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The Food of Coarse Fish

being

The Interim Report on the Coarse Fish Investigation

by

P. H. T. HARTLEY, B.Sc.

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FOREWORD.

The investigation on coarse fish, which the Association is undertaking for the National Federation of Anglers, was started in the spring of 1938. During the summer of that year Mr. P. H. T. Hartley, Assistant Naturalist in charge of this investigation, toured those parts of the country where coarse fish predominate, attending netting operations and making contacts with the people most closely concerned with the development of the fisheries. By the autumn of 1938 East Anglia was selected as the most satisfactory centre for research, and Mr. Hartley established his laboratory at the village of Barrington on the upper reaches of the Cam, a centre from which the Norfolk Broads, the fenlands, the Trent and other rivers and canals in the Midlands, were reasonably accessible.

In January, 1939, routine work was started on selected waters, especially parts of the Norfolk Broads, the old West River, which is part of the original course of the Ouse before the construction of the Bedford Levels, the upper reaches of the Cam, and the Grantham Canal. Difficulties in transport after the outbreak of war made it impossible for the full programme of netting expeditions to be carried out at those stations furthest from the base, but by the end of 1939 a good quantity of information had been accumulated. Owing to the uncertain conditions of research work in war-time and the long delay which is likely before the final results of the investigation are published, it was decided to prepare this short account of some of the results obtained during the first year's intensive work.

The problems to be solved were originally envisaged in the following five categories: (1) the food of coarse fish in different environments and at different stages in their life histories, (2) their growth-rates in different environments, correlated if possible with food supply and the physical and chemical conditions of the water, (3) breeding habits, (4) the factors which reduce the number of fish, such as angling, predators, parasites and disease, (5) the possibilities of artificial propagation as a means of increasing the supply of fish where desirable. The work to date has involved the collection of information in each of these categories except the last. Research on artificial propagation was postponed until more is known about the balance between food supply and the population of fish, so that there should be more reliable means of determining whether a given water could be improved by adding more fish, or whether it already had too many for its best productivity. This publication is restricted to the first category of problems, namely feeding habits, because the information on this subject is the most complete and is thought to be of special interest to those who are concerned with the conservation and improvement of fisheries, as well as to those who are interested primarily in the capture of fish.

Wherever possible Mr. Hartley has used English rather than scientific names for the fish themselves and the small animals and plants which form their food, the scientific name being given only when the organism or group of organisms is first mentioned. Nevertheless, to those not intimate with the smaller forms of under-water life a few words of explanation may be helpful. In the major categories of food organisms, " molluscs " include on the one hand all the water-snails such as the well-known *Limnaea pereger* and on the other hand the bivalved shellfish such as the little pea-mussels, *Pisidium*. " Insects " are divisible into a number of orders of which the most important mentioned are the ephemeropterans (may-flies, etc.) and the dipterans (two-winged flies such as gnats and midges, one family, the Chironomidae, being particularly important as food for fish). The " crustaceans " are divided into two groups for present purposes: firstly the bottom-living forms including the crayfish (*Astacus*), the freshwater shrimp (*Gammarus*) and the water-louse (*Asellus*), and secondly the very small forms grouped together as planktonic crustaceans, which include the cladocerans or water-fleas, the copepods (*Cyclops*, etc.), and the ostracods. The category " plants and algae " includes all the large sized water vegetation, namely the water-weeds, and the filamentous algae which often grow into a kind of mat on the bottom, known as flannel-weed. The category " diatoms " includes for present purposes all the microscopic unicellular algae, although some of those found in the stomachs of fish are not diatoms in the strict botanical sense.

The publication of this pamphlet at a time when every resource of the country is being put towards the national effort, warrants a few remarks on the place of freshwater fisheries in war-time. Although the recreational importance of fish has not entirely disappeared, fresh waters now attract more attention as a possible source of additional food or feeding stuffs than for sport. The eel, one of the most nutritious of fish, offers the greatest opportunity for development as human food, since British waters are by no means cropped to capacity, while the usual continental sources of imported eels are no longer available. A campaign has in fact been started by the Ministry of Agriculture and Fisheries with a view to increasing the capture of eels from British rivers and lakes wherever possible. In addition there are big areas of water, such as the Norfolk Broads, the Lake District and the Cheshire meres, from which considerable quantities of coarse fish could be taken by netting, trapping, and such-like means. We know that at least some of these waters are suffering from too many fish, and that a big reduction in their populations, such as would result from war-time exploitation, would probably lead to improved conditions for angling after the war. Many of these coarse fish are either too small or too muddy in flavour to be worth serious consideration as an important contribution to human food supplies, but they can be used to great advantage as feeding stuffs, either fresh or when converted into high-grade fish meal. Such temporary uses to which fish may be put now, and the anticipated period of reconstruction in fisheries after the war, gives an added importance to biological research, such as that undertaken by Mr. Hartley.

E. B. Worthington, *Director*.

Wray Castle,
August, 1940.

THE FOOD OF COARSE FISH

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THE INTERIM REPORT ON THE COARSE FISH INVESTIGATION

by

P. H. T. HARTLEY, B.Sc.

CONTENTS.

INTRODUCTION.

? abundance of the various foods

Remarkably little has been published on the feeding habits of the non-salmonid fishes of British fresh waters. Regan (1911) refers in general terms to feeding habits in his handbook, and in recent years there have appeared one or two papers dealing with the food of individual species. The following report briefly summarizes the results obtained from the examination of the stomach contents of some 2,700 fish, belonging to 19 species, which were obtained during 1939 (table I). The report is offered as a contribution to the more exact knowledge of the bionomics of freshwater animal communities; but the writer hopes that it will also prove not uninteresting to sportsmen.

The results of all examinations of gut contents were analysed, species by species, upon a simple basis of the presence of different types of food. Foodstuffs were divided up into six main categories—fish, molluscs, insects, crustaceans, higher plants together with filamentous algae, and diatoms—and the occurrence of members of any of these categories was recorded for each fish. No account was taken in this preliminary survey of variations within the main groups; one or one thousand specimens, of one or of ten species, were recorded as one occurrence of organisms of the category to which they belonged. Table II was prepared upon this basis of occurrence, and figure 1 presents these results graphically. This figure shows the percentages in which the different categories of food occurred in each species of fish during the year 1939, and enables the feeding habits of any one species to be compared with those of all the other species investigated.

Table 1. Number and localities of fish examined in 1939.

