*a*) the mean lengths of the eels containing the different food organisms, and (*b*) the diet of three size groups of eels, namely those of 35 cm. and less in length (snigs), those 36–50 cm. representing eels of typical lake size and those of more than 50 cm. regarded as larger lake eels. It appears from Table 2(*a*), when the difference in the numbers of speci-

mens in each group is taken into consideration, that size has no significant influence upon diet, although possibly the mean length of the eels eating Chironomid larvae indicates that they are primarily the food of the smaller fish. The impression that size has little effect on diet is also given by Table 2(*b*) which shows that Mollusca are the main food of eels of all sizes, although the lower frequency figures for the smallest fish are suggestive. There is some indication that aquatic insect larvae are not so important to eels of over 50 cm. and none of these fish had eaten Chironomid larvae. Table 3 gives the seasonal food of the Windermere eels as presented by monthly data, except for those of September to December which have been considered together. The mean lengths of the eels for the different months is of much the same order so that size has not affected the seasonal results. Seasonal differences in the diet are not much marked. Molluscs are eaten at all times and always in numbers relatively large to those of other foods. There is a tendency for a higher proportion of the fish to be feeding on aquatic insect larvae during May and June than in the remaining time which is primarily due to the number feeding on nymphal Ephemeroptera, chiefly *Ephemera danica* in May, their emergence time, and on these nymphs and Trichoptera larvae in June.

Table 4. *Food of yellow eels in Cunsey Beck; 42 fish*

	Stream feeding (16)				Probably stream feeding (9)				Lake or stream feeding (17)			
	Individual organisms		Fish containing		Individual organisms		Fish containing		Individual organisms		Fish containing	
Food organism	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Polycentropid larvae	69	47·5	11	68·0	43	79·5	9	100	—	—	—	—
Hydroptila sp. larvae	—	—	—	—	—	—	—	—	3	3·5	1	5·9
Hydropsyche sp. larvae	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Trichopt. l. indet.	2	1·7	2	12·5	1	1·9	1	11·1	2	2·3	2	11·8
Ephemerella ignita nymphs	44	30·5	8	50·0	—	—	—	—	—	—	—	—
Baëtis spp. nymphs	10	6·8	1	6·2	—	—	—	—	—	—	—	—
Ephemeropt. n. indet.	—	—	—	—	1	1·9	1	11·1	2	2·3	2	11·8
Chironomid larvae	—	—	—	—	2	3·7	1	11·1	43	50·0	4	23·5
Chironomid pupae	—	—	—	—	1	1·9	1	11·1	—	—	—	—
Simulium larvae	6	4·1	2	12·5	—	—	—	—	—	—	—	—
Tipulid larvae	1	0·7	1	6·2	—	—	—	—	1	1·2	1	5·9
Oligochaeta	1	0·7	1	6·2	1	1·9	1	11·1	27	31·5	6	35·5
Gammarus pulex	3	2·1	2	12·5	2	3·7	1	11·1	1	1·2	1	5·9
Sialis larvae	—	—	—	—	1	1·9	1	11·1	1	1·2	1	5·9
Limnaea pereger	—	—	—	—	—	—	—	—	1	1·2	1	5·9
Mollusca indet.	3	2·1	2	12·5	1	1·9	1	11·1	2	2·3	2	11·8
Fish	3	2·1	2	12·5	—	—	—	—	—	—	—	—
Odonata nymphs	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Winged Trichoptera	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Others	—	—	—	—	1	1·9	1	11·1	3	3·5	2	11·8
Totals	145	100·0			54	100·0			86	100·2		—

