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OBSERVATIONS ON THE FISH POPULATION OF ROSTHERNE MERE, CHESHIRE

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Rostherne Mere is a deep natural lake with a steep shore profile. It has extensive reed bed but rather little shallow open water. It is highly productive. The lake was fished with gill nets and funnel traps for 2½ years. The fish population is mainly roach, perch and pike. Curves of length for age, and regressions of weight on length were produced for these three species. Rostherne roach are the fastest growing British population so far described. The growth of perch was also fast but that of pike is rather slow. The representation of year classes in the roach population was very uneven, 75% belonged to the 8+ age group and a further 13% were 4+. This could not be explained by selective sampling.

The analysis of food of roach was only qualitative, but for perch and pike both the occurrence and points methods were used. Perch of more than 6 cm. fed largely on emerging chironomids in spring and early summer, then all age groups switched to cannibalism on their own fry. Pike fed predominantly on perch. The correlation in pike between predator size and prey size was less well marked than in Windermere, but estimations of the relative importance of various size groups of prey showed that although the large pike took many fry, the bulk of their food was derived from a small number of large prey.

Some data on the development of gonads, times of spawning and on sex ratios are also recorded.

Introduction

Rostherne mere, situated between Knutsford and Altrincham, is the largest, deepest, and most northerly of the meres which lie in the Shropshire–Cheshire plain. Its origin is uncertain, but probably results from subsidence following salt solution in the underlying saliferous beds at the time of the retreat of the last ice sheet (Taylor *et al.*, 1963). The chief feeder stream rises 2½ miles to the south-west, passes through Mere mere and falls steeply into the lake. The outflow eventually reaches the Mersey. Beds of *Phragmites* extend round more than half the shoreline, there are smaller beds of *Typha* and *Carex*, and occasional patches of *Nuphar* and *Nymphaea*. Apart from the northern end, where there is a peat bog, the entire shore is composed of fine sand. In summer there is an abundant phytoplankton and zooplankton, but the benthos is present only in the littoral and sublittoral zones (Walsh, 1965). This appears to result from the steep profile of the lake edge (Fig. 1) and the severe deoxygenation of the hypolimnion and the mud bottom in summer. This deoxygenation is at least partly caused by the high organic content of the mud resulting from the faeces of the large flocks of birds which roost there, especially in winter (Brinkhurst and Walsh, 1967).

In the past, interest in the fish fauna was aroused by the presence in Rostherne of the smelt, *Osmerus eperlanus*, but Ellison and Chubb (1968) note that no definite record of the presence of this fish can be accepted after 1922. The work described in this paper was part of a survey of the fish fauna of the mere in which it was intended to examine and measure the growth rates of the principal species and study their feeding habits, reproduction and movements.

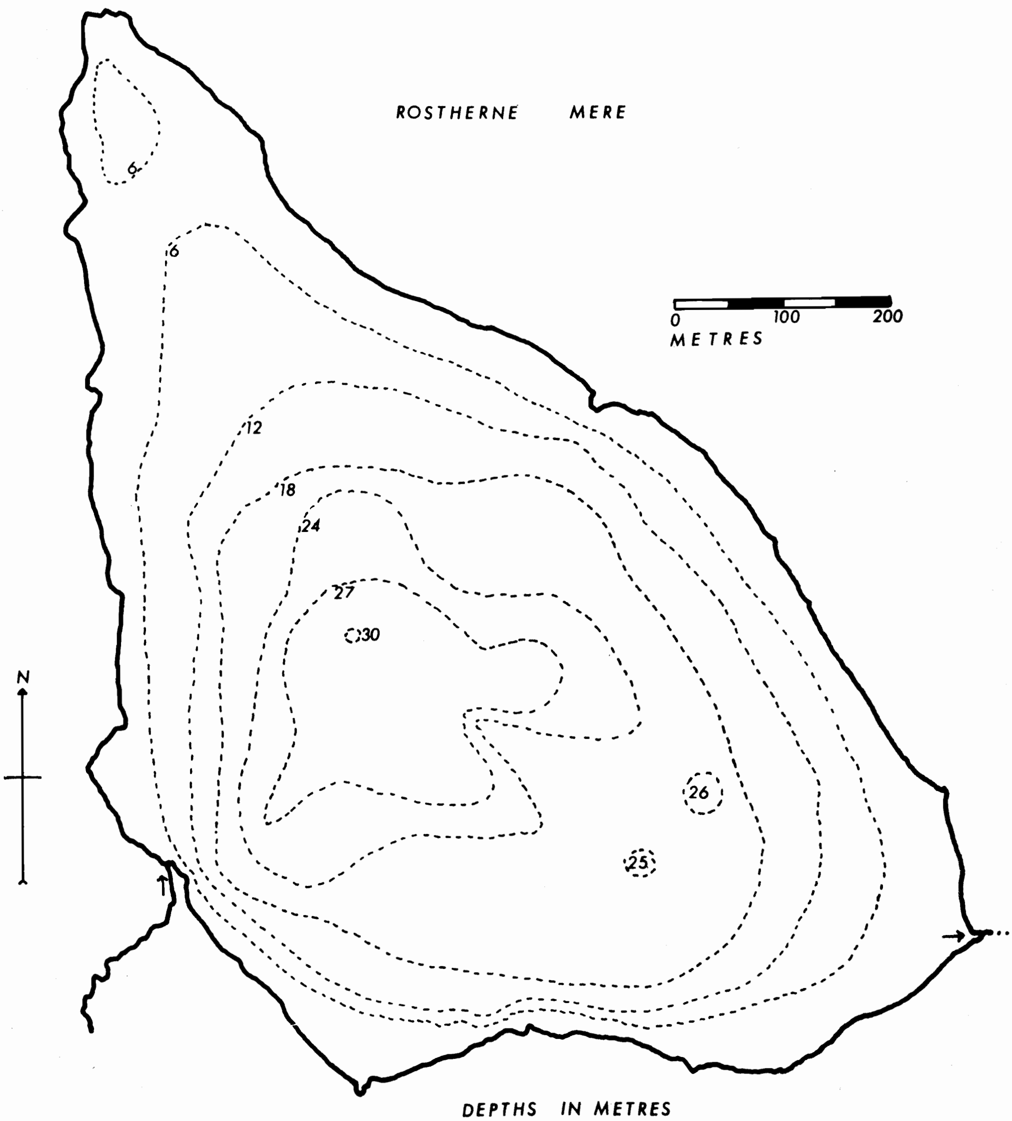

Fig. 1.

Methods

From October 1962 to February 1964 the mere was fished monthly with gill nets of 19·5 mm., 26 mm., 32 mm. and 45 mm. bar mesh. From March 1964 to April 1965 netting was carried out twice a month and additional nettings were made with gill nets of 9 mm., 38 mm. and 64 mm. bar. The majority of the nets were bottom set from the shore to a depth of about 13 m., but the 45 mm. and 38 mm. nets which were primarily intended to catch pike were set at the surface, again mainly near the shore. Some neutral buoyancy nets were set at various depths in the middle of the mere, occasional bottom settings were also made in the middle at 20 to 26 m.