	Total	Old West River, Cambs.	R. Cam, Barrington & Shepreth Brook	R. Cam, at Dimock's Cote Bridge	R. Granta, Cambs.	Madingley Upper Pond, Cambs.	Norfolk Broads	Grantham Canal, Cotgrave, Notts.	Bridgewater Canal, Lancs.	Other Localities
Smelt	1	—	—	—	—	—	1	—	—	—
Pike	56	5	43	—	—	—	2	6	—	—
Eel	27	1	21	—	—	—	5	—	—	—
Crucian Carp ...	1	—	—	—	—	1	—	—	—	—
Gudgeon	147	—	70	1	76	—	—	—	—	—
Tench	13	3	—	1	—	3	3	3	—	—
Minnow	19	—	19	—	—	—	—	—	—	—
Dace	53	2	48	—	—	3	—	—	—	—
Roach	1298	134	68	30	117	50	589	171	109	30
Rudd	129	12	—	1	2	48	60	—	—	6
Silver Bream ...	95	68	—	6	—	—	—	19	—	2
Bream	514	29	—	25	—	—	435	17	—	8
Bleak	8	8	—	—	—	—	—	—	—	—
Loach	11	—	11	—	—	—	—	—	—	—
Perch	138	10	5	1	3	35	30	53	—	1
Ruffe	77	4	—	—	—	—	73	—	—	—
Bullhead	12	—	12	—	—	—	—	—	—	—
3-spined Stickleback	129	3	126	—	—	—	—	—	—	—
Flounder	2	—	—	—	—	—	2	—	—	—

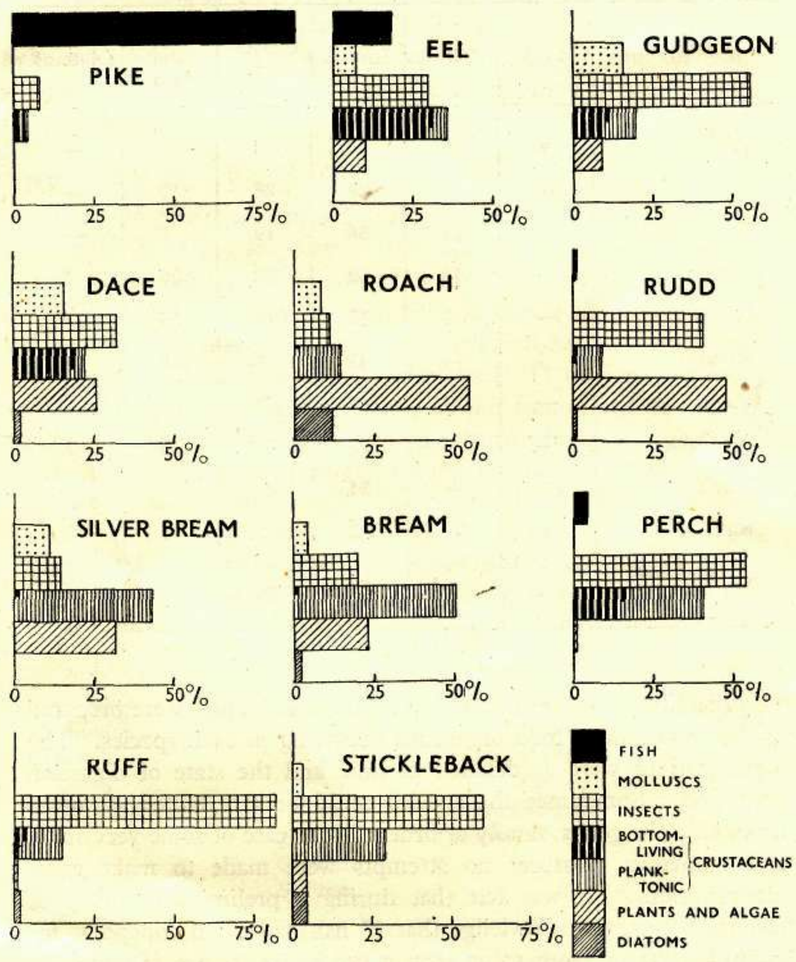

Figure 1. Percentage composition of the diets of coarse fish.

Table II. **Food of fish in 1939: occurrences of different foods expressed as percentages of the total number of occurrences.**

	Fish	Molluscs	Insects	Crusta-ceans	Plants and Algae	Diatoms
Pike	**88**	—	8	4	—	—
Eel	18	7	**29**	**36**	10	—
Gudgeon ...	—	16	**56**	19	9	—
Dace	—	16	**32**	22	26	2
Roach	—	8	11	14	**55**	12
Rudd	1	—	**41**	9	**48**	1
Silver Bream ...	—	11	14	**43**	32	—
Bream	—	4	20	**51**	23	2
Perch	4	—	**54**	41	1	—
Ruffe	—	—	**82**	15	1	2
Three-spined Stickleback ...	—	3	**60**	29	4	4

In addition to the analyses shewn in table II, lists were prepared of the recognizable food organisms occurring in each species. The identifications were as detailed as time and the state of digestion permitted. Sometimes the species could be ascertained, at other times only the genus, family or order: in the case of some very small and numerous creatures no attempts were made to make exact identifications. It was felt that during a preliminary survey of feeding habits, the knowledge that 20 fish had eaten copepods, for example, was of more value than a list of 20 species of copepods eaten by one fish. For reasons of economy these lists have not been printed, but copies have been filed in the library of the Freshwater Biological Association at Wray Castle, where they are available for examination.

The lengths of fish have been measured in centimetres from the snout to the fork of the tail, or, when the tail is not cleft, from snout to tip of tail.

I should like to express my gratitude to Mr. Ernest Bullard and Mr. A. J. Rudd, of the Norfolk Fishery Board, for their constant help and hospitality: to Mr. J. S. Jackson, of Warrington, for many samples of roach: and to Mr. Geoffrey Vinter for fish from Cambridgeshire rivers.

THE PIKE, *Esox lucius.*

Only 56 pike were opened during 1939: these fish were mostly 20-45 cm. (8-18 in.) in length, the smallest measuring 16.8 cm. (6.6 in.), and the largest 55 cm. (21.6 in.). Their food (fig. 1 and table II) consisted largely of small fish, occurring in 42 pike out of the 56, with a few insects and crustaceans. The fishes most frequently eaten (table III) were roach and stickleback (11 occurrences each) with gudgeon (7 occurrences) next in importance. Four of six different insect remains were those of ephemeropterans; the fresh-water shrimp (*Gammarus pulex*) occurred twice, and the crayfish (*Astacus fluviatilis*) once.

Table III. **Pike, 1939: recognizable food organisms, with the number of fish in which each occurred.**

Gudgeon	7	*Ephemera* adult	1
Minnow	2	Larva of *Ephemera* ...	1
Roach	11	„ „ *Baëtis*	1
Loach	1	„ „ *Centroptilum* ...	1
Stickleback	11	Chironomid larva ...	1
		Tabanid „ ...	1
Crayfish ...	1		
Shrimp ...	2		

It would seem that pike will feed on any fish of suitable size and shape, and that the species taken depend upon availability. The food fishes of pike in Windermere (Allen, 1939) were mostly different species from those eaten in East Anglia and the Midlands. The two lists of food fishes are compared in table IV.