(*b*) *Food of yellow eels in Cunsey Beck*

The Cunsey Beck, from which the 42 eels considered in the following account were taken, is a stream about 8 yd. wide, which flows out of Esthwaite Water and into Windermere. In order to obtain information about the food of eels in running water several attempts were made to capture the fish from the beck. The method used, a hand net, since a tank and trough trap was not feasible, was tedious and yielded only 11 eels. There is, however, a trap for the capture of migrating (silver) eels situated some 90 yd. below the outflow of the beck from Esthwaite Water and in August and September 1943, 31 yellow eels, mostly small, containing food were found in this trap. It appears likely that they were swept into the trap either from the beck or the lake, by floods. Five of these trapped fish contained *Ephemerella ignita* or *Simulium* or both and are therefore considered, with the 11 hand-caught specimens, as beck fish; nine of them, since they contained *Polycentropus flavomaculatus*, are regarded as probably feeding in the stream and the remaining 17, the origin of which could not be recognized, are presented as lake or stream feeders (Table 4). The 42 eels examined were taken in June (1), July (8), August (26), September (6) and October (1). They ranged in length from 13 to 62 cm. with a mean length of 28·8 cm., the majority being 26–29 cm., four specimens only being over 40 cm.; the average length for the 16 undoubted beck specimens is 24·8 cm. It may be presumed that the age for length relationship of these 26–29 cm. = 5 years in fresh water. The eels were too few in number to consider diet in relation to size or season.

In the 16 beck fish Trichopteran larvae formed the greatest percentage by number of the food organisms eaten and occurred with greater frequency than any other food, the dominant species being a Polycentropid, probably *Polycentropus flavomaculatus*. This result is corroborated by the nine trapped fish probably of beck origin. The rest of the diet was composed mainly of aquatic insect larvae, predominantly Ephemeroptera and Diptera. In the seventeen eels which may have been of stream or lake origin Oligochaeta and Chironomidae predominated. The former were not identified but from their setae and general appearance most of them seemed to be earthworms, a point substantiated by their high incidence in the trapped eels which suggests that they became available food as a result of the floods.

The results of the stomach examinations are given in Table 5. Chironomid larvae and Ephemeroptera nymphs may be regarded as the most important foods, the former primarily from the numbers consumed and the latter from the high proportion of fish in which they occurred. The remaining food organisms, which are chiefly aquatic insect larvae, are not present in any great numbers nor have many fish fed on them. One eel only, a specimen 23 cm. long, had eaten a fish, a minnow.

An interesting point arises if these results are considered conjointly with those obtained from the yellow eels of Cunsey Beck. At both places aquatic insect larvae are the main food, but whereas Ephemeroptera nymphs (small specimens usually) are eaten to the same extent at both stations the importance of Chironomid larvae and larval Trichoptera is reversed at the two stations. This reversal may be an expression of faunistic differences in the two waters; but it seems more likely that it is related to the marked difference in the size of the eels examined from the Leven and the Cunsey, the specimens from the former being much smaller (14·4 cm. average) than those from the beck.

Table 5. *Food of yellow eels in River Leven; 32 fish*

Food organisms	No. of individual organisms	% of total organisms	No. of fish containing	% of fish containing
Chironomid larvae	118	61·5	9	27·0
Chironomid pupae	3	1·6	2	6·2
Ephemerella ignita nymphs	29	15·1	8	25·0
Baëtis sp. nymphs	9	4·6	6	18·7
Ephemeropt. n. indet.	5	2·6	5	15·6
Plecoptera nymphs	10	5·2	5	15·6
Rhyacophila sp. larvae	1	0·5	1	3·1
Hydropsyche sp. larvae	2	1·1	2	6·2
Trichopt. l. indet.	3	1·6	1	3·1
Asellus sp.	8	4·1	3	9·5
Corixid	1	0·5	1	3·1
Oligochaeta	2	1·1	2	6·2
Fish	1	0·5	1	3·1
Others	1	0·5	1	3·1
Totals	193	100 0		

(*c*) *Food of yellow eels in the River Leven*

The Leven, a fairly quickly flowing river of some 30–40 yd. wide is the outflow from Windermere. The 32 eels considered below were caught in its upper, non-tidal part. During the course of investigations carried out on elvers of the River Leven some specimens of small yellow eels, 'snigs', were captured in the tank and trough traps set for elvers, in addition to these a few others were taken by hand: 23 of the trapped 'snigs' and nine of the hand-caught ones contained food and although these fish provide only a little information it has been thought worth while to record it. The eels were taken in May (9), June (4), July (9), August (5) and September (5). They ranged from 8·0 cm. (one specimen) to 25 cm. in length, with a mean of 14·4 cm. The age for length relationship for such eels may be given as 8·0 cm. = 1, 25 cm. = 5 and 14·4 cm. = 2 years in fresh water. Since the fish were so few in number, the data from the specimens have been considered irrespective of time of capture or of their size.