A series of single funnel wire mesh traps were set at depths from 1–16 m., and similar traps were installed in pairs in the inlet and outlet to catch fish moving to and from the streams and the mere.

The nets were set for periods of 24 hours; the catch of each net was examined separately. The weight, fork length, sex and stage of gonad development were recorded, together with the details of capture, subsequently the stomach contents were analysed and the age determined from scales or opercular bones.

Results and discussion

The fish population was found to be predominantly perch *Perca fluviatilis* L., roach *Rutilus rutitus* L. and pike *Esox lucius* L. The catches included three tench, *Tinca tinca* L., a single bronze bream, *Abramis brama* L. three brown trout, *Salmo trutta* L. and two probable roach and bream hybrids. The common loach, *Noemacheilus barbatula* L., the bullhead, *Cottus gobio* L. and the three-spined stickleback, *Gasterosteus aculeatus* L. were common in pike stomachs at certain times of year, and were occasionally taken in the traps at the inlet and outlet. The monthly totals for the three main species are set out in Table 1.

Table. 1. *Monthly total catches of roach, perch and pike in Rostherne Mere*

	1963										1964												1965		
	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	J.	F.	M.
Roach	1	10	88	69	23	52	28	39	10	8	1	4	39	17	38	29	62	60	48	19	19	7	—	3	2
Perch	1	3	118	57	54	46	15	11	5	3	5	5	18	55	241	52	125	84	90	32	9	26	5	4	2
Pike	15	7	19	6	4	1	8	7	6	7	10	4	22	27	15	27	25	24	18	10	4	8	—	—	—

The roach

(a) Age and Growth

The growth of Rostherne roach is shown in Fig. 2. The curves are derived from two kinds of estimate. Mean lengths were calculated from the opercular bones of a sample of 100 fish. The opercular bone of Rostherne roach was extremely easy to read. When viewed by reflected light against a dark background the summer growth appeared light, merging into a dark winter band which ended abruptly with the commencement of the summer growth of the following season. False bands were rare. The innermost winter band was rarely visible, but its presence was checked by reference to the scales, and by a small number of Walford plots (Walford, 1946). The analysis of age was considerably simplified by the fact that 75 per cent of the catch consisted of a single year class with identical growth patterns. The relationship between the length of the opercular bone and the length of the fish was tested by plotting fish length against the projected length of the operculum measured from the centre of the socket to the posterior margin of the bone along a line at right angles to the margin. The points approximated closely to a straight line passing through the origin, although the very uneven size distribution of the sample caused the points to be rather bunched. It was concluded that growth of the roach operculum was probably isometric and that no serious inaccuracies would result from this assumption. From the fourth year the means have also been plotted from the entire catch after correction to eliminate the effects of the unfinished growth of the current season. Because sample numbers each month were small in any but the slowly growing nine year olds it was decided to follow Williams (1967) and assume that 80 per cent of growth took place between June and October and 20 per cent in March and April. The appropriate proportion of the mean annual increment for each age group was then subtracted from the length of each fish to give the corrected length. Monthly totals and mean length of the males and females of each year class are shown in Table 2. The corrected directly observed plots were then checked against the back calculations and found to be in good agreement. The final curve uses back calculations for the first three years and corrected direct observations thereafter. There is a perceptible and increasing difference between the means for males and females from the fourth year, this has also been noted by Cragg-Hine and Jones (1969). Rostherne roach grow faster than any British population yet described, and compare favourably with the majority of known estimates from Europe. A selection of these are given by Williams (1967) and Cragg-Hine and Jones (1969). The weight length relationship of male and female roach were calculated separately using the formula, $\text{Log } W = \text{Log } A + b \text{ Log } L$, where W = weight, L = Length, A = a constant and b is an exponent. The fish used were all caught between June and September to eliminate differences caused by development of gonads. The following values for the regression were obtained.

Males $\text{Log } W = -2{\cdot}35 + 3{\cdot}49 \text{ Log } L$ (53 fish)

Females $\text{Log } W = -2{\cdot}32 + 3{\cdot}45 \text{ Log } L$ (52 fish)

The difference between the sexes is not significant.

(*b*) *Population structure*

The catch contained 14 year classes, but nearly 75 per cent of the entire catch came from the 1955 year class, and a further 13 per cent from the 1959 year class, (Table 2), similar variations have been recorded for perch by Le Cren (1955). The result cannot be explained by gill net selectivity. The 1955 year class was in the majority in the catches of the 26, 32, 38 and 45 mm. nets, the 1959 year class was taken in 19·5 and 26 mm. nets. The intervening year classes accounted for only 8 per cent of the total catch in these nets. The 9 mm. net caught only 4 roach, although it was highly successful in catching small perch, and had been effective in catching roach elsewhere. A small number of roach fry were seen in the autumn of 1963, and a few more were taken from the stomachs of perch at a time when perch fry were a large proportion of the food of older perch. The 1959 and older year classes were all mature in 1963. There is at present no evidence to show how this uneven representation of year classes has arisen. Poor survival of eggs or newly hatched fry in most years appears to be the most likely cause. Poor survival at later stages cannot be entirely ruled out, but as so few young roach were found either in the nets or in the stomachs of predators this seems less likely than a widespread failure to survive the earliest stages of the life history. Lack of spawning can be excluded, as mature roach were very nearly as abundant in the catch as mature perch, all appeared to have spawned by the end of June in each of the years studied.

Table 1 shows that female roach predominated in all year classes except 1955 and the small sample of the 1962 year class. Hartley (1947) showed that in the waters which he examined females were in the majority in roach over 3 years old, and their dominance increased with age. The dominance of males in the 1955 year class

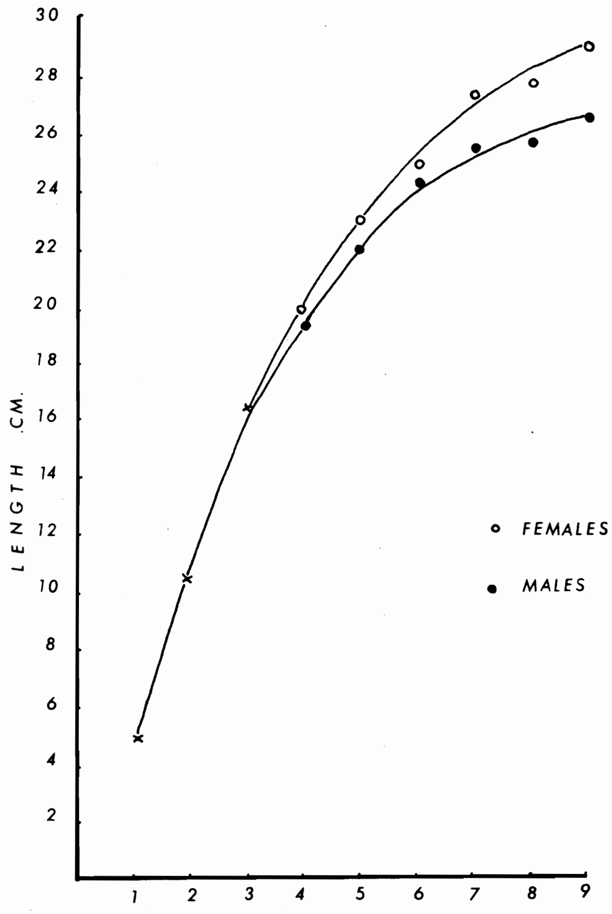

FIG. 2.
Age and growth of roach.

is therefore surprising. A chi-squared test was carried out, making the assumption that the male: female ratio would be expected to be no more than 3 males to 5 females, as in the next large year class in 1959. On this basis the ratio in 1955 is highly significant ($p = <0{\cdot}001$), a further chi-squared test showed that the sex ratio is also just significantly different from a 1:1 ratio ($p = <0{\cdot}05$); no explanation of this anomaly can at present be offered.