Table IV. Pike: comparison of food fishes in Windermere (data from Allen, 1939) with those in East Anglia and the Midlands.

	Windermere	East Anglia and Midlands
Brown trout	2	—
Gudgeon	—	7
Minnow	9	2
Roach	—	14
Loach	—	1
Perch	42	—
Stickleback	8	17

There is a marked similarity, on the other hand, between the insect foods in the two samples. In Windermere, 6 out of 7 occurrences of insects were members of the Ephemeroptera (nymphs of the mayfly, *E. danica*): in the 1939 results of the Coarse Fish Investigation, 4 out of 6 insect remains belonged to the same order.

Bolam (1913) recorded a curious seasonal change in the diet of pike in a lake in Wales. " In May we were annoyed to find neither trimmers nor ' otters ' of any use, and the number caught in the nets was less; and the autopsies shewed that the pike were feeding on the fresh-water shrimp (*Gammarus pulex*). Not only the small jack, but great fellows up to twenty pounds were gorged with them, and during this time they were more delicate in flavour than at any other time . . . This diet satisfied them all through the month of May each year, but at no other season did we find a trace of shrimps amongst their food." Coward (1914 and 1927) recorded the water-louse (*Asellus aquaticus*), the cladoceran *Leptodora* and aquatic beetle larvae from the stomachs of pike caught in the Cheshire meres.

Allen (1939) found that out of 32 pike caught between October and March, 14 (44%) were empty, while between April and October,

only 19 out of 71 contained no food. In 1939, I found 8 out of 27 pike (29.5%) to be empty in the period of January to March and October to December, and 5 empty fish out of 31 (13%) in the warmer half of the year. These figures suggest that pike feed more constantly in summer than in winter, but the numbers examined are too small for a conclusion on this point.

THE EEL, *Anguilla vulgaris*.

Twenty-seven eels were examined during 1939, varying in length from 9 to 61 cm. (3.5 to 24 in.). They were found to have a largely carnivorous diet, with a catholic taste in foods (fig. 1 and table II). The eel was found to rank next to the pike as an active predator upon other fishes; remains of fish were found in five specimens (18% occurrence). The only recognizable species was the bullhead (*Cottus gobio*), which was found twice. Crayfish and freshwater shrimps were favourite foods, each having been eaten by five eels. The number of fish on which such a conclusion may be based is, unfortunately, very small, but the mean lengths of eels containing different foods (table V) suggest that there is a change from a diet of molluscs, insects and planktonic crustaceans in the younger eels, to one of fish, bottom-living crustaceans and, perhaps, plants in the older eels. Plants were never found alone in an eel's stomach; twice they were discovered with the remains of a fish, and once with the remains of crayfish. There is a possibility that fragments of plants were bitten off in a sudden spring upon active prey, and not deliberately eaten.

Table V. Eel, 1939: mean lengths of fish containing different foods.

Food	Fish	Molluscs	Insects	Crustaceans: Cray-fish	Crustaceans: Fresh-water Shrimps	Crustaceans: Plank-tonic Crusta-ceans	Plants
Number of Fish ...	5	2	9	5	5	2	3
Mean length in cm. ...	54·5	25	23·5	53·5	37·5	12·5	57·5

THE GUDGEON, *Gobio gobio.*

Insects formed rather more than half (56%) the food of the gudgeon (fig. 1 and table II). Molluscs and crustaceans in roughly equal proportions, with a little plant matter, completed the diet. Aquatic dipteran larvae—chironomids, *Simulium* sp. and tipulids—made up 77% of the recognizable insect foods and larvae of Ephemeroptera contributed 11%. There was some tendency for a change in the composition of the crustacean diet as size increased. The mean length of gudgeon containing bottom-living crustaceans was 13.0 cm. (5.1 in.), while that of the fish containing planktonic forms was 9.4 cm. (3.7 in.). There is certainly no winter fast, but there may be some fasting just after the spawning season. In the four three-monthly periods, January—March, April—June, July—September and October—December, the percentages of empty fish were 17, 27, 40 and 12.5: the highest monthly percentage of empty fish was 52% in July.

THE DACE, *Leuciscus leuciscus.*

Dace were found to eat more animal food (fig. 1 and table II) than their congeners the roach and rudd. Insects were the food occurring most frequently (33% of total occurrences); crustaceans (22%) and molluscs (16%) made up the animal food. Plants, and a single occurrence of diatoms, formed 29% of the diet. Only 53 dace were examined during 1939, and of that number 23 were empty. A sample of 30 fish containing food is too small to permit anything but the most cautious comparison with the feeding habits of other species. Mention may be made of a qualitative similarity between the insect foods of roach and dace, and of the fact that freshwater shrimps, and not planktonic forms, were the crustacean food most frequently occurring.

THE ROACH, *Rutilus rutilus.*

The first analysis of the food of the roach (fig. 1 and table II) shewed that vegetable matter—higher plants, algae and diatoms—formed the bulk of the diet; that crustaceans came next in importance, and that molluscs and insects were also eaten. The year 1939 was divided into six periods of two months each, and the percentage occurrence of food organisms of the different categories was calculated for each period (fig. 2, A to F). In every period vegetable matter was the most important food. In three periods out of the six (A, C and D), crustaceans were the principal animal food; in two periods (B and E) insects were most numerous, and in one (F) molluscs predominated.