(*d*) *Food of migrating eels*

This account is based on 60 eels caught over a period of years in the traps set on the Cunsey Beck. The trap which is situated some 90 yd. below the outflow of the stream from Esthwaite Water was erected and is operated by the Freshwater Biological Association and it fishes the whole width of the stream. It is in operation from July to November and is for the capture of eels which are migrating to the sea, such fish being characteristically in the silver phase having a silver belly and large eyes. Some of the eels caught, although clearly

seaward migrants, had not developed fully these characteristic features but were turning from the yellow to the silver phase. When the trap was first used no distinction between the fully silver and the transitional form was made, although later the two forms were distinguished, with the result that of the 60 migrants containing food 21 (18♀ and 3♂) may be taken as silver eels, the remainder being the transitional forms, although probably including some silver specimens. Thus, although the following account is better regarded as referring to the feeding habits of seaward migratory eels, it does provide some evidence that the silver eel takes food, a fact of some interest since it is usually alleged that it does not do so. Petersen (1894), for example, attributes the fact that baited hooks catch far more yellow than silver eels to the greater voracity of the former, 'a fact which is fully borne out when we examine the contents of the stomachs of eels which have been caught in other ways; the silver eels generally contain nothing, though it may happen [that they do contain food?], particularly when the eel has perhaps not quite finished the change of its dress. When it is migrating and in its full, characteristic dress, I never saw any food in its stomach'. Of course, many undoubted silver eels taken in the Cunsey trap did not contain food and the alimentary canal had the shrunken appearance associated with silvering.

The 60 migrating fish taken during the period of the 'run' August to October consisted of 57 females ranging from 50 to 70 cm. in length with a mean of 58·2 cm. and 3 males, 40 and 41 cm. long. The age of the former would lie between 11 and 14, an eel of 58·2 cm. being 11 years in fresh water, and the three males would have spent about nine years in fresh water.

The results of the stomach examinations are given in Table 6. From the situation of the trap 90 yd. below the outflow from Esthwaite Water it is most likely that the stomach contents represent the feeding in the lake rather than in the beck, since having been stimulated to leave the lake it is improbable that the eels would pause in the short stretch of stream above the trap. The table shows only the number of eels containing any particular food organism and the expression of these data in percentage terms, since other data were not always recorded. The diet is varied and contains most of the kinds of food organisms which were found in the yellow eels of Windermere, the River Leven or the Cunsey Beck. Molluscs, Trichoptera and Diptera occurred with the greatest frequency and among these the occurrence of *Chaoborus ?crystallinus* De Geer was of interest since none of the yellow eels of Windermere contained larval Diptera of this genus. Fish had been eaten to an appreciable extent, in one case four minnows were found in one stomach, but before concluding that migrating eels eat more fish than yellow eels it must be noted that the minnows, perch, etc., which are sometimes washed into the trap, may have been eaten when captive.

4. DISCUSSION

In Table 7 the results obtained are summarized, the food organisms having been grouped into six main categories. The number of individual organisms in each category is given, this figure being expressed as a percentage of the total organisms, and the number of fish containing each category is noted, each such number being expressed as a percentage of the total number of fish examined. It is evident from the table that the eel feeds chiefly on bottom-living

Table 6. *Food of migrating eels taken in the trap on Cunsey Beck;* 60 *fish*

Food organisms	No. of fish containing	% of fish containing
Limnaea pereger	4	6·6
Valvata piscinalis	2	3·3
Pisidium/Sphaerium	6	10·0
Planorbis spp.	2	3·3
Mollusca indet.	7	11·7
Leptocerid larvae	3	5·0
Polycentropid larvae	2	3·3
Phryganea sp. larvae	1	1·7
Trichopt. l. indet.	11	18·4
Chironomid larvae	8	13·4
Chironomid pupae	2	3·3
Tipulid larvae	3	5·0
Chaoborus larvae	4	6·6
Phoxinus	4	6·6
Perca	2	3·3
Salmo trutta	1	1·7
Fish indet.	5	8·3
Baetid nymph	2	3·3
Ephemeropt. n. indet.	2	3·3
Coleoptera larvae	4	6·6
Sialis larvae	3	5·0
Odonata nymphs	1	1·7
Corixid	2	3·3
Oligochaeta	2	3·3
Gammarus pulex	1	1·7
Ostracods	1	1·7
Winged insects (terrest.)	2	3·3
Winged Ephemeroptera	1	1·7
Others	7	11·7
Debris	2	3·3