(*c*) *Food*

No detailed survey of roach food was undertaken as the habit of grinding the food with the pharyngeal teeth makes the quantitative estimation of different food items almost impossible. Much of the food consisted of Mollusca, with considerable amounts of both macrophytes and algae. *Asellus*, *Gammarus* and Chironomid larvæ were common. Larvae of Trichoptera, *Sialis lutaria* and a large species of *Cyclops* were also seen occasionally. The diet appeared to be typical for the species.

Table 2. *Monthly totals, mean lengths and*
taken from Rostherne

	1962		1961		1960		1959		1958		1957	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
1963												
May							181(2)	173(1)			232(1)	
June							182(3)	175(2)				
July							177(2)	187(1)				
Aug.							203(4)	210(2)				265(1)
Sept.							212(5)	198(2)				
Oct.-March							211(9)	202(8)	216(5)		258(4)	236(2)
1964												
April							213(1)	207(1)				232(1)
May		84(1)		122(1)			216(6)	202(3)				
June			120(1)				220(1)	229(1)		235(1)		
July	81(1)						232(4)	222(4)	242(4)	223(1)		
Aug.		99(1)					241(2)		248(2)		249(1)	245(1)
Sept.							236(4)	222(4)	249(3)		283(1)	
Oct.-March 1965		103(1)			161(1)		246(9)	223(3)	245(1)		268(2)	
%	0·5		0·3		0·2		13		3		2	

Table 3. *Monthly totals, mean lengths and percentage representation*
taken from Rostherne between March 1964 and

	1964	1963		1962		1961		1960		1959	
	Unsexed	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
March and April 1964		51(5)	53(3)	86(16)	85(20)	148(2)	151(2)	194(7)	168(3)		204(1)
May 1964		51(4)		89(7)	88(54)	143(1)	133(2)	200(32)	191(9)	235(5)	231(1)
June 1964				96(6)	94(2)	138(4)		200(25)	185(7)	224(3)	202(1)
July 1964	36(1)	80(3)	80(1)	113(35)	102(23)			205(20)	192(5)	260(3)	
Aug. 1964		84(12)	84(9)	123(29)	118(14)			222(6)	212(1)	260(1)	
Sept. 1964	46(6)	93(3)	97(6)	130(12)	131(6)	188(3)		226(17)	210(7)	252(3)	232(2)
Oct. 1964 to March 1965	42(1)	106(7)	104(7)	139(17)	133(7)	182(4)	181(2)	229(10)	215(3)		
%	1	19		32		3		20		3	

percentage representation of each year class of roach
between May 1963 and March 1965

1956		1955		1954		1953		1952		1951		1950	
Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
	258(1)	272(35)	255(45)										
	241(2)	274(16)	249(45)							305(1)	262(1)	315(2)	
275(1)	262(2)	276(10)	250(1)			310(1)							
	248(2)	278(19)	260(21)	280(1)									
285(1)	250(2)	289(10)	260 (6)							304(1)		307(1)	
284(3)	242(3)	278(19)	261(33)	285(8)		300(1)		286(2)				310(1)	
		286(7)	260(6)	282(1)									
		281(4)	258(22)										
	263(2)	283(2)	258(18)										
281(1)		288(27)	265(20)										
		292(30)	270(20)			287(1)		305(1)		306(1)			
		289(20)	275(16)										
		293(12)	267(23)										
3		75		2		0·4		0·4		0·5		0·5	

of each year class of perch
March 1965.

1958		1957		1956		1955		1954	
Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
248(2)			273(1)	312(20)	255(1)	304(4)			
263(6)	236(2)	282(10)		289(6)	253(1)	286(6)		300(2)	
259(9)	229(2)	270(15)	243(2)	288(8)	282(2)	289(7)	285(1)	296(3)	
268(3)	248(1)	280(12)	257(2)	293(5)	277(1)	305(1)			
280(1)		289(1)	261(2)	281(1)		297(2)	294(2)	304(2)	
260(1)		279(10)	256(3)	272(2)	264(1)	298(5)	276(2)		
255(1)		279(10)		285(3)		276(1)	281(1)	304(1)	
4		9		4		4		1	

(d) Reproduction

In 1964 spawning took place from mid to late June; all fish caught in July were spent. The redevelopment of gonads began towards the end of August, but full size was not attained until May 1965.

The almost complete absence of the younger age groups from the samples makes it difficult to be certain about the ages at which spawning first occurs. All 4 year olds seen were maturing. Of the seven younger fish only one, a 2+ male of 10·3 cm., was certainly maturing.

The perch

(a) Age and growth

The mean annual growth was determined by back calculation from the operculum and by direct measurement of all fish caught between November and April. After correction for allometry the back calculations agreed very closely with the direct measurements; the latter have been used in Fig. 3. The growth of females outstrips the males after the third year, this coincides with maturity for the females, but many

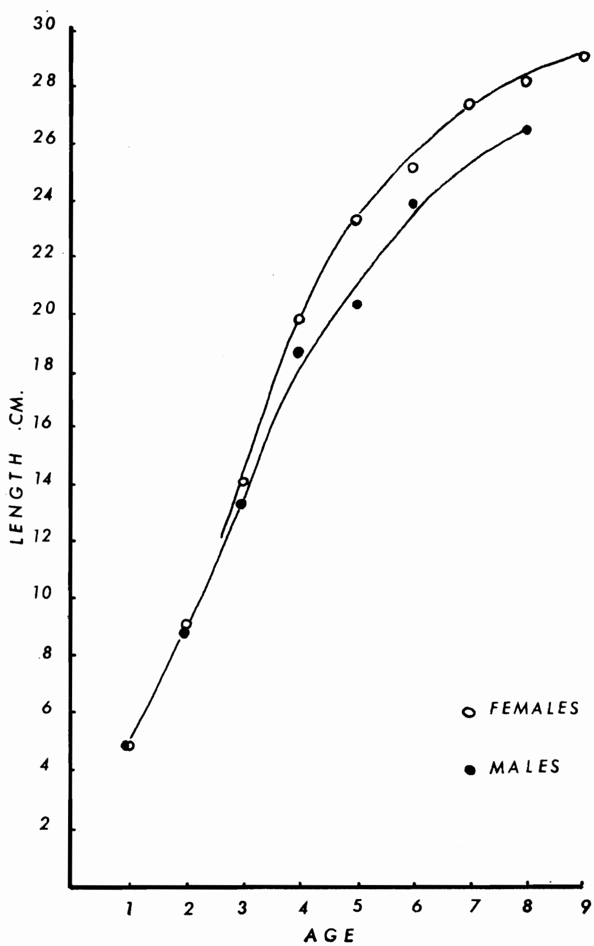

FIG. 3.
Age and growth of perch.

of the males mature at one or two years. The growth of Rostherne perch is fast compared to that in other British waters and compares well with data from continental waters given by Williams (1967). The monthly plots of the mean length of each year class given in Table 3, showed that most of the season's growth in length takes place in June, July and August, but there was also some growth in May and September, particularly in the younger fish.