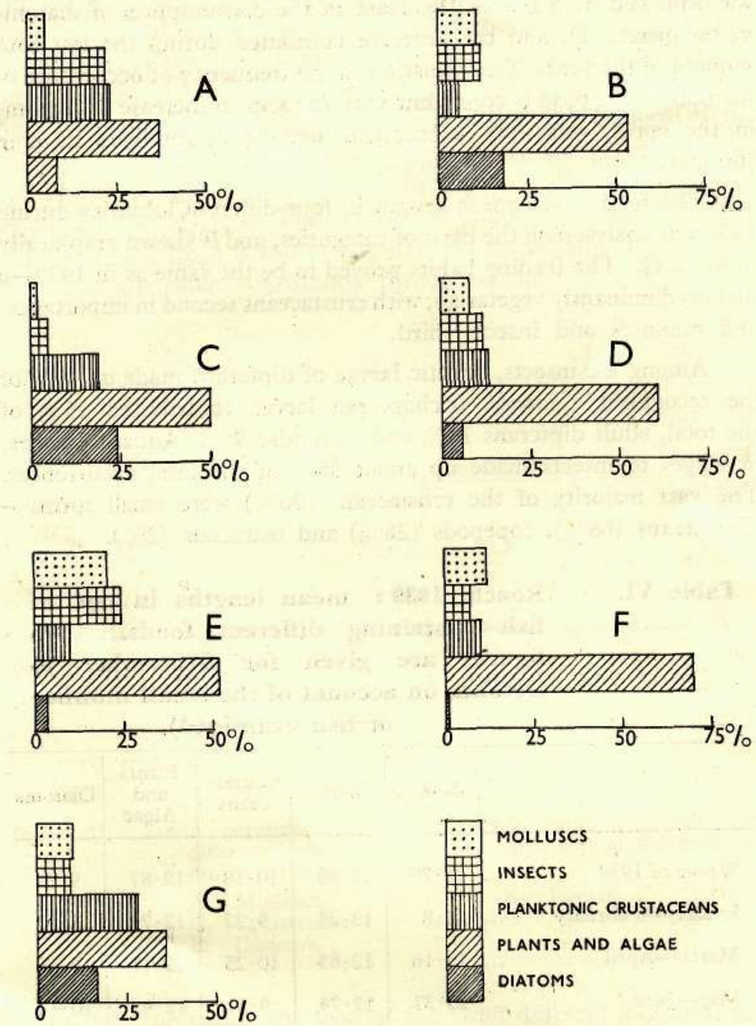

Figure 2. Roach: percentage composition of the diet at different times of the year.
A. January-February, 1939. B. March-April, 1939.
C. May-June, 1939. D. July-August, 1939.
E. Sept.-October, 1939. F. Nov.-December, 1939.
G. Four months in 1938.

The percentage occurrence of diatoms increased from the first period to the second, and from the second to the third. This increase was followed by a marked decrease in the consumption of diatoms in the period D, and the decrease continued during the last four months of the year. This variation in the frequency of occurrence of diatoms in the food is consistent with the known increase of diatoms in the spring, and the subsequent decline in numbers in high summer.

The food of the roach caught in four different localities during 1938 was analysed on the basis of categories, and is shewn graphically in fig. 2 G. The feeding habits proved to be the same as in 1939—a diet predominantly vegetarian, with crustaceans second in importance, and molluscs and insects third.

Among the insects, aquatic larvae of dipterans made up 48% of the recognizable forms: trichopteran larvae contributed 15% of the total, adult dipterans 10% and Corixidae 9%. Aquatic species, or stages of insects made up about 85% of the total occurrences. The vast majority of the crustaceans (96%) were small forms—cladocerans (68%), copepods (26%) and ostracods (2%).

Table VI. Roach, 1939: mean lengths in cm. of fish containing different foods. (No figures are given for September to October on account of the small number of fish examined).

	Molluscs	Insects	Crusta-ceans	Plants and Algae	Diatoms
Whole of 1939	14·79	12·99	10·18	12·87	9·79
January—February ...	14·8	13·25	9·22	12·79	8·92
March—April	15·16	12·63	10·25	12·77	9·58
May—June	15·37	12·79	9·31	12·92	10·14
July—August	14·88	13·3	12·41	13·82	12·28
September—October ...	—	—	—	—	—
November—December ...	13·73	13·31	9·63	11·99	—

The mean lengths of the fish consuming foods of the different categories were calculated for each of the six two-monthly periods and for the whole year 1939 (table VI). It emerges from the examination of the table that crustaceans and diatoms are, on the whole, the food of the smaller fish, and that molluscs are mostly eaten by the larger roach. Additional evidence of this change in diet is given in fig. 3, where the percentage length frequency distributions of the fish eating foods of the different categories are compared with the percentage length frequency distribution of all the specimens examined during 1939. The close correspondence between the two curves in both fig. 3 B and D suggests that insects and higher plants + algae are eaten consistently throughout life.

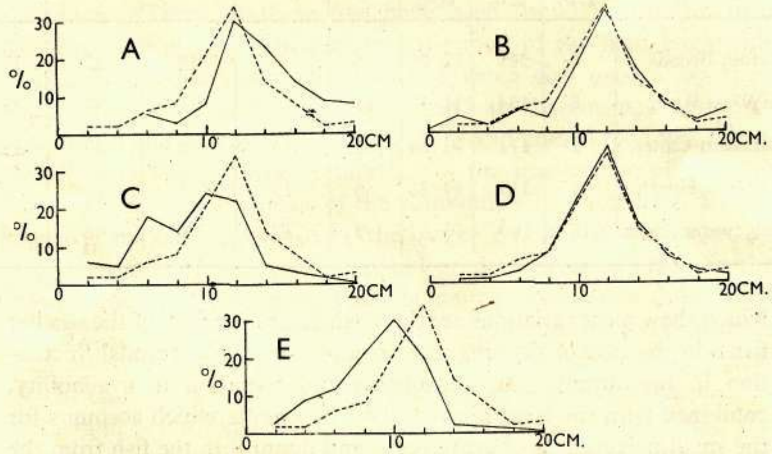

Figure 3. Roach: percentage length frequency distributions of fish eating different foods (solid lines) compared with all fish examined during 1939 (broken lines).
A. Molluscs. B. Insects.
C. Crustaceans. D. Plants and Algae.
E. Diatoms.

When comparing the food of fish from different localities, it is essential to allow for the changes in diet which accompany changes in size. When the length frequency distributions of samples are substantially different, variations in food may be merely an expression of this difference in size, and of no real bionomic significance.

The diets of roach from five different localities are shewn in table VII: in all cases more than 100 fish were examined during 1939. The percentages of molluscs, insects and plants from the five localities are all of the same order of magnitude. The two categories

Table VII. Roach, 1939: diet of fish from five localities, expressed as percentages of the occurrences of all foods.

Locality	Number of Samples	Number of Fish	Mean length of All Fish in cm.	Percentage Occurrences of				
				Mol-luscs	Insects	Crusta-ceans	Plants +Algae	Dia-toms
Norfolk Broads ...	6	589	12·09	6	5	19	52	17
Old West River ...	8	134	11·32	11	12	17	52	8
Grantham Canal	2	171	12·63	12	13	6	52	17
R. Granta, Hinxton	1	115	14·21	6	15	1	77	1
Bridgewater Canal	12	109	13·67	9	12	9	66	4

which shew most variations are those which are the food of the smaller fish: in the case of diatoms there is also a marked seasonal fluctuation in the supply. It is probably this variation in availability, combined with the large mean size of the sample, which accounts for the small percentages of crustaceans and diatoms in the fish from the R. Granta, which were caught in July. The localities from which these fish were taken are very different—a chain of lakes and dykes subject to tidal influence, a sluggish fenland river, two canals, one of them deserted, and a swift, well-keepered trout-stream. In view of this diversity of habitat, the diets of these five populations of roach are remarkably similar.

From the results so far obtained, it is possible to make the following generalizations on the food of the roach in England:—

(1) The roach is omnivorous; but it eats more vegetable than animal food.

(2) Planktonic crustaceans and diatoms are food of the younger fish.

(3) Insects, vascular plants and algae are eaten throughout life; but they increase in importance in the diet as the consumption of crustaceans and diatoms decreases.

(4) Molluscs are a food of the older fish.