invertebrates and of these molluscs predominate in the eels from Windermere and aquatic insect larvae in those from Cunsey Beck and the River Leven. This distinction is, however, in all probability due to the difference in the size of fish examined from the lake and the running waters (it has already been suggested that such a difference explains the different diet of Cunsey and Leven eels) and also almost certainly an expression of a difference in the faunistic conditions prevailing between Windermere and the two streams. In connexion with the latter it may be

Table 7. *Summary of food of yellow and migrating eels in Windermere catchment area; number of fish examined in brackets*

Locality ...	Windermere (106)				Cunsey Beck (42)								River Leven (32)				River Leven	
					Stream (16)				Probably stream (9)				Lake or stream (17)					
	Individual organisms		Fish containing		Individual organisms		Fish containing		Individual organisms		Fish containing		Individual organisms		Fish containing		Individual organisms		Fish containing		Migrating eels (60) Fish containing	
Food organisms	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mollusca	1504	74·80	91	86·0	3	2·1	2	12·5	1	1·9	1	11·1	3	3·5	3	17·6	—	—	—	—	18	30·0
Aquatic insect larvae	341	17·00	52	49·0	134	92·4	16	100·0	49	90·6	9	100·0	52	60·4	9	53·0	180	93·4	30	94·0	32	53·5
Crustacea	151	7·45	22	20·8	3	2·0	2	12·5	2	3·7	1	11·1	1	1·2	1	5·9	8	4·1	3	9·5	2	3·3
Oligochaeta	12	0·60	3	2·9	1	0·7	1	6·2	1	1·9	1	11·1	27	31·4	6	35·5	2	1·0	2	6·2	2	3·3
Fish	1	0·05	1	0·9	3	2·1	2	12·5	—	—	—	—	—	—	—	—	1	0·5	1	3·1	12	20·0
Others	2	0·10	2	1·9	1	0·7	1	6·2	1	1·9	1	11·1	3	3·5	2	11·8	2	1·0	2	6·2	9	15·0
Totals	2011	100·0			145	100·0			54	100·0			86	100·0			193	100·0				

noted that from the quantitative data given by Moon (1934) and Humphries (1936) one may deduce that in Windermere molluscs are relatively much more abundant than aquatic insect larvae (exclusive of the Chironomidae) and that from general observation I have gained the impression that the molluscan fauna of the Cunsey and the Leven is appreciably poorer than that of the lake. It appears that the food of eels, like that of other fish, is governed, to some extent at least, by the food organisms present.

Surface food, as represented by terrestrial insects which have fallen on to the water or by the adult forms of insects with aquatic larvae, is almost absent from the stomachs. This doubtless is related to the fact that the eel lives primarily on the bottom of the lake or stream. The incidence of surface food was negligible among the many thousands of New Zealand eels examined by Cairns (1941, 1942*a*, *b*).