The weight length relationship was determined from samples of fish caught between June and September. The values obtained for the regression were:

Immature	$\text{Log } W = -2\cdot24+3\cdot34 \text{ Log } L$	(47 fish)
Males	$\text{Log } W = -1\cdot94+3\cdot13 \text{ Log } L$	(54 fish)
Females	$\text{Log } W = -2\cdot00+3\cdot17 \text{ Log } L$	(70 fish)

The regression for the immature fish was significantly different from the adults ($p<0\cdot001$), but there is no difference between the sexes when mature.

Le Cren (1958) showed that in Windermere perch growth in each season was quite closely correlated with the number of "degree days" on which the surface temperature exceeded 14 °C. Although there was insufficient data to attempt such a correlation in Rostherne, plots of mean surface temperature and percentage monthly growth of the 1960 year class showed that in the summer of 1964 the temperature already exceeded 14 °C. in May, while the greatest increase in length took place between July and August. This was the time of maximum water temperature. No year class showed much increase in length before June, when the water had already been at 14 °C. for more than a month. These few observations in Rostherne suggest that the relationship between temperature and growth is different from that in Windermere. This is perhaps not surprising in view of their different situations. The marked increase in length between July and August in Rostherne coincided with a change of diet, while the lack of growth in the early part of the summer is probably a result of spawning.

(*b*) *Population structure.*

At the times of these observations variations in year class strength in Rostherne were less marked than others which have been recorded in the Lake District by Le Cren (1955). Fig. 4 shows the total number of each year class taken in 1963 and 1964 in gill nets of four mesh sizes; 19·5, 26, 32 and 45 mm. Each year class was represented in at least three net sizes. The fishing effort with the three smaller sizes was identical. There was less effort with the 45 mm. net, but data from it have been included because this swells the numbers for the older fish without changing the pattern revealed by the smaller nets. Fig. 4 is therefore no more than a useful indicator of relative abundance for all year classes before 1961. It is clear that 1960, 1957 and probably 1955 were all strong years. The 1962 and 1963 year classes are also well represented in the monthly samples given in Table 3, but they were caught in traps and occasional settings of 9 mm. gill nets, so numbers cannot be compared directly with the other year classes.

Greater fry survival in hot summers has been postulated by Le Cren (1958) to explain synchronous variations in year class strengths in a number of Lake District waters. In Rostherne, however, the 1959 year class was weak, although this was a very hot summer. Neither 1960 nor 1957 were particularly hot. The summer of 1955 was hot, and this was the year of strong year classes of both roach and perch in Rostherne. Alm (1952) suggested that a dominant year class maintained its position

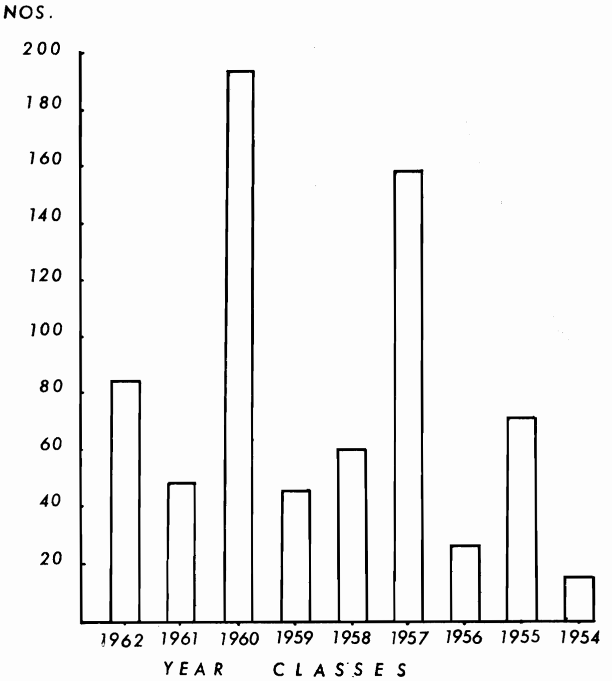

FIG. 4.
Total numbers of perch of each year class taken in 1963 and 1964.

in the waters which he studied by predation on the fry of later years. Although Rostherne perch do prey heavily on their own fry, the presence of three strong year classes does not suggest that predation has materially affected the population structure. The variations in year class strength are less marked than those recorded by Alm and Le Cren, so it seems that the factors controlling these fluctuations act less severely in Rostherne. Both fry survival and predation may play a part but no final explanation is possible.

(*c*) *Food*

A points method of food assessment was used similar to that employed by Hynes (1950). The basis of the method was the allotment of 24 points to a stomach subjectively considered to be full, 12 points to a stomach which was half full, etc. The point allotment was then divided among the food items on the basis of their volume relative to the total food volume. A minimum of one point was allocated to any food item identified. A total of 32 points was allocated to a distended stomach, this category was reserved for examples in which the food filled the stomach and extended back into the oesophagus. For analysis the data were divided into three size groups; from fish from 6·0 to 11·9 cm., from 12·0 to 17·9 cm., and above 17·9 cm. Each stomach was flushed into a petri dish and examined under a low-power binocular microscope. Where fish remains were present they were counted and measured as far as was possible.