Neuhaus (1936) found that, in the neighbourhood of Stettin, roach up to 6 cm. (2.4 in.) long ate planktonic diatoms, and green algae; fish from 6—15 cm. (2.4—6 in.) ate plants, algae, diatoms and copepods; and that the main food of fish over 15 cm. in length was molluscs. Neuhaus's list of molluscs included *Dreissensia polymorpha*, *Valvata piscinalis*, *Bythinia tentaculata*, *Hydrobia* and *Cardium*. Three of these five have been found in English fish. Walker (Spicer, 1939) investigated the food of roach in Highfields Lake, Nottingham, and distinguished three size groups by their feeding habits. Fish up to 8 cm. (3.1 in.) ate diatoms and desmids; between 8 and 15 cm. (6 in.) both plant and animal food was taken, but " there was a marked preference at the smaller end of this size range for the small animals of the plankton, viz., water-fleas, and an equally marked preference at the larger end for plant material." Roach over 15 cm. shewed a marked predominance of plants in the food " and the small proportion of animal food eaten diminished rapidly . . . until the bigger fish were found to be feeding quite exclusively on the larger plants." Stadel (1936) opened 127 roach, 5—20 cm. (2—7.9 in.) long, from the Elbe, and found that crustaceans and a few oligochaets were the food of the smaller fish; the larger specimens contained crustaceans, a larger proportion of oligochaets and molluscs. Sponges and *Cordylophora* " seemed to be prized by the roach," and the remains of insect larvae and fish were found but once each. Stadel considered the proportion of plant food to be low, but he mentioned that the diet of a few fish was almost exclusively vegetarian, diatoms and filamentous algae predominating. Dobers (1922) listed aerial insects, chironomid larvae and ephemerid nymphs, cladocerans, copepods, algae and diatoms as foods of the roach. Berry (1935) found that in the Hampshire Avon, in winter, " the chief item of diet appeared to be snails, chiefly *Limnaea* sp.": one fish of 210 grm. contained a perch 6.5 cm. (2.6 in.) in length. Patterson (1929) recorded that roach fed ravenously on filamentous algae.

It will be seen that the results of several workers differ in detail (indeed, it would be surprising if they did not), but agree in substance. The decrease in consumption of planktonic crustaceans and diatoms as the fish grow older, and the increase in the number of molluscs eaten, may be regarded as well established changes in the feeding habits. The dominance of vegetable foods in the diet is emphasized by Neuhaus and by Walker.

Table VIII. Roach: percentages of fish containing food in each month.

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
1938 ...	—	—	—	76·5	—	87·5	—	88	—	—	—	100
1939 ...	67	81	85	72	88	97	96	97	71	84	80	24

In table VIII are shewn the percentages of fish containing food in four months of 1938, and in every month of 1939. It will be seen that during 1939 the percentage of fed fish is highest in the summer months and lowest in mid-winter, but that there is little indication of a similar tendency in the admittedly incomplete figures for 1938. In fig. 4 the percentages of fed fish in all the specimens examined during each month of 1939 are compared with the percentages of fed fish in each sample of ten or more individuals. There is little uniformity between sample and sample in the winter and spring months—in January the percentages vary from 50 to 78, in May from 56 to 99, in November from 53.5 to 98, and in December from 17 to 73. In contrast with this variation, the three months of mid-summer shew consistently high percentages of feeding fish. During June, July and August there were no samples in which less than 80% of the roach contained food.

Stadel (1936) mentioned that, in the Elbe, roach took only a very small amount of food during October, November and December. Berry (1935) working on the Hampshire Avon, found that, in winter, " several roach stomachs examined were empty, but fish which had been feeding were gorged," and that " speaking generally, if one fish of a batch was empty, the others netted at the same time would also be empty. It would seem, therefore, that fasting is controlled

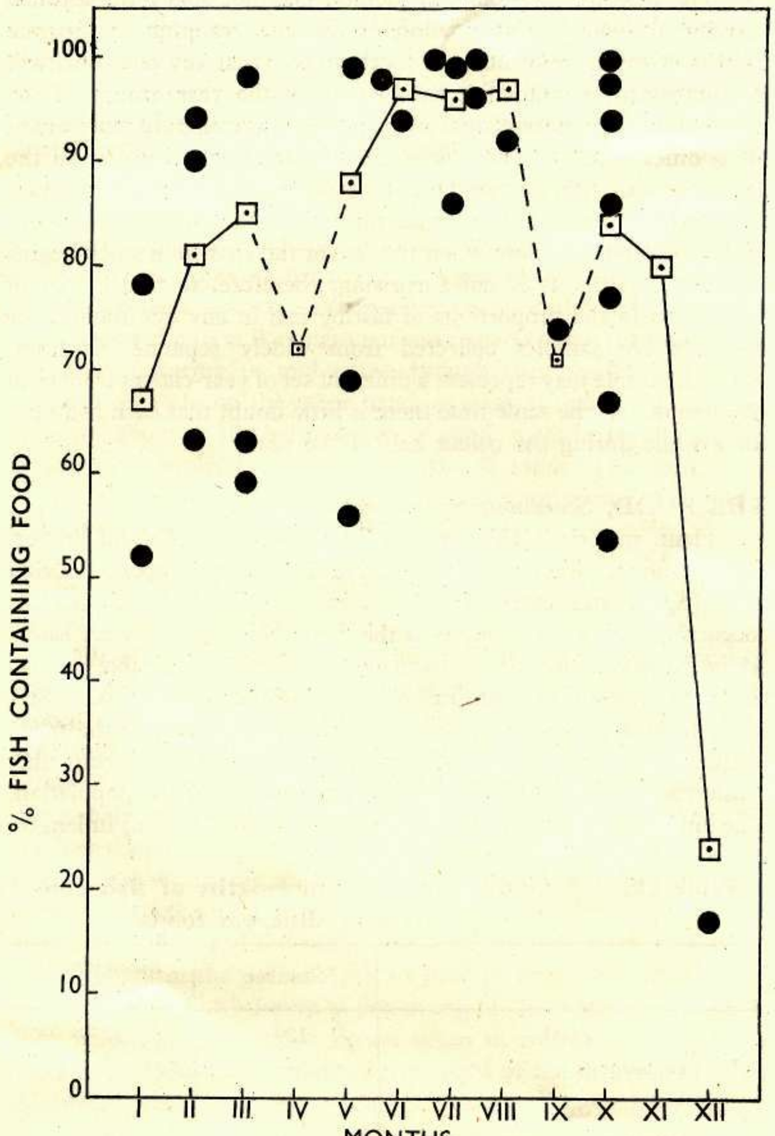

Figure 4. Roach: percentage of fish containing food in each month of 1939.
Squares=percentage for all fish examined.
Circles=percentage in each sample of 10 or more fish.

by some obscure physiological factors, and not solely by seasonal scarcity of food." Examination of the age grouping in separate catches of roach from the same locality show that any one shoal will not necessarily contain fair samples of all the year groups of the population. The proportions in which the year groups are represented often differ widely. There is evidence that in some species all the age-groups of fish do not fast at the same time: in the flounder (*Pleuronectes flesus*), for instance, the fast of the smaller, immature fish is drawing to a close when the fast of the spawning stock begins (Hartley, 1940). It is not surprising, therefore, to find a lack of uniformity in the proportions of fasting fish in any one month, for not only are samples collected from widely separate localities, but each sample may represent a different set of year-classes from each population. At the same time there is little doubt that each fish fasts for a while during the colder half of the year.

