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FOOD AND FEEDING RELATIONSHIPS IN A COMMUNITY OF FRESH-WATER FISHES

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(With 3 Figures in the Text)

1. INTRODUCTION

In the majority of researches upon the food of fishes attention has been fixed upon one species, and the other members of the community in which that species lives are considered chiefly as predators or as potential foods. Yet, it is generally realized that the factor of interspecific competition for supplies may be fully as rigorous as intraspecific competition in its limiting effects upon multiplication, growth and well-being. Nikolsky (1945) has named as the first problem in fish biology 'the study of the feeding habits of different species in order to understand the qualitative and quantitative connections between fishes and their food organisms. The results would be the knowledge of the dynamics of the food chains in a water body....'

Among others, Swynnerton & Worthington (1940) and Radforth (1940) in Great Britain; Alm (1917, 1921, 1922) in Sweden; Clemens, Dymond & Bigelow (1924) in Canada; Nurnberger (1930), Ewers (1933), Ewers & Boesel (1935), Boesel (1937) and Van Oosten & Deason (1937) in the United States; and Dobers (1922) and Stadel (1936) in Germany have published accounts of the foods of several species of fresh-water fish from one water. In some of these papers competition between species is not explicitly discussed, although information upon the subject is implicit. More recently, Frost (1946) has considered the food relationships of most of the species of fish in Windermere.

Between the end of 1938 and the beginning of 1941 the Freshwater Biological Association maintained a substation for the study of the biology of coarse (non-salmonid) fish at Bulbeck Mill, in the village of Barrington, Cambridgeshire. This laboratory was situated on the upper reaches of the River Cam, or Rhee, near the inflow of a small tributary, the Shepreth Brook. The fishing in a short length of the main river, and in nearly half a mile of the Shepreth Brook, was under the control of the Association. The Ouse and Cam Fishery Board kindly appointed the author, who was in charge of the investigations, an honorary bailiff, with powers to take fish by any method and at all seasons.

2. DESCRIPTION OF THE HABITAT

A map of the area from which all the fish investigated came is given in Fig. 1. The 'run' of the mill, from which the undershot wheel had been removed, is the upper limit on the main river. Below the mill the river widens into a pool about 40 ft. (13 m.) across and 6 ft. (2 m.) deep in the middle. The south bank of this pool is steep-to, with the remains of a system of revetments. The north shore is of gravelly chalk mud, steeply shelving and much grown up with *Epilobium* sp. After some 20 yd. (20 m.) the pool becomes shallower and the river thereafter flows over a bottom of gritty chalk mud in a channel 30 ft. (9 m.) wide and 2–4 ft. (*c.* 1. m.) deep. On the northern side there is a steep grass-grown bank, on the south there are grazing meadows which are under water in times of flood.

A dismantled eel-trap above the mill drains into a narrow dyke, much choked with reeds (*Phragmites communis*) and reed-mace (*Typha* sp.). This dyke curves round to join the main river at the foot of the pool below the mill.

The upper part of the Shepreth Brook runs between rows of pollard willows (*Salix* sp.) in a channel about 10 ft. (3 m.) wide, floored with clean gravel; the water is only a few inches deep. Half a mile from its junction with the river, the brook is joined by an almost stagnant creek which lies parallel to the main river among willow holts and orchards. The bottom of this creek is thickly covered with sodden leaves and fine mud. Below the mouth of this creek the brook is about 10 ft. (3 m.) wide and much overhung with willows. The water is 1–3 ft. (0·3–1 m.) deep, with a muddy bottom in the deeper stretches and a gravelly bottom in the shallows.

During the period of observation, the river rose and fell through a range of 37 in. (1 m.), the highest levels being in January and May 1939, and February and March 1940. In times of flood the north bank of the Cam and the slightly embanked south side of the Shepreth Brook were the shores of a wide, shallow lake. A gang of river cleaners cleared some of the mud and growing weeds from the main river each summer. Shepreth Brook was cleaned out at longer intervals.

This branch of the Cam rises from chalk springs at Ashwell, and flows through agricultural country. The water is alkaline, with a pH of 8·3–8·4 and is usually turbid with chalk mud. The water of Shepreth Brook has a similar pH value, but is very clear. I am indebted to Mr R. S. A. Beauchamp for analyses of the water from the river, the brook and the dyke made at the end of April 1939 by the members of the Cambridge Zoology Department hydrobiological course (Table 1).

The records at once show the great variations in temperature conditions which fish living in small waters must endure. On several occasions the animal community of the upper Cam was subject to greater changes of temperature within one month than animals living in the English Channel would experience within a year (Harvey, 1928). The temperature variations within the day were also large. It must be emphasized that the two daily readings were not necessarily the maximum and minimum temperatures for the period, with the result that the mean daily ranges given in Table 2 may be regarded as minimal.

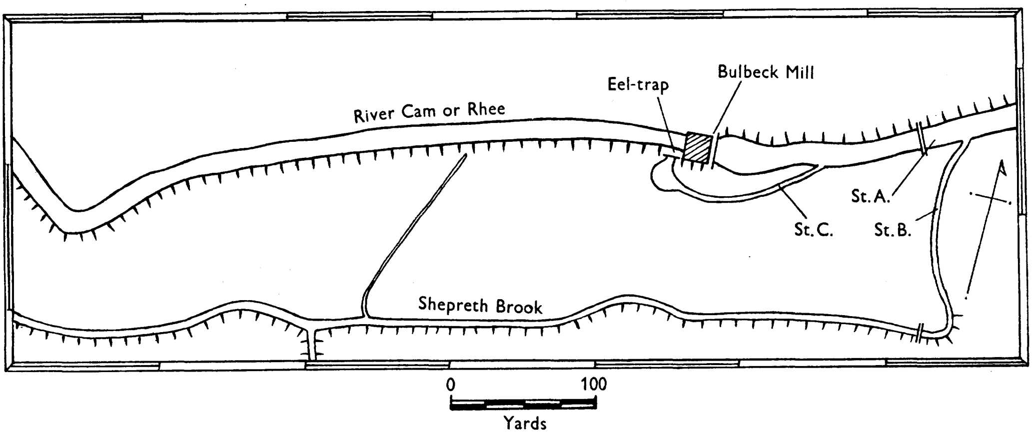

Fig. 1. River Cam and Shepreth Brook at Barrington, Cambridgeshire. The embanked shores of the river and brook are hachured.