Table 4. *A monthly analysis of the food of perch between 6·0 and 11·9 cm. in length. Points are an index of stomach fullness explained in the text*

Month	April		May		June		July		August		September		October		November		Dec.-March	
Total fish	46		46		6		47		33		22		8		3		32	
No. empty	5		11		3		5		5		6		3		3		14	
% empty	11		24		50		11		15		27		38		100		44	
Total points	313		307		31		374		415		156		48		—		171	
Av. points per stomach	7		7		5		8		13		7		6		—		5	
	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%
P. fluviatilis	—	—	—	—	—	—	16	42	19	84	24	15	—	—	—	—	—	—
R. rutilus	—	—	—	—	—	—	8	2	24	6	—	—	—	—	—	—	—	—
Unidentified fish	—	—	—	—	—	—	4	3	5	7	—	—	—	—	—	—	—	—
Diptera pupae	7	21	9	33	1	3	5	9	3	1	—	—	—	—	—	—	—	—
Diptera larvae	9	30	10	32	—	—	6	16	—	—	6	12	—	—	—	—	6	11
Trichoptera larvae ..	6	4	—	—	—	—	—	—	—	—	12	8	—	—	—	—	—	—
Corixa sp.	—	—	—	—	—	—	17	9	—	—	8	10	2	4	—	—	12	14
Sialis lutaria	13	21	18	6	—	—	—	—	—	—	—	—	—	—	—	—	9	16
Dytiscid larvae	9	3	—	—	—	—	8	2	—	—	—	—	—	—	—	—	—	—
Asellus aquaticus	6	8	5	3	—	—	—	—	—	—	14	17	6	13	—	—	9	28
Gammarus pulex	—	—	—	—	—	—	6	3	6	1	—	—	13	33	—	—	14	25
Daphnia sp.	9	6	—	—	15	97	12	16	—	—	11	22	20	41	—	—	—	—
Cyclops sp.	4	8	8	26	—	—	—	—	—	—	7	17	4	8	—	—	6	4
Macrophytes	—	—	1	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	—	—	—	—	—	1	+	6	1	—	—	—	—	—	—	—	—

Table 5. *A monthly analysis of the food of perch between 12·0 cm. and 17·9 cm. in length. Points are an index of stomach fullness explained in the text*

Month	April		May		June		July		August		September		October		November		Dec.-March	
Total fish	8		48		60		35		47		33		9		7		32	
No. Empty	0		3		7		5		5		5		1		1		6	
% Empty	—		6		12		14		11		15		13		14		23	
Total points	84		435		497		308		481		248		79		63		190	
Av. points per stomach	11		9		8		9		10		8		9		9		6	
	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%
P. fluviatilis	20	24	18	16	32	25	23	37	19	85	23	56	—	—	24	38	—	—
Unidentified fish	—	—	8	6	12	5	5	5	—	—	7	29	12	30	—	—	3	2
Diptera pupae	6	7	11	60	7	28	5	3	3	6	2	2	—	—	—	—	—	—
Diptera larvae	11	26	3	1	6	9	6	6	—	—	3	1	4	5	12	59	2	3
Trichoptera larvae	—	—	—	—	3	1	—	—	—	—	1	+	—	—	—	—	—	—
Corixa sp. nymphs	—	—	—	—	3	2	13	8	15	3	—	—	18	23	—	—	6	3
Odonata	—	—	—	—	7	3	—	—	—	—	—	—	—	—	—	—	—	—
Sialis lutaria	9	32	11	8	3	1	8	5	—	—	—	—	10	25	—	—	11	76
Asellus aquaticus	9	11	—	—	8	11	—	—	6	3	3	2	12	15	—	—	4	6
Gammarus pulex	—	—	6	6	12	15	18	6	3	1	6	9	—	—	—	—	8	8
Daphnia sp.	—	—	4	3	—	—	8	29	3	2	1	+	—	—	—	—	—	—
Leptodora kindti	—	—	—	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—
Cyclops sp.	—	—	1	1	1	+	—	—	1	+	3	1	—	—	1	3	1	1
Hirudinea sp.	—		—	—	6	1	—	—	2	+	—	—	—	—	—	—	—	—
Mollusca indet.	—	—	—	—	—	—	3	1	—	—	—	—	—	—	—	—	—	—
Macrophytes	—	—	2	+	—	—	—	—	2	+	—	—	1	1	—	—	1	1
Unidentified	—	—	—	—	7	3	—	—	—	—	—	—	—	—	—	—	—	—

Table 6. *A monthly analysis of the food of perch more than 17·9 cm. in length. Points are an index of stomach fullness explained in the text*

Month	April		May		June		July		August		September		October		November		Dec.-March	
Total fish	22		251		184		166		68		67		41		22		36	
No. Empty	3		24		22		19		11		15		17		3		12	
% Empty	14		10		12		11		16		22		41		14		33	
Total points	234		1,599		1,371		949		640		625		143		131		216	
Av. points per stomach	11		6		8		6		9		9		3		6		6	
	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%	Average points	%
P. fluviatilis	—	—	16	5	17	2	13	66	17	91	15	89	11	72	17	50	20	72
R. rutilus	—	—	—	—	18	1	—	—	—	—	2	+	—	—	—	—	—	—
C. gobio	—	—	4	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified fish	—	—	9	1	4	1	5	9	4	4	4	11	2	8	5	4	7	6
Diptera pupae	11	33	8	61	14	63	2	5	—	—	1	+	—	—	—	—	—	—
Diptera larvae	9	12	5	8	4	4	2	5	1	1	—	—	1	1	2	2	1	1
Trichoptera larvae	—	—	3	1	3	+	1	+	—	—	—	—	—	—	—	—	—	—
Corixa sp. nymphs	—	—	1	+	2	1	2	+	—	—	—	—	1	1	—	—	—	—
Zygoptera nymphs	—	—	—	—	15	2	—	—	—	—	—	—	—	—	—	—	—	—
Sialis lutaria	20	44	4	8	3	2	1	+	1	+	1	+	5	15	4	9	4	14
Dytiscid larvae	—	—	2	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haliplid larvae	—	—	—	—	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Asellus aquaticus	6	12	3	2	6	11	7	4	1	+	1	+	—	—	8	18	3	6
Gammarus pulex	—	—	4	4	7	9	6	1	—	—	—	—	1	1	6	9	3	1
Daphnia sp.	—	—	7	7	3	1	4	4	1	1	—	—	—	—	—	—	—	—
E. lamellatus	—	—	—	—	1	+	—	—	—	—	—	—	—	—	—	—	—	—
Leptodora kindti	—	—	—	—	—	—	3	5	3	3	—	—	—	—	—	—	—	—
Cyclops sp.	—	—	4	2	1	+	1	+	1	+	1	+	1	1	1	2	—	—
Ostracoda	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hirudinea	—	—	1	1	3	1	—	—	—	—	—	—	1	1	3	2	—	—
Pisidium sp.	—	—	—	—	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Gastropoda indet.	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Macrophytes	—	—	1	1	3	+	1	+	—	—	—	—	—	—	5	3	—	—
Unidentified	—	—	—	—	3	1	1	+	6	1	—	—	—	—	—	—	—	—

Hynes (1950) criticizes the points method because of its subjectivity, the investigator may be prejudiced in his allotment of points. This was found to be true in this analysis. Histograms of total points allocated and numbers of stomachs examined showed that in every month the 18 point category was far below what might have been expected from the number in the 12 and 24 point categories. However, Hynes also pointed out that most other methods of analysis are also subjective, and that some give a spurious impression of accuracy. The advantages of the points method lie in its speed and its avoidance of precision which is difficult to achieve or justify on stomachs containing organisms which vary in the rates at which they are digested, and degree to which they can be recognized.

Tables 4, 5 and 6 present an analysis of the food by month and size of perch. The data from December to March have been pooled. The columns headed "average points" show the average for only the stomachs in which the item appeared, not for the total number of stomachs in the month's sample. In other words the figures give an indication of how much of the stomach was taken up by the relevant food item in the fish in which it was found. The column headed "%" gives the percentage of the total points in each month which were allocated to each food item. A + sign indicates that the item made up less than 0·5 per cent of the total points allocated in the month, all other percentages have been rounded to the nearest whole number.