THE RUDD, *Scardinius eryophthalmus*.

Plant material (48% of the total occurrences) and insects (41%) made up the bulk of the food of the 129 rudd opened during 1939 (fig. 1 and table II): crustaceans (9%), fish and diatoms (occurring once each) completed the diet. No molluscs were eaten. Aerial forms contributed no less than 61% of the recognizable insects: there were remains of moths in 7 fish out of 48 netted on February 8th, 1939, from a pool surrounded by trees. Comparison of the mean lengths of the fish taking different foods (table IX) suggests that crustaceans were a food of the younger members of the population. The only rudd which had eaten a fish was 16 cm. (6.3 in.) in length.

Table IX. Rudd, 1939: mean lengths of fish containing different foods.

	Number	Mean length in cm.
Total	129	12·9
Fish containing:		
Insects	47	11·59
Crustaceans	9	(9·2)
Plants	54	13·63

Only 20 rudd were caught in the months April to September, and 19 of these had fed. Of the 109 fish caught during the colder half of the year, 73% contained food: but in a sample of 38 rudd taken on December 13th, 1939 (included in the 109 above), only 15 (39%) had food in their stomachs. There may, therefore, be a winter fasting period, but the material available was not large enough to establish the fact.

In feeding the rudd appears to combine the rôles of active carnivore and browsing herbivore. Its general habit is to haunt the mid-waters and surface. When numbers of rudd and roach were kept in stew-ponds at Barrington, it was remarked that the rudd always remained hovering in mid-water, though they would shoal when alarmed. Roach, on the other hand, as soon as they sighted a man, flounced about on the bottom of their pond, with the result that they were soon completely hidden in clouds of mud. The rudd is one of the few fish which does not find an important source of supply in the mud-burrowing chironomid larvae.

THE BREAM, *Abramis brama*.

The stomach contents of just over 500 bream were examined during 1939. The fish varied from 3—40 cm. (1.2—15.7 in.) in length. First analysis of the organisms found (fig. 1 and table II) indicated a diet in which crustaceans formed more than half the total occurrences of food. Insects and plants were next in importance; some molluscs and a few diatoms were eaten. The number of fish was considered to be too small to permit sub-division into six two-month periods, so the data for the bream were analysed into four periods of three months each. The diets in each of these periods are shewn in fig. 5 A to D. Crustaceans were always the most abundant food, though in the period April to June insects were found almost as frequently. The number of fish eating molluscs was always small. Fig. 5E shows the diet of bream taken in two localities in 1938. There was a close resemblance to the food of the fish caught in the following year.

There was a marked change in diet with size. In table X the length frequency distribution and mean lengths of all the bream

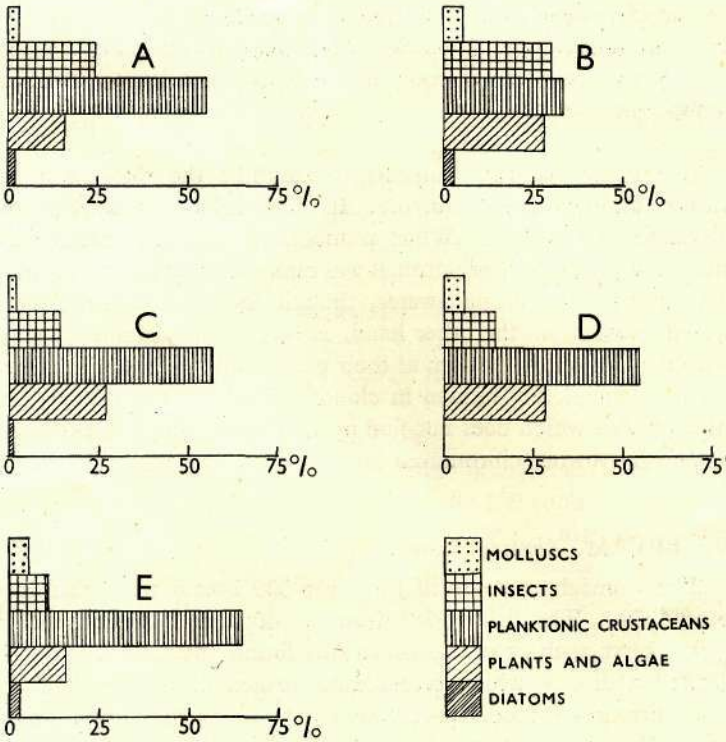

Figure 5. Bream: percentage composition of the diet at different times of the year.
A. January-March, 1939. B. April-June, 1939.
C. July-September, 1939. D. Oct.-December, 1939.
E. Two months in 1938.

examined during 1939 are contrasted with the length frequencies and mean lengths of the fish containing food of each category. Crustaceans and diatoms were the principal food of the smaller fish. As the fish grew older they ate more insects and plants. Fish of 18 cm. (7.1 in.) and over ate some molluscs.

Table X. Bream, 1939: length frequency distributions and mean lengths of all fish examined, and of fish containing different foods.

	No. of Fish	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30 to 35	36 and over	Mean length in cm.
		%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	
All Fish examined	514		3	1·5	5	7·5	7·5	18	18	15	8	5	3	1	2	3	1	17·26
Food: Molluscs ...	20	—	—	—	—	—	—	5	5	**15**	**15**	**15**	5	10	**15**	5	10	24·6
Insects ...	100	—	—	—	1	2	2	**17**	**17**	**14**	**14**	6	5	1	7	11	3	21·1
Crustaceans	257	—	0·2	3	8	9	**11**	**24**	**24**	**14**	3	2	0·2	0·2	0·2	1	—	15·44
Plants and Algae ...	117	—	—	—	1	4	7	**18**	**18**	**23**	8	7	4	2	3	3	1	18·95
Diatoms ...	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	(14·25)

Ninety-four per cent of the insect remains were those of chironomid larvae; and of the crustaceans 99% were planktonic: cladocerans (46%), copepods (47%) and ostracods (6%). Stadel (1936) opened 126 bream from the River Elbe, and found that in those with lengths of less than 26 cm. (10 in.), crustaceans (copepods and phyllopods) were first in importance as foods, and tubificid worms second. Bream more than 26 cm. long ate more tubificids, and fewer crustaceans. Stadel found some plant remains, and mentioned that no molluscs were eaten, although they were available in great numbers. At Stettin (Neubaur, 1926) larvae of midges were the principal food of bream, with some traces of the crustaceans:—*Leptodora*, *Daphnia* and ostracods. In Highfields Lake, Nottingham, according to Walker (Spicer, 1939) bream up to 12.5 cm. (4.9 in.) in length fed almost entirely on planktonic organisms—especially *Daphnia* and ostracods. Fish of more than 12.5 cm. seemed to be omnivorous, eating the larger species of planktonic and bottom-living animals, and some plants.