Table 1. *Analysis of water samples from the River Cam, Shepreth Brook and Bulbeck Mill Dyke. Late April* 1939

All values expressed as p.p.m.

	River Cam St. A	Shepreth Brook St. B	Dyke St. C
O_2	15	16	16
$-CO_3''$	276	258	246
NH_3'	0·1	0·02	0·04
$-NO_2''$	0·014	0·009	0·014
$-NO_3''$	7·5	—	—
SiO_2	11·0	11·0	11·0
$-P_2O_5'''$	0·26	0·26	0·26

The temperature of the water of the main river was taken twice daily, at 09.30 and 16.30 hr. (G.M.T.), in the pool just below the mill. The water there had been well mixed by pouring over the lip of the mill run. Table 2 shows the mean morning temperature for each month, the mean daily range (that is, the mean difference between the morning and afternoon temperatures), the highest and lowest temperatures recorded during each month, and the mean air temperature at 09.30 hr.

Yet in June 1939, and May 1940, the daily range averaged more than 3·1° C. The greatest differences between morning and afternoon temperatures were 5·90 on 20 April 1939 (when the difference between the maximum and minimum air temperatures for the day was 17·40) and 5·8° on 13 August 1940 (when the mean range of air temperature was 10·5°).

Daily variation of temperature was greater in summer than in winter. There was a marked lack of regularity in the ranges of temperatures on successive days. For example, on 10 May 1939, the range of temperature for the day was 3·9°; on 11 May it was 0·3°. On 24 May 1939 the day's range of temperature was 4·5°; on 25 May it was 0·1°. The animals living in such a habitat must be strongly eurythermal.

3. MATERIAL AND METHODS

The fish examined were caught by a variety of methods—by trapping, by seine-net and hand-net, by spearing, snaring and shooting and by 'fair angling'. Except in the case of very small species and juveniles the vast majority of the specimens were secured in traps.

The traps used were made on the lobster-pot principle. Each trap (Fig. 2) consisted of a cylinder of wire-netting lying on its side, having one end closed and the other fitted with a funnel of netting opening inwards. The first trap used was professionally built, with two compartments, each having a funnel of copper wire. All the rest of the 'fleet' were home-made, of ½ in. mesh chicken netting on a frame-work of thick galvanized wire. The entry end of each trap was fitted with a projecting hood of wire-netting, designed to increase the effective diameter of the funnel.

The 'fleet' used consisted of a dozen traps. These were dropped singly into likely places in the river and brook, with the entrance downstream. Drifting weed and rubbish settled thickly on the hoods and tops of the traps, and it is probable that the entrances appeared as gaps in obstructions in the path of the fish. It was found that certain places, especially where the water was deep and the bank steep, were profitable, and traps were kept steadily at work there.

Table 2. *Temperature conditions (in °C.) in the River Cam at Barrington, Cambridgeshire, 1939 and 1940*

Mean T., mean temperature for month at 09.30 hr.; Max., highest temperature recorded during month; Min., lowest temperature recorded during month; Range, mean difference between temperatures at 09.30 and 16.30 hr.

1939	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Water:												
Mean T.	5·12	5·86	6·14	9·1	11·02	13·5	15·5	15·69	13·97	8·93	8·47	6·2
Max.	8	9	8	12	14	16	17	17	17	11	10	10
Min.	0	3	4	6	7	11	13	14	9	5	5	3
Range	0·71	1·33	1·93	2·47	2·92	3·16	1·41	2·0	1·42	1·19	0·61	0·61
Air:												
Mean T.	5·5	6·0	7·02	10·9	12·91	17·42	18·25	16·6	14·83	8·28	8·6	4·55
1940												
Water:												
Mean T.	1·45	2·91	5·88	8·77	12·17	15·68	15·72	15·89	11·9	8·03	7·0	4·14
Max.	2	8	8	11	15	18	17	19	16	10	10	7
Min.	0	0	2	5	9	12	13	11	7	3	2	1
Range	0·43	0·78	1·71	2·27	3·13	3·01	2·91	2·86	3·0	2·4	0·99	0·79
Air:												
Mean T.	−1·96	2·07	5·15	9·07	13·24	17·7	15·98	15·99	13·8	7·43	6·47	3·05

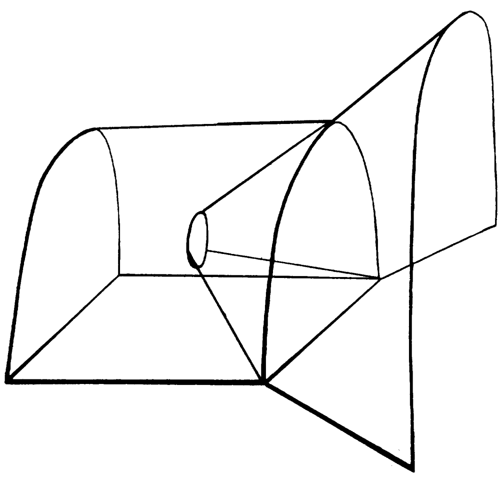

Fig. 2. Framework of fish-trap.

Fish were removed through a small door in the top of the trap. Some fish of the smaller species were caught in traps consisting of a glass jam jar with a tin funnel entrance projecting inwards. Traps of both kinds were set unbaited.

Other traps were moved about, working the less likely stretches of water. A number of fish were taken by dropping traps into 'lies' from which they had been seen to swim. Traps were lifted twice daily in winter and thrice daily in summer. Occasionally, when the water was low, traps were placed in a row across the brook and the fish were driven towards them by trawling a bag-net from the banks.