It was rather unexpected to find that so few fish are eaten, since records from other European waters indicate that they occur to some considerable extent in the diet (see below). This may be due, to some extent, to the size of the eels examined from the Windermere catchment. Cairns (1941, 1942*a*, *b*) found that in New Zealand the trout eaten by long-finned eels (*Anguilla dieffenbachii* Gray) of 40–75 cm. long were all fingerlings or fry, since apparently eels of this size could not swallow anything larger; whereas in eels of over 75 cm. there was a 'predominance of trout [adult fish] in the diet'. A somewhat crude attempt to see the size of salmonid fish that a yellow eel could swallow was made by opening the mouth of the eel and inserting individuals of different sizes. It was found that an eel of 40 cm. long could just take a fingerling trout (5 cm.), one of 50 cm. easily took a 9·5 cm. salmonid and one of 75 cm. or more could take an 11 cm. salmon parr. The mean length of the eels examined from the River Leven and the Cunsey Beck was 14·4 and 28·8 cm. respectively and thus a salmonid fingerling would be too large a prey for such eels. There seems no reason why they should not swallow alevins or young fry; but since none of the eels was captured in spring, when these fish would be present, there is no evidence on this point. Other species of fish, such as minnows and sticklebacks, would appear to present prey of suitable size to the eels of the Cunsey and the Leven, but probably the number examined was insufficient to establish the incidence of fish in the diet. The eels examined from Windermere covered a wide range in size and had a mean length of 45 cm., and it seems unlikely that such eels would fail to find prey of suitable size among the varied fish population of the lake. The fact that when confined, as in perch traps, or tethered as line bait, perch and minnows are eaten suggests that the eel, being primarily benthic, finds that in the lake these and all except the bottom-living species of fish, such as bullhead and loach, etc., are difficult to capture and out of its range. In view of this suggestion it may be noted that the bullhead (*Cottus gobio* (L.)), the loach (*Nemachilus barbatula* (L.)), the lamprey (*Lampetra fluviatilis* (L.)), and the gudgeon (*Gobio gobio* (L.)), all benthic fish, comprise by far the greatest part of the fish diet of over 100 eels examined from the River Cam (Hartley, 1940 and unpublished data).

Observations on the food of eels in fresh waters made by various investigators are of interest for comparison with those obtained from Windermere. The many references to the food of individual eels from British waters will not be noted here, but Hartley's detailed examination of 27 (1940) and 87 (unpublished data) eels from East Anglia, mainly from the River Cam, shows that aquatic insect larvae, *Astacus*, *Gammarus* and fish are the foods occurring most frequently in the stomachs. Hornyold (1926), generalizing from observations made in France and Spain, notes that in rivers, lakes and ponds eels feed on snails, slugs, crayfish, aquatic insect larvae, frogs and fish; he also notes that annelids, including leeches, are eaten and sometimes elvers in greater or lesser quantities. Schiemenz (1910) in a general account of the food of eels in German waters states that *Asellus* and *Gammarus* are the food of 'pencil-sized' specimens, larger ones feed on molluscs, insect larvae, aquatic worms and fish, such as burbot (*Lota lota* (L.)) and stickleback (*Gasterosteus*) and in spring the eel eats fish spawn. Wundsch (1916) found that in the Steinhuder lake the eels of an average length of 45 cm., fed on fish, aquatic insect larvae and Cladocera and in Paddenpfuhl those of an average length of 36 cm. ate insect larvae, predominantly *Corethra* (*Chaoborus*), and in Aeppelsee aquatic insect larvae, fish and molluscs were the chief foods of eels. Struck, quoted by Schiemenz (1910), notes that in the Schmollensee eels which 'lived on *Mysis* in one year turned to plankton during a year when this was abundant'. These observations indicate a diet that is, in general, much like that of the eels of the Windermere catchment area, but one in which fish is appreciably more important, a contrast probably due to local faunistic conditions and to the type of water investigated The consumption of Cladocera (*Leptodora*, *Bosmina*, etc.) by the 45 cm. eels of the Steinhuder See had no parallel in the Windermere region, although such organisms are abundant in the lake.

Eels are alleged to feed on carrion, but Schiemenz (1910) maintains that when found near carrion the eel is not feeding upon it but is in search of the *Gammarus*, snails, etc., which are consuming the dead matter. Fishermen on Windermere consider that the bait set in yellow eel traps is useless when it becomes rotten.

There is an opinion among scientific investigators and practical fishermen that yellow eels show two forms, a broad-headed type having a flat, muscular head and thick lips (*breitkopf*) and a narrow-headed

type with more pointed head and thinner lips (*spitzkopf*). It is maintained that the two forms have different feeding habits, that the broad-heads are predators and feed on fish and the narrow-heads are not so (*friedfisch*) but feed on aquatic insect larvae, snails, etc. Schiemenz, however, states (1910) and demonstrates (1935) that there is no such hard and fast distinction, there being at most a tendency for the *spitzkopf*, since they are the smaller to be the *friedfisch* and the *breitkopf* being larger to be the predators; a similar conclusion was reached by Torlitz (1922) and may be deduced from the data given by Wundsch (1916). Sivertsen (1938) showed that in Norway in fresh water insect larvae and snails formed the main food of both types of eel. The eels examined from the Windermere catchment were not divided into the broad and narrow-headed forms but it is my recollection that the fish from the lake, primarily feeding on molluscs, included both types.