There is a well marked winter fast: the monthly percentages of bream containing food are shewn in table XI.

Table XI. Bream, 1939: monthly percentages of fish containing food.

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Number of Fish Examined ...	77	28	68	1	46	18	151	2	—	—	78	45
Percentage of Fish containing Food	39	50	72	—	91	100	93	—	—	—	32	27

THE SILVER BREAM, *Blicca bjoernka.*

Ninety-five silver bream were opened during 1939. The close resemblance of this species to the common bream is not only morphological: the diet of the silver bream (fig. 1 and table II) with crustaceans first and plants second as the most important foods, was very like that of its nearest relative. The examination of recognizable organisms emphasized this resemblance, as shewn by the comparison of the dominant forms in the two species (table XII).

Table XII. Common and Silver Bream, 1939: comparison of percentage occurrences of dominant foods.

Food Organisms	Common Bream	Silver Bream
	Percentage of recognizable insects	
Chironomid larvae ...	94	67
	Percentage of recognizable crustaceans	
Cladocerans	46	50
Copepods	47	42
Ostracods	6	6

The mean length of fish containing molluscs and insects exceeded the mean of all the silver bream examined, while that of the crustacean feeders was less (table XIII). This suggests a change in diet with increasing size similar to that in the common bream.

Table XIII. Silver Bream, 1939: mean lengths of fish containing different foods.

	Number	Mean length in cm.
Total	95	12·5
Fish containing:		
Molluscs	11	13·55
Insects	14	13·3
Crustaceans	43	11·5
Plants	32	12·7

In 188 silver bream from the Elbe (Stadel, 1936) the food was of molluscs, oligochaets and crustaceans: in the larger fish the number of crustaceans eaten decreased, and molluscs and oligochaets became the more important forms of diet. Stadel recorded that the consumption of food in November and December was noticeably small. In the fish which I examined during 1939, only 12 out of the 30 specimens (40%) caught in the periods of January to March and October to December contained food: 55 (85%) of the 65 fish caught between April and September had food in their stomachs. The reduction in the percentage of fed fish during the six colder months seems to confirm the existence of a winter fasting period.

THE PERCH, *Perca fluviatilis.*

The perch (fig. 1 and table II) is carnivorous in habit: plant foods were found in only two of the 138 fish examined. Insects made up more than half (54%) of the diet, with chironomid larvae, and the larvae of alder flies (*Sialis* sp.), trichopterans and agrionids as the dominant forms.

In the crustaceans, which made up 41% of the food, the water-louse and freshwater shrimp were of importance in the larger fish, and copepods in the smaller. O'Donoghue and Boyd (1934) found that in 10 perch from West Loch, St. Abb's, insects were the most numerous food, chironomid and other dipteran larvae and pupae making up the bulk of the diet; crustaceans, chiefly freshwater shrimps, came next in importance, and molluscs were found in two fish. Allen (1935) found that in Windermere chironomid larvae and pupae were the most important insect food. Brofeldt (1922), Dobers (1922) and Stadel (1936) gave lists of food organisms found in perch in Germany: these lists emphasize the importance of insects and crustaceans. Brofeldt and Stadel recorded molluscs and leeches as foods of the perch.

There is a marked change in diet with increase in size. The mean lengths of perch eating different foods are shewn in table XIV. The smallest fish ate planktonic crustaceans and insects; as they grew bigger, the consumption of planktonic crustaceans decreased, and more bottom-living crustaceans were eaten. The larger individuals ate some fishes.

Table XIV. Perch, 1939: mean lengths of fish containing different foods.

	Total	Fish	Insects	Bottom-living Crustaceans	Planktonic Crustaceans
Number of Fish	138	6	83	21	39
Mean Lengths in cm. ...	10·52	16	9·58	12·45	8·83

Changes in diet with change in size have been recorded several times. Brofeldt (1922) recorded that perch under 10 cm. (3.9 in.) in length ate planktonic crustaceans: the fish above that size ate bottom-living crustaceans, insect larvae, worms and snails, and the larger perch ate small fishes. Dobers (1922) regarded perch of 11 to 15 cm. (4.3—5.9 in.) as only occasional predators on young fish. Allen (1935) found that " in summer the food of the perch changes with the size of the fish: fish less than 14 cm. in length feed chiefly on plankton, those between 14 and 18 cm. in length feed on the bottom fauna, and those over 18 cm. in length feed on fishes." " In the winter these perch which in summer fed upon the larger plankton species and the bottom fauna, feed upon the smaller plankton animals. This change occurs because the animals which they eat

in summer are not available in winter." Röper (1936) found that perch of one summer lived upon littoral and planktonic crustaceans; in fish aged two or more summers, littoral insect larvae were dominant, until a size of 15 cm. was reached, when larger animals, including fish, were eaten.

In the fish examined during 1939, no evidence of a winter fast was found. On the other hand, Allen (1935) found an increased percentage of empty fish from Windermere during the winter months, and Stadel (1936) recorded that there were 18 empty fish out of 26 taken from the Elbe between December and February.

THE RUFFE, *Acerina cernua*.

Seventy-seven ruffe were examined during 1939. Seventy-three of them came from the Norfolk Broads, the other 4 from the Old West River in Cambridgeshire. The food of this species (fig. 1 and table II) was almost entirely of animal origin, with insects strongly dominant (82% of the total occurrences). 92% of the recognizable insects were chironomid larvae. The smaller ruffe had eaten some planktonic crustaceans: the mean length of fish containing cladocerans, copepods and ostracods was 7.4 cm. (2.9 in.), as compared with the mean length of all the fish examined, which was 9.9 cm. (3.9 in.). The mean lengths of fish containing bottom-living crustaceans and insects were 9.8 cm. and 10 cm. Brofeldt (1922) listed chironomid and sialid larvae, water-lice, small crustaceans, *Tubifex* (a small worm) and *Clepsine* (a small leech) as foods of 26 winter-caught ruffe, and noted a change from planktonic to bottom-living food with increasing size. Dobers (1922) recorded insects and crustaceans, with chironomid larvae dominant, as food of the ruffe. Stadel (1936), who examined 201 fish from the Elbe, found that ruffe under 8 cm. (3.1 in.) ate copepods, and those of a larger size freshwater shrimps: there was a correlation between the occurrence of different types of crustaceans and their seasons of maximum abundance. Stadel found that some leeches were eaten, and that molluscs were common in ruffe of more than 13 cm. (5.1 in.). Brofeldt and Stadel both drew attention to the lack of a winter fast in the ruffe. In confirmation of this, the results of the investigation during 1939 (table XV) gave no evidence of a seasonal decrease in food consumption.