A list of the fish examined is given in Table 3. Routine investigation consisted of measurement of the length overall, and to the fork of the tail in those species with a cleft caudal fin; observation of the sex and gonad condition; and the examination of the contents of the stomach and gut. Since most of the fish were trapped, no estimates of the 'fullness' of the digestive tracts could be made. In certain species scales were collected for age determination, and the fishes were weighed.

The foods contained in the stomach and gut were identified and enumerated as exactly as their condition permitted. Unfortunately the cyprinid fishes grind their food to fragments before swallowing it and a tangled mass was found consisting of insect legs and shards and other food remnants, mixed with mud and mucus. Since the investigation of the foods of fishes from this area was but a part of a larger programme, it was impossible to examine and count the organisms in every sample of food in detail. An arbitrary scale was therefore used—'few', 'some', 'several', 'many' and 'very many'. When compiling lists of organisms eaten, numerical values were given to these standards: 'few', 3; 'some', 5; 'several', 7; 'many', 20; and 'very many', 40. In the table of food organisms found (Table 5), the fish in which all or most of the enumerations are on this basis are marked with an asterisk. Since the values allotted are most conservative, the numbers of different organisms stated to have been eaten by these fish should be regarded as minimal.

In the autumn of 1938 there had been a severe pollution of the main river by an alkaline outflow from a cement works farther upstream, and many fish were killed thereby. The Shepreth Brook was not affected. The fishes caught in the main river were, therefore, recolonizing the depopulated area from the lower reaches, or from the tributary streams.

fish, showing both the number of fish in which each organism occurred and the number of this organism found in all the fish of each species investigated. These lists are shown in Table 5. Tables 4 and 5 form the basis of discussion of the food and feeding habits of the fish and the possibilities of competition between one species and another.

On the basis of feeding habits, the fish of the Barrington district may be divided into four groups:

(1) Specialist predators upon a single prey—the pike.

(2) Fish taking a wide variety of foods—the eel and the brown trout.

(3) Fish taking a diet in which insects and plants predominate—roach, dace and minnow.

(4) Fish eating a diet in which insects and crustaceans predominate—gudgeon, bullhead and stickleback.

Perch and loach were not classified; the latter species probably belongs to the fourth group.

Table 3. *Species of fish examined*

	Total	River Cam	Shepreth Brook	Mill Dyke	No data
Pike (*Esox lucius* L.)	62	38	19	1	4
Eel (*Anguilla anguilla* (L.))	125	27	81	14	3
Gudgeon (*Gobio gobio* (L.))	391	99	273	19	—
Minnow (*Phoxinus phoxinus* (L.))	126	24	101	1	—
Dace (*Leuciscus leuciscus* (L.))	231	161	63	7	—
Roach (*Rutilus rutilus* (L.))	166	125	23	15	3
Loach (*Nemacheilus barbatula* (L.))	16	6	3	7	—
Perch (*Perca fluviatilis* L.)	8	—	8	—	—
Bullhead (*Cottus gobio* L.)	84	21	58	4	1
3-spined stickleback (*Gasterosteus aculeatus* L.)	227	151	34	42	—
Brown trout (*Salmo trutta* L.)	30	4	26	—	—

4. FOOD AND FEEDING RELATIONSHIPS OF THE FISHES

The foods of the fish were listed in two ways: first, in order to find out the general feeding habits of each species; and secondly, to discover the organisms on which each species had fed. In the investigation of feeding habits, the foods were divided into a number of categories—fish, molluscs, insects, Crustacea, vascular plants and filamentous algae, diatoms, etc.—and lists were made of the number of fish of each species in which foods of any of these categories were found. In this first analysis no account was taken of the relative abundance of the different foods: one insect larva or a hundred larvae were alike listed as one occurrence of insect food. The occurrences of food of the different categories in each species of fish are shown in Table 4, both in actual numbers and in expression of these numbers as percentages of the total. The percentage occurrence of foods of the different categories are also shown in Fig. 3.

After this first analysis had been made, lists were prepared of the recognizable organisms found in each

The dietaries of the members of these groups must now be compared, in order to find out what degree of competition may exist within each group, and to what extent the members of the different groups may compete with one another. In the absence of data upon the density of the food organisms, and the proportion removed by fish predation in the course of the year, 'competition' here means nothing more exact than 'taking an appreciable proportion of a common food', without any implication that the supply of that food was a limiting factor.

(1) The fish-eating pike is the end-point of many food chains in fresh waters. Trout and eels eat several of the same fishes as pike, and the insect and crustacean foods taken by juvenile pike are also eaten by a number of other species of fish. An adult pike may eat the actual fish which competed with it in its youth. Pike are remarkable as the only fresh-water fish eating sticklebacks in any numbers (14 occurrences and 20 individual preys).

(2) Of the fish of the second group, brown trout and eels, which show no specialization of feeding habits, brown trout are the more remarkable for the

Table 4. *Food of fish in the River Cam and Shepreth Brook*, 1939–41

The number of occurrences (=of fish containing) of food of each category is shown: and in each species of fish, the occurrences of food of each category are expressed as percentages of the total occurrence of foods (=total fish containing foods) of all categories.