It is clear that from time to time a wide variety of organisms are eaten by Rostherne perch, but most of them are unimportant. The smallest size group had the most variable feeding pattern. Cannibalism on fry is important in July, reaches a peak in August and then falls away. Dipteran pupae are important during the main time of their emergence in April and May, dipteran larvae are also important then but also occur in other months. *Sialis lutaria* larvae are important from December to April, *Asellus aquaticus* and *Gammarus pulex* are also mainly a winter food. Planktonic crustacea do not seem to be important for this size group, although as in Windermere (Smyly, 1952) they formed the bulk of the diet of the perch below 6·0 cm. No detailed estimates were made of the diet of these smallest perch.

The medium sized perch of 12·0 to 17·9 cm. show cannibalism for a longer time than the smaller group, although for these too it reaches its peak in August. Dipteran pupae are the dominant prey in May, and are important in June. *Sialis* larvae are again important in winter, but *Asellus* and *Gammarus* occur irregularly.

The largest perch of 18·0 cm. and above are notable for their extensive cannibalism which occurred at all times except April, when the sample was small. As in the other groups it reaches a peak in August, but is dominant from July to March. Dipteran pupae are important in April and dominant in May and June. The pattern for *Sialis*, *Asellus* and *Gammarus* is similar to that in the medium sized perch.

Previous investigations into the diet of perch have produced results of two kinds. Although some workers found no change of diet with increasing size of perch, the majority have recorded such changes. Allen (1935) showed that in Windermere, perch of less than 16·5 cm. ate plankton, perch from 11·5 cm. to 19 cm. ate bottom fauna, and that perch of more than 16·5 cm. ate fish. Hartley (1947) reached similar conclusions for perch from East Anglia. Antosiak (1963) found that in some Polish lakes perch began to prey on fish, chiefly perch fry, when 13–15 cm. in length and 4–5 year old. At this size invertebrates were still consumed, but accounted for progressively smaller percentages as the fish grew. In Rostherne, with an increase in size of the perch, fish do become more important as prey, but the seasonal changes in diet are even more marked. The abrupt change to cannibalism from a diet of dipteran pupae which took place in July was extremely striking, especially in the larger fish. Healey (1954) also noted a high incidence of summer cannibalism in Lake Barnagrow.

Healey, and Antosiak (1963), concluded that availability of food was more important than predator size in determining diet. In some of the Irish lakes studied by Healey this resulted in heavy predation on zooplankton even for perch of 25 cm. in length. In Rostherne only the smallest perch eat much zooplankton, and cannibalism is a more important source of food than the littoral or sublittoral invertebrate fauna. This is an accurate reflection of availability since the shallow water fauna is restricted, and high turbidity of the water in summer might make zooplankton feeding difficult. If this were so it could explain the relatively poor growth of Rostherne perch in their first year.

(*d*) *Reproduction*

Spawning in both 1963 and 1964 took place in late April and May. The redevelopment of gonads for the following year commenced in late August and was well advanced by the end of the year. The males matured earlier than the females (Table 7). This shows that although 89 per cent of males first spawned at the end of their second year of life no females of the same year class spawned until the end of their third year, about half at the end of their fourth year, but not all until the end of their sixth year of life. On the other hand the sex ratio, which is approximately 1 male: 2 females for perch in their third year, moves steadily further in the direction of female dominance with increasing age (Table 8). The 1956 year class is possibly aberrant in this respect, although the sample is small.

Table 7. *Percentages of maturing perch in a sample of age groups 1–5*

Age	1+	2+	3+	4+	5+
Males	89(53)	100(14)	100(12)	100(12)	100(9)
Females	0(23)	3(31)	53(36)	91(34)	100(19)

Table 8. *Sex ratios of a sample of perch in different year classes*

Year class	1962	1961	1960	1959	1958	1957	1956	1955
Males : Females	1:1·9	1:3·6	1:3·7	1:5	1:5·2	1:6·4	1:2·5	1:7·5
Sample size	94	23	142	18	31	67	21	34

The pike

(*a*) *Age and Growth*

The ages, average length and length range of each age class of the sample of 241 pike taken from Rostherne are shown in Table 9. A graph of mean length for age is given in Fig. 5.

Table 9. *Average length, length range and age of a sample of 241 pike taken from Rostherne in 1963–1964*

Age	MALES			FEMALES		
	Av. Length	Numbers	Length Range	Av. Length	Numbers	Length Range
0+	220 mm.	4	179–258 mm.	149 mm.	3	120–185 mm.
1+	317 ,,	15	191–396 ,,	329 ,,	13	265–392 ,,
2+	357 ,,	35	281–435 ,,	384 ,,	36	200–565 ,,
3+	437 ,,	10	335–505 ,,	417 ,,	17	346–501 ,,
4+	461 ,,	14	395–532 ,,	492 ,,	12	400–585 ,,
5+	547 ,,	3	531–570 ,,	583 ,,	5	534–634 ,,
6+	570 ,,	6	460–620 ,,	608 ,,	8	530–780 ,,
7+	644 ,,	7	570–750 ,,	656 ,,	14	595–800 ,,
8+	632 ,,	4	570–690 ,,	727 ,,	9	605–805 ,,
9+	660 ,,	2	634–685 ,,	740 ,,	10	670–780 ,,
10+	662 ,,	1	—	819 ,,	4	775–895 ,,
11+	665 ,,	1	—	841 ,,	4	760–895 ,,
12+	765 ,,	1	—	740 ,,	1	—
13+	702 ,,	1	—	890 ,,	1	—

The opercular bones of Rostherne pike were found to be unsuitable for ageing. Many did not have the annual banding pattern seen in specimens from Windermere (Frost and Kipling, 1959). Readings of age had therefore to be made mainly from scales.

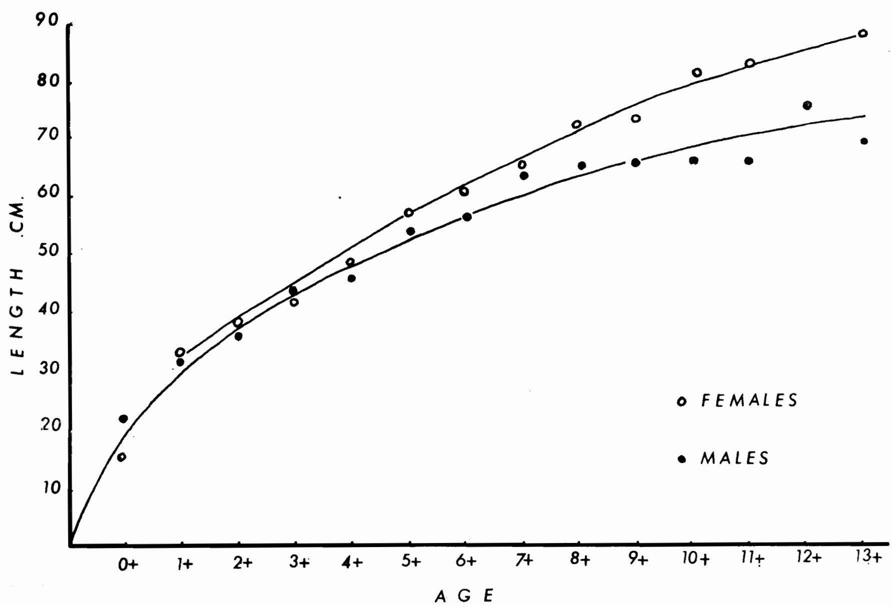

FIG. 5.
Age and growth of pike.