The relationship between the feeding habits of the eel and those of the fish associated with it, particularly trout and young salmon, may be discussed in the light of the information obtained from the Windermere catchment area. The conditions in a lake are well illustrated by reference to Windermere since data on the food of brown trout (*Salmo trutta* L.), char (*Salvelinus a. willughbii* (Günther)), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and minnow (*Phoxinus phoxinus* (L.)) are available. Here the food of the trout consists principally of *Limnaea*, *Gammarus* and the larvae and pupae of aquatic insects (Allen, 1938); the char feeds chiefly on planktonic Crustacea, Chironomid larvae and pupae and to some extent on *Gammarus* (Frost, unpublished data); fish, *Gammarus* and the insect bottom fauna provide the main foods of perch of 16·5–18·5 cm. long; the adult pike feeds primarily on fish and to a very small extent on aquatic insect larvae (Allen, 1935; Frost, unpublished data) and the food of the minnow consists of Cladocera, Copepoda and algae (Frost, 1943). Comparison of this evidence with that in Table 1 suggests that the food requirements of the eel coincide appreciably with those of the trout and to some extent with those of the perch, they exhibit little in common with those of the char and pike and nothing with those of the minnow. It may also be deduced from the same comparison that the eel is seldom a predator upon the other members of the fish community in Windermere (a view somewhat modified by the evidence of trapped perch) and that it is rarely preyed upon by other fish.

The relationship between the food of the eel and that of other members of the fish community in running water cannot be determined directly on evidence from the Cunsey Beck and River Leven, since there are no data on the food of other fish in these waters. Some indication, however, of the relationship is obtained if the information obtained from the Cunsey and Leven eels is compared with that obtained from trout, salmon (*Salmo salar* L.) and minnow, the important species of the Cunsey Beck and River Leven, from other waters. Investigations of the food of brown trout from rivers and streams of widely different types show that aquatic insect larvae, particularly the Chironomidae, Ephemeroptera and Trichoptera, are of primary importance as food organisms. The same has been found for the feeding of young salmon, and it has also been shown that in a small river these organisms enter, although to a lesser extent, into the diet of minnows (Frost, 1943). Since such larval insects form the chief food of the yellow eels of the Cunsey Beck and the River Leven the food requirements of the three fish have much in common with that of the eel. There is evidence, provided mainly by the larger migrating specimens, that the eel preys upon fish. Studies of the stomachs of fish from other rivers indicate that the eel in running waters is not a forage fish.

The interrelationship between the eel and trout and young salmon as illustrated by the data from the Windermere catchment area may be further considered under the headings: (1) the extent to which the two types of fish exploit the same food supply, (2) the eel as a predator upon the salmonids, and (3) the eel as a food for salmonids:

(1) It has been shown that in Windermere the food of yellow eels and trout is to an appreciable extent the same and that the diet of the eel in Cunsey Beck and the River Leven is much like that of the trout and young salmon of any stream. Whether or not this exploitation of the same source of food results in competition will depend on the adequacy of the food supply and the density of the fish population, points on which there are no adequate data for this locality. The eel population, however, may be assumed to be considerable for there is a 'good run' of elvers up the River Leven, and on the River Wyre, a smaller Lancashire river, a similar 'good run' has been estimated, from trapping experiments, to be some 1,000,000 elvers annually.

(2) The eels from the Windermere catchment do not support the view that they are predators upon trout and young salmon, but this is more than likely explained by the pelagic habits and size of trout in the lake and the limited nature of the data obtained from the beck and river (pp. 46–7). Information from river keepers and from the literature indicates that the eel does prey on salmonids in rivers, the alevins, fry and parr stages living in running water presenting the eel with fish of suitable size, and the habit of the trout of frequenting shallows being favourable to the bottom-living habit of the eel. The depredations of the eels of New Zealand upon trout fry and adults is stressed by Cairns (1941, 1942*a*, *b*).