	Mammals		Amphibia		Fish		Mollusca		Insecta		Myriapoda		Arachnida		Crustacea		Oligochaeta		Vascular plants and filamentous algae		Diatoms	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pike	—	—	—	—	45	**85**	—	—	5	**9**	—	—	—	—	3	**6**	—	—	—	—	—	—
Eel	1	**1**	—	—	28	**19**	7	**5**	36	**24**	—	—	—	—	66	**44**	2	**1**	8	**5**	—	—
Gudgeon	—	—	—	—	—	—	60	**12**	281	**57**	—	—	1	/	119	**24**	1	/	27	**6**	2	/
Minnow	—	—	—	—	—	—	—	—	65	**43**	1	**1**	5	**3**	14	**9**	—	—	32	**21**	34	**23**
Dace	—	—	—	—	—	—	22	**9**	135	**53**	—	—	—	—	16	**6**	—	—	56	**22**	27	**10**
Roach	—	—	—	—	—	—	35	**19**	66	**36**	—	—	1	**1**	13	**7**	—	—	55	**30**	12	**7**
Loach	—	—	—	—	—	—	—	—	13	**(65)**	—	—	—	—	7	**(35)**	—	—	—	—	—	—
Perch	—	—	—	—	1	(10)	—	—	3	**(30)**	—	—	—	—	6	**(60)**	—	—	—	—	—	—
Bullhead	—	—	—	—	—	—	1	**1**	58	**58**	—	—	—	—	39	**39**	3	**3**	—	—	—	—
3-spined stickleback	—	—	—	—	—	—	7	**2**	150	**51**	—	—	1	**1**	69	**24**	1	**1**	42	**14**	23	**8**
Brown trout	1	**1·5**	1	**1·5**	8	**13**	4	**7**	29	**48**	—	—	1	**1·5**	13	**21**	2	**3**	2	**3**	1	**1·5**

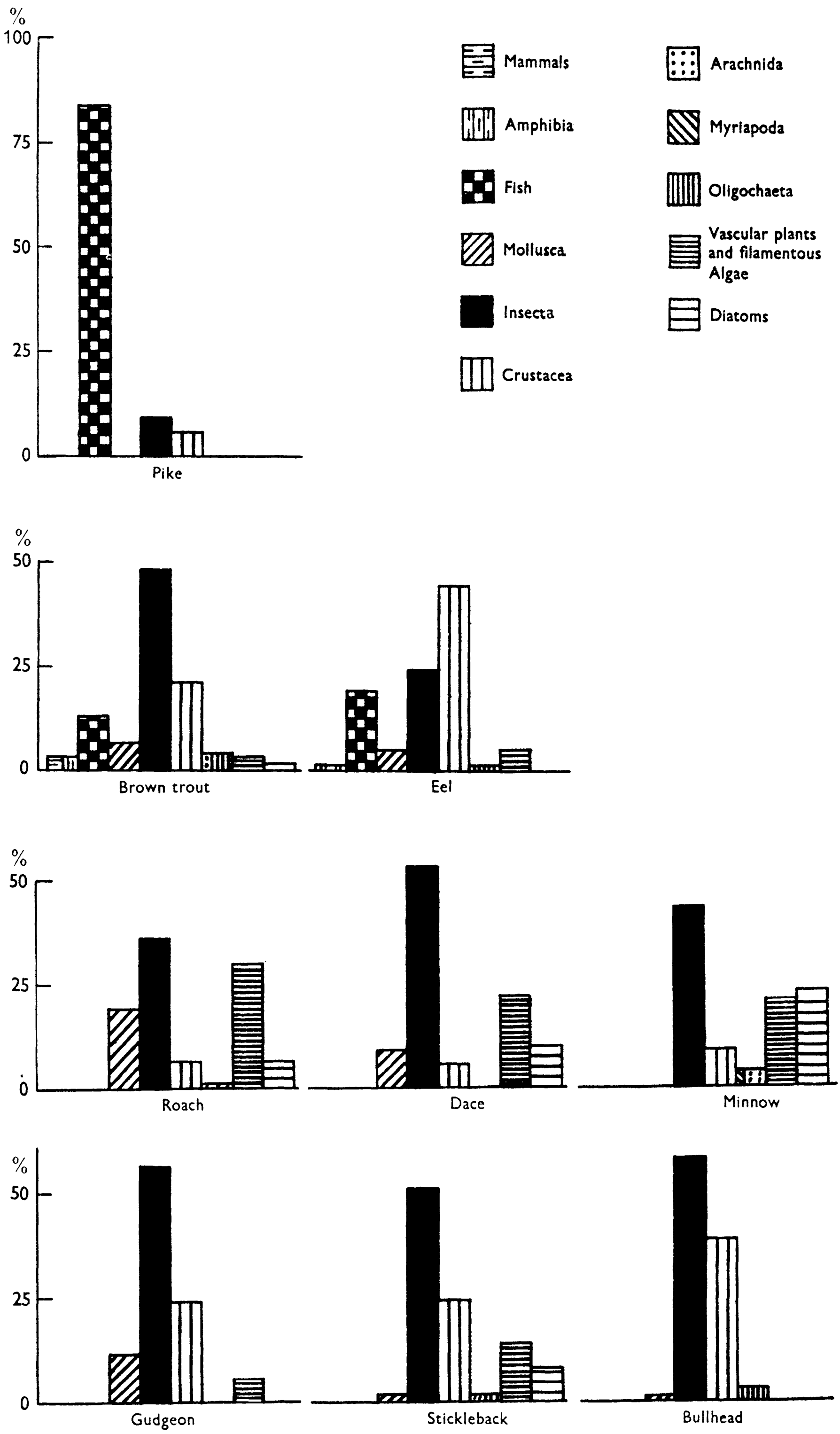

Fig. 3. Food of fish in the River Cam and Shepreth Brook at Barrington, Cambridgeshire, in 1939–41. In each species of fish the occurrences of different foods are expressed as percentages of the total occurrences of foods of all kinds.

Table 5. *Food of fish in the River Cam and Shepreth Brook*, 1939–41

The number of fish in which each food was found is shown, and (when the numerical method of expression is suitable) in italics—the total number of each food organism.