Back calculation from pike scales of length at the ends of previous years is known to be unreliable for Windermere pike (Frost and Kipling, 1959), and a further series of measurements (Banks, 1968) showed it to be unreliable in pike from the fens. It was therefore decided to draw the graph of age and mean length from the direct observations on the length of the fish when caught. Since fish were taken throughout the growing season this leads to some uncertainty about the probable mean length of each age group. In theory these lengths can be corrected to give values for growth in a full year, as for roach, but the variations in growth between fish of the same age were so large (Table 9) that the numbers available in most age classes were too small to make meaningful corrections. Fig. 5 therefore shows uncorrected values in which ages have been designated 0+, 1+, 2+, etc., instead of 1, 2, 3, to underline this difference.

Table 9 and Fig. 5 show that the mean lengths of the females are larger for all ages except 0+ and 3+, but the difference is not significant for any age below 8+. Female pike normally show faster growth from about the third year. It is not clear why this difference does not appear clearly in Rostherne until so much later.

The growth of Rostherne pike is slower than Windermere. This is perhaps surprising in view of the rapid growth of perch and roach, but it may be explained by some comments of Frost and Kipling (1967), who point out that the pike feeds by sight, and will therefore have more hours of good visibility for hunting in seasons of fine weather. They also suggest that limited visibility resulting from turbidity may impede the pike in the capture of its prey. In summer Rostherne is turbid, Secchi disc readings are less than 1 m. during August and September (Walsh, 1965) and visibility may well be poor enough to slow pike growth. Calculations were made of the regression of weight on length of a number of categories of pike, giving the following results.

Immature Log W = $-2 \cdot 52 + 3 \cdot 30$ Log L (45 fish)
Males Log W = $-1 \cdot 88 + 2 \cdot 91$ Log L (21 fish)
(caught July–October)
Males Log W = $-1 \cdot 95 + 2 \cdot 95$ Log L (22 fish)
(caught December–March)
Females Log W = $-2 \cdot 20 + 3 \cdot 08$ Log L (31 fish)
(caught July–October)
Females Log W = $-1 \cdot 91 + 2 \cdot 93$ Log L (48 fish)
(caught December–March)

The regression for immature pike differs significantly from the others. The value for the exponent b is rather surprisingly greater in the immature fish, indicating that length for length they are fatter than the mature ones. The males show no significant difference between winter and summer, but the regression coefficients for the two samples of females differ significantly and apparently show that females become thinner in winter, despite the development of the gonads.

(*b*) *Food*

Species identified from Rostherne pike stomachs are given in Table 10. The seasonal percentage occurrence of various food organisms is given in Fig. 6. This shows that perch are the dominant food throughout the year, and in no quarter did any other fish exceed 8 per cent of occurrences. There is some diversification of feeding in the spring and early summer. There is no evidence of a winter fast, although the percentage of empty stomachs is slightly higher in the autumn and winter quarters.

Table 10. *Organisms identified in a sample of 241 pike stomachs*

Annelida	Hirudinea:	*Erpobdella octoculata*
Arthropoda	Crustacea:	*Gammarus pulex, Asellus aquaticus*
	Insecta:	Chironomidae, larvae and pupae.
		Dytiscidae, larvae.
		Limniphelidae, larvae.
		Corixa sp., nymphs.
		Odonata, nymph indet.
Mollusca.	Gastropoda:	Valvata sp.
Chordata.	Pisces:	*Rutilus rutilus* (roach)
		Gasterosteus aculeatus (stickleback)
		Perca fluviatilis (perch)
		Cottus gobio (bullhead)
		Noemacheilus barbatula (stone loach)
		Esox lucius (pike)
	Aves:	Anseridae, indet.

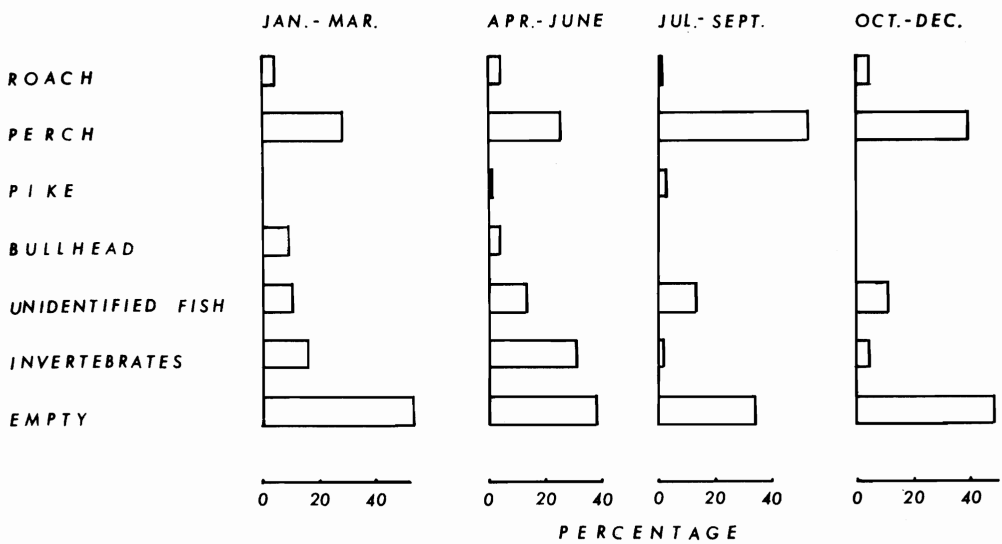

Fig. 6.
Seasonal percentage of the major items in the diet of pike.

The relationship between size of predator and size or type of prey is given in Fig. 7. The percentages have been calculated after subtracting the number of empty stomachs from the total stomachs for the quarter. Five pike between 10 and 19·9 cm. were also caught, but they have been omitted from the Figure, three contained small perch fry, the other two were empty. Predictably, the largest percentage of invertebrate feeding takes place at the lower end of the size range, but no size group had less than about 20 per cent occurrences of invertebrates. The largest prey are found in pike over 60 cm., but it is notable that large numbers of fish of less than 5 cm., mostly perch fry, occur in the majority of pike up to 60 cm. in length. These results are in general agreement with the findings of Healey (1956) in Irish lakes, Willemsen (1965) in Holland and Banks (1968) on the Fens, but contrast with Windermere where Frost (1954) showed a more marked correlation between prey and predator size.