Table XV. Ruffe, 1939: number of fed and empty fish in each period of three months.

Period	I-III	IV-VI	VII-IX	X-XII
Number of Fish containing Food ...	9	13	25	27
Number of Fish empty ...	1	1	—	—

THE STICKLEBACK, *Gasterosteus aculeatus.*

Insects formed 60%, and crustaceans 29%, of the food of the stickleback (fig. 1 and table II). A few small molluscs, and some plants and diatoms were also eaten. 80% of the recognizable insects were aquatic dipteran larvae, and 16% were ephemeropteran larvae. 80% of the occurrences of crustaceans were of copepods; other planktonic forms, *Chydorus* sp. and ostracods, made up another 18%. Crustaceans seemed to be most important as foods in the winter months; in the period January to March crustaceans were found more frequently than insects, but the latter group occurred in more fish during the rest of the year (table XVI). There was no winter fast.

Table XVI. Stickleback, 1939: number of fish containing insects and crustaceans in each period of three months.

Period	I-III	IV-VI	VII-IX	X-XII
Insects	31	38	6	28
Crustaceans	34	4	1	11

OTHER SPECIES OF FISH.

A few fish belonging to six other species were examined. The numbers were far too small to allow any deductions to be made about the usual feeding habits; but the results obtained are summarized in table XVII for comparison with the foods of other species.

Table XVII. Summary of data about other species of fish.

Species	Locality	No. Examd.	Composition of Diet No. of Occurrences	Remarks
SMELT *Osmerus erpelanus* ..	Ranworth Little Broad, Norfolk ..	1	Crustaceans .. 1	Copepods
MINNOW *Phoxinus phoxinus* ..	R. Cam, Barrington, Cambs.	16	Insects .. .. 9 Crustaceans .. 4 Plants + Algae .. 7 Diatoms 2	
	R. Granta, Ickleton, Cambs.	3		
BLEAK *Alburnus lucidus* ..	Old West River Cambs.	8	Insects .. 5 Plants + Algae .. 3	
LOACH *Nemachilus barbatula*	R. Cam, Barrington ..	11	Insects .. .. 8 Crustaceans .. 4	Dipteran larvae + planktonic crustaceans
BULLHEAD *Cottus gobio* ..	R. Cam, Barrington Grantham Canal, Cotgrave, Notts. ..	11 1	Insects .. .. 9 Crustaceans .. 4	A very mixed diet, including benthotic crustaceans
FLOUNDER *Pleuronectes flesus* ..	Ranworth Little Broad, Norfolk ..	2	Fish .. .. 2 Insects .. .. 1 Crustaceans .. 1	One fish, 18.5 cm. long, contained two roach, each 3.5 cm. long

DISCUSSION.

The study of the food of coarse fishes in English waters has shown that it is difficult to assign a clearly defined ecological niche to each species. Even the pike, the predatory fish *par excellence* of fresh water, has been shown by Balfour-Browne (1906) to feed upon small crustaceans when young, and so to change the part it plays in the fish community as it grows bigger. The perch shows a similar change in the constitution of a purely animal dietary, and the ruffe also appears to be a carnivore, altering its food but once when it changes from planktonic to bottom-living foods. With these exceptions freshwater fishes show diets so varied that it is almost impossible to assign to any one species a type of food necessary for its existence, or a feeding habit which marks it off clearly from the other members of the community. It has been found that in most localities the roach is predominantly herbivorous in habit, yet there is evidence from the composition of the diet of 68 roach from the upper reaches of the River Cam—molluscs 32%, insects 30%, crustaceans 5%, plants and algae 32%, diatoms 1%—that the species can exist, and indeed thrive, upon an animal diet. Again 69% of the occurrences of food organisms in 48 rudd from a pond in Cambridgeshire were of insects, while 77% of the food of 59 rudd from the Norfolk Broads was of vegetable origin.

In the summaries of the feeding habits of each species it will be seen that a few food organisms—chironomid larvae, freshwater shrimps, copepods and the cladocerans *Chydorus* and *Bosmina*—occur repeatedly and that they are highly important foods of the fish which eat them. These inter-specific similarities suggest that the distinction between the diet of one species and another lies rather in the proportions in which the most numerously occurring food stuffs are eaten rather than in the exploitation of totally different sources of supply. In writing of the feeding habits of the animals living in one community it is difficult to avoid the use of the word " competition." In many cases there may be true competition between two or more species for a food organism which is not available in numbers sufficient to supply the entire needs of all predators upon it. But at times the word cannot legitimately be employed. In the upper reaches of the Cam, for example, great masses of filamentous algae float down the river during the late summer, and are stranded along the banks and upon shoals: it is not to be believed that in the presence of so vast a supply there is an active competition between the roach and dace which eat algal food. In the following paragraphs, therefore, the phrase " to compete with " means no more than " to exploit the same source of supply " expressing no opinion on the adequacy or inadequacy of the provision.

It will, of course, be realized that all the species of fish mentioned in this paper are not living together in a single community, so the nature of the " competition " will vary from place to place. In the upper reaches of the Cam, for example, roach share the available plant foods with dace, the insects with dace, gudgeon and brown trout, the diatoms with minnows and the planktonic crustaceans with sticklebacks. In the Norfolk Broads roach find themselves in competition with bream for copepods and cladocerans, with ruffe and perch for insects and with rudd for plants. At some stages in its life history a species may have no competitors at all. In all cases the nature of the intra-communal competition must change with the varying success of the year classes of the different rivals. These

annual variations, working with the changes in feeding habits which accompany changes in size, will tend to prevent the establishment of an absolutely stable equilibrium of inter-specific relationships and of intra-specific nutritional conditions.

There is no evidence that freshwater fish communities are so constituted as to contain only one representative of each type of feeding habit. Ruffe live side by side with young perch, and feed upon the same small invertebrates. Eels and brown trout from one river contain the same animal foods, and show the same catholic choice of diet. But the best example of this lack of assortment in fish communities is the case of bream and silver bream. In all localities where silver bream have been caught, bream have been netted also. The two species are so much alike that it is often necessary to count the fin-rays or scales to distinguish them. Their foods have been found to be remarkably similar. Usually there is only a partial community of feeding habits between one " rival " and another, but here two closely related fishes are seen to occupy a single ecological niche.

So the conclusion is reached that there is little that is rigid in the organization of communities of coarse fish, and much that is mutable. There are no assemblies of specialists, each playing a part in a nicely adjusted microcosm, but rather groups of " rivals," each species affecting the habits of those with which it lives, and by them influenced in its own behaviour. Though marked preferences for this or that diet exist, most species have more or less generalized feeding habits, and are enabled to maintain themselves in the face of varying circumstances by flexibility of behaviour rather than by notable efficiency in a single method of existence.

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