	Pike		Eel		*Gudgeon		*Minnow		*Dace		*Roach		Loach		Perch		Bullhead		*3-spined stickle-back		Brown trout	
	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.
Mammals																						
Apodemus sylvaticus (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Microtus sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphibia																						
Rana temporaria L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Fish																						
Anguilla anguilla (L.)	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phoxinus phoxinus (L.)	3	*3*	2	*5*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gobio gobio (L.)	7	*7*	3	*3*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	*3*
Rutilus rutilus (L.)	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nemacheilus barbatula (L.)	3	*3*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cottus gobio L.	3	*3*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gasterosteus aculeatus L.	14	*20*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Cyclostomata																						
Lampetra fluviatilis (L.)	—	—	7	*12*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mollusca:																						
Lamellibranchiata																						
Sphaerium sp.	—	—	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	1	*2*	—	—
Gastropoda																						
Hydrobia jenkinsi Smith	—	—	1	*1*	10	*189*	—	—	6	*107*	11	*107*	—	—	—	—	—	—	1	*1*	3	*43*
Ancylus fluviatilis (Müll.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Limnaea pereger (Müll.) and sp.	—	—	4	*27*	—	—	—	—	1	*1*	—	—	—	—	—	—	—	—	1	*4*	1	*1*
Planorbis sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arachnida																						
Aranaeid indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*2*
Limnocarid indet.	—	—	—	—	—	—	—	—	—	—	1	*10*	—	—	—	—	—	—	—	—	—	—
Hygrobatid indet.	—	—	—	—	—	—	1	*1*	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—
Hydracarinids indet.	—	—	—	—	1	*1*	3	*3*	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—
Myriapoda																						
Myriapoda indet.	—	—	—	—	—	—	1	*3*	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Insecta:																						
Ephemeroptera																						
Ephemera sp., adult	1	*1*	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—	—	—	—	—	3	*6*
Ephemera vulgata L. and sp., nymph	1	*1*	3	*7*	—	—	1	*1*	1	*7*	—	—	—	—	—	—	2	*2*	—	—	3	*4*
Leptophlebia cincta (Retzius) and sp., nymph	—	—	1	*4*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*3*
Baetis sp., nymph	1	*1*	2	*8*	8	*87*	1	*2*	3	*5*	—	—	1	*1*	—	—	1	*1*	11	*22*	1	*1*
Centroptilum sp., nymph	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—
Ephemeropteran indet., adult	—	—	—	—	—	—	—	—	1	*20*	—	—	—	—	—	—	—	—	—	—	1	*1*
Ephemeropteran indet., nymph	—	—	11	*48*	24	*82*	2	*3*	6	*30*	3	*23*	2	*4*	—	—	6	*8*	9	*11*	3	*10*

Table 5 (*continued*)

	Pike		Eel		Gudgeon		Minnow		Dace		Roach		Loach		Perch		Bullhead		3-spined stickle-back		Brown trout	
	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.
Insecta (*continued*):																						
Hemiptera																						
Corixa striata (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Corixids indet., adult	—	—	—	—	—	—	1	1	4	5	1	1	—	—	—	—	—	—	2	3	4	8
Corixids indet., nymph	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	1	1	—	—
Megaloptera																						
Sialis lutaria (L.), larva	—	—	3	3	15	19	—	—	4	8	3	5	1	1	2	2	7	9	1	1	4	4
Trichoptera																						
Rhyacophila dorsalis (Curt.), larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Hydroptila sp., larva	—	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	—	1	1	1	3
Polycentropus sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Hydropsyche sp., larva	—	—	2	2	2	2	—	—	3	5	—	—	—	—	—	—	4	10	—	—	1	1
Phryganea sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptocerus sp., larva	—	—	—	—	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Molanna angustata Curt. and sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3
Glyphotaelius sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Limnophilus sp., larva	—	—	1	1	4	7	—	—	—	—	—	—	2	3	—	—	1	1	—	—	—	—
Anabolia nervosa Curt., larva	—	—	1	1	—	—	—	—	18	37	2	5	—	—	—	—	1	1	—	—	4	5
Stenophylax sp., larva	—	—	—	—	2	4	—	—	11	24	—	—	—	—	—	—	2	2	—	—	2	2
Halesus sp., larva	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	1	7
Trichopteran indet., adult	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	2	22
Trichopteran indet., larva	—	—	2	4	12	15	2	3	35	87	3	6	1	2	—	—	2	2	1	1	10	35
Lepidoptera																						
Moths indet., adult	—	—	—	—	—	—	—	—	1	7	—	—	—	—	—	—	—	—	—	—	1	2
Caterpillars indet.	—	—	3	4	—	—	—	—	3	3	1	1	—	—	—	—	—	—	—	—	1	1
Coleoptera																						
Dytiscus marginalis L. and sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3
D. marginalis L. and sp., larva	—	—	1	1	4	5	—	—	1	1	2	3	—	—	1	1	1	1	—	—	4	6
Hydroporus sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Hygrobia hermanni (Fab.), adult	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Dryops sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gyrinus sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Helodes sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Coleopteran indet., adult	—	—	2	2	8	11	2	3	18	31	2	6	—	—	—	—	—	—	—	—	9	95
Coleopteran indet., larvae	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—