Table 11. *Quarterly variations in the relative importance of different sizes of prey to different size groups of pike*

Pike Size	Prey Size: Under 5 cm. Quarterly weights					5–9·9 cm. Quarterly weights					Over 15 cm. Quarterly weights				
	1st	2nd	3rd	4th	Total Weight (grams)	1st	2nd	3rd	4th	Total Weight (grams)	1st	2nd	3rd	4th	Total Weight (grams)
10–19·9 cm.	—	—	2	1	3	—	—	—	—	—	—	—	—	—	—
20–29·9 cm.	2	8	2	1	13	—	21	—	—	—	—	—	—	—	—
30–39·9 cm.	20	—	96	7	123	35	84	14	133	266	—	—	—	—	—
40–49·9 cm.	26	1	84	22	133	140	77	28	—	245	—	—	200	—	200
50–59·9 cm.	—	16	6	3	25	—	7	7	—	14	—	200	200	—	400
Over 60 cm.	—	—	2	73	75	21	—	21	35	77	—	2,600	—	600	3,200

The presentation of stomach analysis data by means of the occurrence method, as in Fig. 6 and 7, tends to over emphasize the importance of small organisms. In order to correct this impression an attempt was made to assess the relative nutritional importance of each size group of prey fish by multiplying an average weight for each size group by the numbers of individual prey identified in the group. Lengths or length estimates had been recorded for all fish prey, these were converted to weights from weight for length data obtained from fresh perch and roach. The following average weights were used.

Prey size.	Less than 5 cm.	5–9·9 cm.	over 15 cm.
Weight.	1 g.	7 g.	200 g.

No prey of between 10 and 14·9 cm. were recorded. Fish of this size were rare in the lake at the time of this work. The result of this analysis is given in Table 11. This shows that in spite of the large numbers of small fish eaten by all size groups of pike, their total weight is relatively small in the diet of any pike group which can swallow

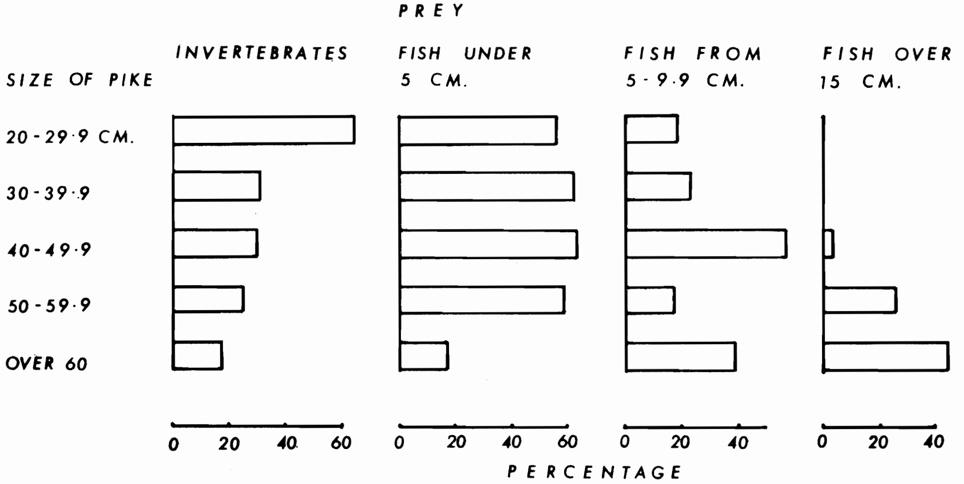

Fig. 7.
Size of pike and percentages of invertebrates and size groups of fish eaten.

larger prey. Frost (1954) concluded that in Windermere external factors such as relative abundance and seasonal availability determine the species of fish prey, but the size of individuals of the fish species eaten is also influenced by the size of pike. For Rostherne it is necessary to add that the size of pike sets only an upper limit to the size of fish eaten, and although the stomachs of big pike may contain many small fish, a small number of large fish provide the bulk of their nutrition.

(*c*) *Reproduction*

Spawning in 1964 took place in late April and May. The redevelopment of gonads commenced in some fish in August and was universal in September. Some fish of both sexes matured at the end of their second year, the majority by the end of their third year, all fish seen in their fourth year were maturing (Table 12). The sexes were equally represented up to the age of 8, thereafter there is a slight preponderance of females (Table 9).

Table 12. *Numbers of immature and maturing pike in age groups 0+ — 3+*

Age Group	0+	1+	2+	3+
Males:				
Immature	7	4	2	0
Maturing	0	6	9	3
Females:				
Immature	2	3	3	0
Maturing	0	6	15	6

Conclusions

The fish fauna of Rostherne is virtually confined to three species, *Rutilus rutilus* (roach), *Perca fluviatilis* (perch) and *Esox lucius* (pike). Although *Cottus gobio*, *Noemacheilus barbatula* and *Gasterosteus aculeatus* were present they were almost entirely found in the region of the inflowing and outflowing streams. A large, productive lowland lake might well carry substantial stocks of other Cyprinids especially *Tinca tinca* (tench) and *Abramis brama* (bream). *Cyprinus carpio* (carp) and *Scardinius erythrophthalmus* (rudd) are also present in many such waters, where they have thrived after introduction, but there is no evidence that they have ever reached Rostherne. Only three tench and bream were taken in 2½ years of intensive netting, so it may be concluded that these species are rare. The reason is probably the sparseness of the bottom fauna and its confinement to the narrow marginal shelf. The roach can survive in reasonable numbers because it is a more versatile feeder. Many of its food items were more characteristically found among the submerged reed stems and surrounding plant debris than on the true lake bottom. Nevertheless the strange age structure of the roach population indicates that for some reason conditions are not often suitable for spawn or fry survival. The very high growth rate of roach may therefore result from the plentiful food for the existing population. The pressure on food resources will be kept down by the sporadic recruitment to the adult population.

The perch is the commonest species. Its food supply comes from three main sources. The fry feed on zooplankton, fish more than 6 cm. long feed on emerging chironomids in spring and early summer, but switch to feeding on their own fry in late July when these reach a length of about 2·5 cm. Without this cannibalism it is unlikely that the perch population could maintain its high growth rate, as the turbidity of the water may make conditions unsuitable for feeding on zooplankton. Further work is being undertaken to test this.

The pike are also common, with many specimens up to 20 lb. in weight, but in contrast to the roach and perch they are rather slower growing than those of most other waters in Britain for which figures have been published.

The over-all impression gained was that the fish population of the mere was in an equilibrium which few natural events could disturb. Some changes might result if the Mersey became clean enough to allow eels to reach the mere. A large reduction in the bird population, especially the roosting gulls, might reduce the productivity and turbidity. Any attendant changes in the plankton would then alter the availability of food to the fish in several ways. At present the turbidity is probably responsible for inhibiting rooted floating plants in the shallow areas. If such weed beds were ever established, together with attendant deposits of fine mud, then perhaps there would be a suitable environment for a larger population of bottom feeding cyprinids like tench and bream, and perhaps more suitable nursery grounds for young roach. For the foreseeable future the fish population of Rostherne seems likely to remain much as it is today.

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