(3) Examination of hundreds of stomachs of trout and young salmon over many years shows that the 'snig' and adult eel are negligible as food for the

salmonids. Hutton (1921) notes that he saw a 12 oz. trout attack an eel 9 in. long; records of such a habit are, however, rare. There is no doubt that trout feed heavily upon elvers during their ascent in spring but the period for this feeding is a short one.

Finally, the points brought out in the preceding paragraphs suggest a policy towards the eel in fishery conservation. In any large lake presenting an association consisting primarily of pike and perch, although the diet of the eel coincides to some extent with that of these fish and the likelihood of the eel preying upon the perch cannot be ignored, there seems little reason to believe that the eel is a detrimental member of such an association. In waters populated primarily by 'coarse' fish (other than pike and perch) it would appear, from a comparison of Hartley's account of the food of such fish in East Anglian waters (1940) with the food of the eel in the Windermere catchment area, that, although the dace (*Leuciscus leuciscus* (L.)), roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erophthalmus* (L.)), bream (*Abramis brama* (L.)), silver bream (*Blicca bjoernka* (L.)) and ruffe (*Acerina cernua* (L.)) feed to some extent on aquatic insect larvae and molluscs, that there would be little probability of serious competition for these foods by inclusion of the eel in a coarse fish community. In any waters conserved for Salmonidae the food requirements of these fish coincide so closely with those of the eel that serious competition between the species may result; this, and the likelihood of the eel being of considerable consequence as a predator on salmon and trout, particularly in running water, but withal of almost negligible value itself as forage for the salmonids, indicate that its presence is undesirable, particularly in running waters.

5. INTERNAL PARASITES

Mention may be made of the parasitic 'worms' which were met with during the investigation. The impression gained during the gut-examinations that very few eels were infested with internal parasites may have been due to unobservance. Nematodes were taken from three eels, a cestode from one and some acanthocephalids from two. The nematodes and cestode were examined by Dr H. A. Baylis of the British Museum (Natural History) and by Miss N. G. Sproston of the Marine Biological Laboratory, Plymouth, to whom I am indebted for their identification. The nematode was *Raphidascaris cristata* (Linstow, 1872) and the cestode *Bothriocephalus claviceps* (Geoze, 1782). Dr H. A. Baylis, of the British Museum (Natural History), informs me that the identity of the species of *Raphidascaris* commonly referred to as *R. acus* (Bloch) is very uncertain, as it is insufficiently described. He has examined some of the material on which Yorke and Maplestone's (1926) figures of '*R. acus*' were based, and believes that it is actually *R. cristata* (Linstow, 1872). Unless Linstow's description of this species is inaccurate, it appears to be distinct from *R. acus*. Dr Baylis recorded *R. acus* and *B. claviceps* from the eels from a Worcestershire pond examined by Hornyold (1922), and also (1939) from eels taken in Hampshire and Berkshire. Acanthocephalids were noted in one eel and recently Miss M. Young of the University of Nottingham, working at Wray Castle on fish parasites, found 15 in one eel, which she identified as *Echinorhynchus truttae* Schrank, 1788, a species already reported by Dr Baylis from English eels. The same worker also found that the lens of the eye of one of the eels was infected with a trematode *Diplostomum* sp.

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7. SUMMARY

1. The food of eels (*Anguilla anguilla*) from the Windermere catchment area has been investigated by the examination of the stomach contents of 106 yellow eels from Windermere, 42 from Cunsey Beck and 32 from the River Leven; the food of 60 seaward migrating eels caught in the trap on Cunsey Beck has also been ascertained.

2. Eels feed almost entirely upon bottom-living invertebrates, molluscs predominating in the Windermere fish and the larvae of aquatic insects in those from the Cunsey Beck and River Leven. This distinction is probably due to the size of the eels examined from the two places being different and differences in the faunistic conditions of the two environments.

3. The number of eels from Windermere feeding on fish is negligible; the virtual absence of fish from the diet of Cunsey and Leven eels may be accounted for by the size of those examined.

4. Some seaward migrating eels, including specimens which were changing from the yellow to the silver phase and those which were wholly silver, contained food.

5. The relationship between the feeding habits of the eel and fish associated with it is discussed, some suggestions for fishery policy being based on the discussion.

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