Hymenoptera																						
Chalcidoids indet., adult	—	—	—	—	—	—	—	—	3	*10*	1	*2*	—	—	—	—	—	—	1	*1*	—	—
Hymenopterans indet., adult	—	—	—	—	1	*1*	2	*3*	3	*6*	—	—	—	—	—	—	—	—	—	—	3	*3*
Diptera																						
Tipula sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—	—	—
Dicranota sp., larva	—	—	—	—	6	*13*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tipulid indet., larva	—	—	1	*1*	2	*4*	—	—	—	—	1	*1*	—	—	—	—	4	*8*	—	—	—	—
Simulium sp., larva	—	—	7	*37*	35	*376*	2	*4*	19	*93*	10	*70*	4	*25*	—	—	4	*5*	4	*6*	1	*3*
Simulium sp., pupa	—	—	—	—	1	*1*	—	—	—	—	2	*6*	—	—	—	—	—	—	—	—	—	—
Tanypus sp., larva	—	—	—	—	2	*28*	—	—	—	—	1	*7*	1	*2*	—	—	—	—	2	*25*	—	—
Corynoneura sp., larva	—	—	—	—	—	—	—	—	—	—	1	*2*	—	—	—	—	1	*1*	—	—	—	—
Forcipomyia sp., larva	—	—	—	—	24	*110*	1	*2*	—	—	—	—	1	*2*	—	—	1	*1*	1	*2*	—	—
Chironomus sp. and chironomid indet., larva	2	*3*	3	*4*	212	*1565*	33	*115*	28	*94*	22	*55*	6	*16*	—	—	16	*68*	67	*285*	—	—
Chironomid indet., pupa	—	—	1	*1*	3	*23*	5	*9*	2	*4*	1	*5*	—	—	—	—	2	*2*	10	*21*	—	—
Culicid indet., pupa	—	—	—	—	—	—	1	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tabanid indet., larva	1	1	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthomyiid indet., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—	—	—
Dipterans indet., adult	—	—	—	—	2	*7*	4	*7*	4	*8*	4	*8*	—	—	—	—	—	—	—	—	10	*80*
Crustacea																						
Potamobius pallipes Lereboullet (=*Astacus fluviatilis* L.)	1	*1*	33	*43*	—	—	4	*4*	1	*1*	—	—	—	—	—	—	3	*3*	—	—	3	*3*
Gammarus pulex (de Geer)	2	*6*	39	*225*	71	*281*	5	*5*	13	*67*	14	*34*	3	*17*	6	*13*	34	*40*	2	*2*	10	*24*
Asellus aquaticus Leach and sp.	1	*1*	2	*2*	—	—	—	—	1	*1*	—	—	—	—	—	—	3	*8*	1	*1*	1	*1*
Oniscus sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chydorus sp.	—	—	—	—	29	*135*	2	*8*	—	—	—	—	3	*5*	—	—	—	—	14	*35*	—	—
Cyclops sp.	—	—	—	—	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Copepoda indet.	—	—	—	—	35	*145*	2	*5*	—	—	2	*8*	1	*2*	—	—	1	1	54	*215*	—	—
Ostracoda indet.	—	—	1	*1*	15	*53*	—	—	—	—	—	—	—	—	—	—	—	—	8	*24*	—	—
Oligochaeta																						
Earthworm indet.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Oligochaete indet.	—	—	—	—	2	*3*	—	—	—	—	—	—	—	—	—	—	—	—	1	*2*	—	—
Hirudinea																						
Herpobdella octoculata L. and sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	3	*3*	—	—	—	—
Plants																						
Sparganium sp.	—	—	—	—	—	—	—	—	7	—	2	—	—	—	—	—	—	—	—	—	—	—
Ulothrix sp.	—	—	—	—	—	—	—	—	4	—	2	—	—	—	—	—	—	—	—	—	1	—
Cladophora sp.	—	—	—	—	—	—	—	—	10	—	10	—	—	—	—	—	—	—	—	—	—	—
Spirogyra sp.	—	—	—	—	—	—	—	—	8	—	1	—	—	—	—	—	—	—	—	—	—	—
Vaucheria sp.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—

wide variety of their diet. Forty-nine recognizable genera or species of prey were found in 30 fish, an average of 1·63 different preys per trout, as compared with an average of 0·26 different preys per eel (33 recognizable on 125 fish). The high proportion of the number of recognizable organisms to number of fish examined which is found in the trout is not due to difference in degrees of mastication, for both trout and eels tend to bolt their food whole. Larval Trichoptera, occurring in 25 out of 30 fish (84 %), were the insect food most often eaten by brown trout, 62 individuals belonging to nine genera being found. Adult beetles, occurring in 13 out of 30 fish (43 %) and adult Diptera in 10 fish (33 %) were next in importance, with some nymphal and adult Ephemeroptera, larvae of beetles and *Sialis* sp. and adult corixids. Trout differed markedly from all other insect-eating fish in these waters in that chironomid larvae formed no part of their diet, and that larvae of *Simulium* sp. were found but once (three larvae in one fish). *Gammarus pulex* occurred in 10 fish (33 % occurrence) and *Astacus fluviatilis* in 3 (10 %). Three trout had eaten *Hydrobia jenkinsi*.

On a basis of occurrence, insects made up 48 % of the diet of brown trout, and Crustacea 21 %. In the eel these proportions were almost exactly reversed, insects, contributing 24 % of the diet and Crustacea 44 %. Ephemeropteran nymphs were the insect food most often taken by eels, 67 individuals being found in 17 eels out of 125 (13·6 % occurrence); 37 larvae of *Simulium* sp. were found in 7 eels (5·6 % occurrence) and trichopteran larvae in 6 (4·8 %). *Gammarus pulex* was the chief crustacean food of eels as well as of trout, being found in 39 fish out of the 125 (31 %), but eels contained more than twice as many gammarids per stomach, 5·8 per fish, as compared with 2·4 in trout. Eels took many *Astacus fluviatilis*, 43 specimens being found in 33 fish (26 %).

(3) In the third group, in which insects and plants are the most important items in the dietary, there is some competition between the three members—roach, dace and minnow—but the proportions in which the more numerously occurring foods were eaten showed considerable differences.

Chironomid larvae occurred in 34 minnows out of 129 examined (26·5 % occurrence), in 24 roach out of 163 (14·5 %) and in 28 dace out of 231 (12 %). The larvae of *Simulium* sp. were found in 19 dace (8 %), in 10 roach (6 %) and in 2 minnows (1·5 %). Trichopteran larvae were the insect food most often taken by dace, 166 larvae belonging to at least five genera being found in 69 fish (30 % occurrence), but only 6 roach (3·5 %) and no minnows contained this food. Nineteen dace (8 %) contained adult beetles, but these insects were found in only 2 roach and 2 minnows. Ephemeropteran nymphs were found in 10 dace (4 %), in 3 roach (2 %) and in 4 minnows (3 %).

The plant foods eaten by these three species consist largely of filamentous algae. In the summer months the production of such algal food is enormous, great mats of 'flannel weed' drifting down the river and stranding in the shallows. In the presence of such a superabundance of plant food it is not to be believed that there can exist any pressure upon the supply for at least half the year, and even in winter long strands of algae are to be found growing on piles and stones. Diatoms are a food of young roach and dace (Hartley, 1947), but they make a substantial contribution to the diet of minnows of all sizes.

Of the crustaceans eaten *Gammarus pulex* occurred most frequently, 34 specimens being found in 14 roach (8·5 %), 67 in 13 dace (5·5 %) and one in each of 5 minnows (4 %). Four minnows had each eaten one very small *Astacus fluviatilis*.

Hydrobia jenkinsi was found in 11 roach (7 %) and in 6 dace (2·5 %).

(4) In the fourth group, in which the food is composed of insects and crustaceans, there is considerable competition between all three members for insect foods, between gudgeon and bullhead for the larger Crustacea, and between gudgeon and stickleback for the smaller.

In gudgeon and stickleback, chironomid larvae were by far the most important food; they occurred in 238 gudgeon out of 391 (61 %) and in 95 sticklebacks out of 227 (42 %). In loach, chironomid larvae were found in 8 (50 %) of the 16 fish examined, and in the bullhead, which took a higher proportion of Crustacea than the other members of the group, chironomid larvae formed the insect food most frequently occurring, being found in 18 fish out of 84 (21·5 %). Of other insect foods, ephemeropteran nymphs were found in 9 bullheads (11 %), 21 sticklebacks (9 %), 32 gudgeon (8 %) and in 4 out of 16 loach. Trichopteran larvae had been eaten by 11 bullheads (13 %), 24 gudgeon (6 %), 3 loach and only 3 sticklebacks (1 %). Gudgeon differed from the other fish of the group in taking many larvae of *Simulium* sp. These were found in 35 fish (9 %).

Gammarus pulex was the food most often eaten by bullheads, being found in 34 fish (40·5 %); 71 gudgeon (18 %) had eaten *Gammarus* and so had 3 loach. The average number of *G. pulex* found in gudgeon was 4 (281 specimens in 71 fish), but in bullheads the average consumption was only a little over 1·1 (40 specimens in 34 fish). The 3 loach which had eaten this food contained 17 between them.

Of the smaller Crustacea, Copepoda were an important food of sticklebacks, being found in 54 fish (24 %). Thirty-four gudgeon (8·5 %) and 1 bullhead had eaten copepods. Twenty-nine gudgeon (7·5 %) and 14 sticklebacks (6 %) had eaten *Chydorus* sp., and 3 loach contained Cladocera of this genus.

The fishes of the community have been divided into four groups, on a somewhat arbitrary basis of differences of general feeding habits: but it is immediately obvious that competition for certain foods is not confined within group limits. Table 6 shows the frequency of occurrence of certain foods, expressed as a percentage of the fish of each species examined in which these foods were found. This table emphasizes both competition within groups and insect diets. There is a certain similarity between the diets of the small bullheads and the relatively large brown trout and eels. Of 21 identifiable foods eaten by bullheads, 9 had also been eaten by both brown trout and eel, 4 by eels only, 1 by brown trout only.

The activities of the fish fauna do not complete the tale of vertebrate predation upon the population of

Table 6. *Animal foods found most frequently in fish from the River Cam and Shepreth Brook in* 1939–41

In each species of fish, the number of fish in which each food occurred is expressed as a percentage of the total number of fish examined.

	Fish	Ephemeropteran nymphs	Trichopteran larvae	Adult beetles	Larvae of *Simulium* sp.	Chironomid larvae	*Potamobius pallipes* (=*Astacus fluviatilis*)	*Gammarus pulex*	Copepoda	*Chydorus* sp.
Pike	73	—	—	—	—	—	—	—	—	—
Brown trout	26·5	26·5	84	43	—	—	10	33	—	—
Eel	22	13·6	—	—	5·6	—	26	31	—	—
Roach	—	—	—	—	6	14·5	—	8·5	—	—
Dace	—	—	30	8	8	12	—	5·5	—	—
Minnow	—	—	—	—	—	26·5	—	—	—	—
Gudgeon	—	8	6	—	9	61	—	18	8·5	7·5
Stickleback	—	9	—	—	—	42	—	—	24	6
Bullhead	—	11	13	—	—	21·5	—	40·5	—	—

Table 7. *Food of aquatic birds, River Cam and Shepreth Brook,* 1939–41

Of the 10 moorhens, 5 were adult and 5 juveniles in down.

	Tufted duck		Common snipe		Moorhen	
	Occ.	No.	Occ.	No.	Occ.	No.
Hydrobia jenkinsi Smith	—	—	1	1	2	3
Ephemeropteran indet., nymph	—	—	—	—	1	1
Sialis sp., larva	1	2	1	8	—	—
Hydropsyche sp., larva	1	4	—	—	—	—
Stenophylax sp., larva	1	1	—	—	—	—
Coleopteran indet., adult	—	—	—	—	3	5
Dytiscus sp., larva	1	2	—	—	—	—
Tipula sp., larva	—	—	2	18	—	—
Simulium sp., larva	—	—	—	—	1	1
Gammarus pulex (de Geer)	1	16	—	—	—	—
Elodea sp.	—	—	—	—	1	/
Sparganium sp.	—	—	—	—	1	/
Carex sp. (seeds)	—	—	—	—	1	(25)
Cladophora sp.	—	—	—	—	1	/

competition between members of different groups. For example, chironomid larvae are an important food of all members of groups 3 and 4 (in which a high consumption of insect food is the common feature of the dietaries). Trichopteran larvae are the most frequently occurring insect foods of both brown trout and dace, and only these two species consume any quantity of adult beetles. The fact that brown trout take no dipteran larvae is a distinction between their the river. Otters (*Lutra lutra*), herons (*Ardea cinerea*), kingfishers (*Alcedo atthis*) and little grebes (*Podiceps ruficollis*) all visited the area. In addition to their direct toll, a number of aquatic birds competed with the fishes for invertebrate foods. The stomach contents of 10 moorhens (*Gallinula chloropus*), 1 tufted duck (*Aythya fuligula*) and 2 common snipe (*Capella gallinago*) from this stretch of the Cam were examined. The food of these birds is shown in Table 7.

Three 'links' of a few food chains have been established by direct observation, and these are shown in Table 8.

Percival & Whitehead (1929) recorded that 'the carnivorous species do not form more than 10% of the total (invertebrate) fauna of a given type of substratum', and Slack (1936) has shown the predominance of an herbivorous feeding habit among trichopteran larvae. Feeding largely upon herbivorous animals, the members of the fish fauna stand in a qualitatively simple relationship to the invertebrate community. Usually there is but one connecting link between plant material and fish, and in group 3 (the fishes of partially vegetarian habit), this link is often omitted. It would be easy to construct many more food chains by deduction, but they would serve only to emphasize the predominance of the simple system: plant—invertebrate herbivore—vertebrate predator.

Table 8. *Food chains in the River Cam and Shepreth Brook*, 1939–41

(1) 31 Mar. 1939	*Spirogyra* sp.	Gudgeon	Pike	—
(2) 27 May 1939	Plant fragments	Chironomid larvae	Stickleback	Pike
(3) 19 July 1939	—	Nymph of *Ephemera* sp., larvae of *Simulium* sp.	Gudgeon	Pike
(4) 27 July 1939	Plant fragments	Stickleback	Pike	—
(5) 7 Oct. 1939	—	Nymphs of *Baetis* sp., larvae of *Simulium* sp.	Minnow	Pike
(6) 1 Dec. 1939	—	Larvae of trichopteran, 2	Stickleback	Pike
(7) 14 Mar. 1940	*Meridion circulare* and *Synedra* sp., many Naviculid indet., 1	Larvae of *Simulium* sp.	Bullhead	—
(8) 9 Apr. 1940	—	Larvae of trichopteran	Stickleback	Pike
(9) 2 June 1940	—	Nymph of *Ephemera* sp. nymph of ephemeropteran, 2, larvae of *Limnophilus* sp., 2, chironomid larvae, *Gammarus pulex*	Loach	Eel
(10) 18 July 1940	Plant fragments and diatom frustules	Larvae of *Simulium* sp.	Dace	—
	Plant fragments	Larvae of *Simulium* sp.	Dace	—
	Plant fragments and diatom frustules	Larvae of *Simulium* sp.	Dace	—
(11) 30 July 1940	—	Nymph of *Baetis* sp., 1, chironomid larva, 1	Bullhead	Pike
(12) 1 Aug. 1940	*Coscinodiscus* sp. and naviculid diatoms	Larva of *Simulium* sp.	Gudgeon	—
(13) 2 June 1941	*Synedra* sp. and naviculid diatoms	Larva of *Simulium* sp.	Trout	—

5. DISCUSSION

When the feeding habits and relationships of the fishes living in the waters at Barrington have been surveyed, it is possible to make three generalizations about them. First, between no two species is there a true identity of feeding habit. The nearest approach to a common dietary is in gudgeon and stickleback. In these two species insects contributed 57 and 51% of the total occurrences of food, and of insect food three groups, ephemeropteran nymphs and larvae of *Simulium* sp. and of chironomids contributed 82 and 89% respectively on a basis of occurrence, and 95 and 93% on a basis of numbers. Yet in the foods of these two species there are contrasts quite as marked as the similarities: *Gammarus pulex* contributed 48% of the crustacean foods found in gudgeon, and only 1·3% in the stickleback. 12% of the gudgeon food was molluscs and only 2% of the sticklebacks. In gudgeon only 6% of the occurrences of food was of plant origin, but in sticklebacks vascular plants and algae contributed 14% of the food, and diatoms 8%. In the same way it has been shown that there is a marked similarity between the insect foods of trout and dace, and wide dissimilarity in the constitution of the rest of their diet.

Secondly, it may be concluded that, with the exception of the fish-eating pike, there is a great degree of general competition between all the fish of the community. While no instance has been found of two species occupying one ecological niche, as bream (*Abramis brama* (L.)) and white bream (*Blicca bjoernka* (L.)) appear to do in some East Anglian waters (Hartley, 1947), none of the species present have clearly defined individual roles to play. Here is no orderly hierarchy of specialists, each fulfilling its part, but rather a loosely organized assemblage in which the members are distinguished by no more than the varying proportions in which they draw upon the constituents of a common stock. It has been shown elsewhere (Hartley, 1940) that most of the 'coarse' fishes show considerable flexibility of feeding behaviour, and it is by no means certain that the balance of relationships revealed in the period 1939–41 will be maintained unaltered. In the absence of any evidence of the actual degree of pressure upon the food supplies it is impossible to say to what extent 'competition' between different species is a limiting factor upon growth and numbers; and the ability of most of the members of the community to live and thrive upon a wide variety of foods will make the effects of the failure of any one source of supply less disturbing of the general balance than they would be in a community in which ecological niches were more clearly defined.

Thirdly, it must be concluded that the organization of this animal community is qualitatively straightforward. There are but two or three steps between the supply of plant material and the end-point of the food chain. This is not to suggest that the ecological relationships within a 'small river' community are entirely simple, but complexities will be quantitative rather than qualitative. It has been shown that the differences between the food requirements of one species and another lie in the different inroads which they make upon the components of a common stock. As the supply of one food becomes more abundant, and of another scarce, so the balance of competition between one species and another will be altered. Though no complete identities of diet have been found, the degree of general competition is such that few of the members of the fish fauna will be wholly unaffected by an enforced change in the diet of some other species.

SUMMARY

1. A short stretch of the upper reaches of the River Cam and one of its tributaries, the Shepreth Brook, contained a community of eleven species of fish. The area is defined and briefly described.

2. An investigation was made of the food of the members of the fish community, and of a few aquatic birds from the same area. It is shown that, on a basis of food, the fish may be divided into four groups:

(*a*) Specialist predators upon a single prey. One species.

(*b*) Fish taking a wide variety of foods. Two species.

(*c*) Fish taking a diet in which insects and plants predominate. Three species.

(*d*) Fish taking a diet in which insects and crustaceans predominate. Four species.

3. It is shown that between no two species is there complete identity of feeding habit, but that there is much general competition between all the fish of the community for certain staple foods.

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