

SUMMARY

1. An apparatus is described which records instantaneous changes in the absorption spectrum of muscle.

2. By means of this apparatus, it is shown that *yellow ferment* and cytochrome *c* are active during the aerobic contraction phase of a gastrocnemius muscle.

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612.61:597.55 *Salmo*

The male sexual stage in salmon parr
 (*Salmo salar* L. juv.)

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[Plate 1]

INTRODUCTION

It has long been known that ripe males occur among salmon parr, i.e. in young individuals, up to 15 cm. long, which have never left their native river. One of us (G. M. K.) has seen them frequently during the last 28 years on the Wye, Towy and Dee. These males have mostly been regarded as occasional precocious males (Calderwood 1930), and there has been no recognition that the male phase may be normal and functional in the fresh-water life of salmon before they migrate to the sea. Recently knowledge of

these so-called precocious males came to one of us, and in view of the peculiar biology of the salmon it was thought that a male phase might be universal and normal in salmon parr (Orton 1937) and an investigation of the problem was begun.

LITERATURE

A century ago Shaw (1840) in a paper proving that parr were the fry of salmon also noticed that male parr with ripe milt accompanied adult female spawning salmon. He concluded that the young males might be fertilizing the eggs, and showed by an experiment with milt from a young male parr and ova from an adult salmon that successful fertilizations could be made, and that the progeny became parr like the male parent. Unfertilized controls in a stream of pure water gave no fry. Further, he reared the progeny of this cross and from one young ripe male again fertilized successfully ova from an adult female salmon.

Similar experiments were successfully repeated later at Stormontfield by Brown in 1862 and by Sir Gibson Maitland at Howietown in 1880 (Day 1885). Davy in 1854 recorded the occurrence of ripe male parr. In 1885 Day summarized the information available on the breeding of salmon from parents which have never descended to the sea, stating:

“(1) that male parrs and smolts may afford milt competent to fertilize ova, but when from fish of the second season, or up to 32 months old, it is (? always) of insufficient strength for strong and vigorous fry to be raised...

(3) that young male Salmonidae are more matured for breeding purposes than are young females of the same age.”

Day and his contemporary naturalists were at pains to show that salmon reared in ponds and enclosed waters could develop gonads. That discovery fostered the notion that ripe male parr are occasional precocious males. Dahl in 1910 recorded high percentages of ripe males among parr and smolt from the rivers of Norway and Finland, and adds that it is evident that many of these would spawn in the ensuing autumn. In 1913 Carr found that parr in the Wye, examined in May, July and October, showed male gonads varying from an undeveloped state to one almost of maturity. He states, along with McNicoll, that the ripening parr will probably remain in the river to spawn before migration. Among 252 fish he found twice as many males as females, counting individuals with a thread-like gonad (stage I) as males. Meek (1916) states that parr may take part in spawning before proceeding to sea. In 1933 Pentelow and others found two kinds of males among Tees smolts, one with very small, the other with large and well-developed testes, and that the latter migrate earlier in the season.

It is clear from this review of the literature that ripe male salmon parr (*Salmo salar*) have been found in the rivers of England, Scotland, Wales, Norway and Finland, and that many authors have expressed the view that some of the males would spawn in company with adult females in the river. Experiments have shown that such ripe male parr have functional sperm. There is uniformity in the description of all female parr stages—in the rivers—as immature. The problem remaining to be investigated is whether the male phase in salmon parr in fresh water is universal and normal before the fish proceed to the sea.

SEX-CONDITIONS OF SALMON PARR IN THE WELSH DEE IN OCTOBER 1937

By the courtesy of the Dee Fishery Board, the Superintendent and bailiffs, to whom our thanks are gladly tendered, samples of salmon parr were obtained from five localities of the River Dee and its tributaries in October 1937, at the beginning of the spawning season. The samples are random collections taken by rod and line and not selected in any other way. Length and girth measurements were made and age and sex-condition determined (see fig. 1). In recording the sex-condition the usual arbitrary phases for the development of the gonad were adopted, with the modifications and significances shown in Table I. An analysis of the gonad phases is given in Table II. Of the 226 fish examined 94 are ripe or ripening males with gonads all in the phases III to VI, 94 are young females of which 92 are in gonad phase II with ova 180 to 250 μ in diameter, and 38 are of doubtful sex with long tubular gonads of phase I. These proportions are fairly maintained in the separate localities examined, except that from Hirnant brook (No. 5, Table II). This brook was nearly dry save for pools at the time of the capture of the fish and yielded no males. It would appear that the males had left the brook under the conditions prevailing; the sample is however a small one.

The fish are mainly two years old, i.e. two summers, as determined by scale-readings, and include some three years (see Table III).

As 41 % of the sample of the population of parr examined, i.e. mainly two-year-old fish, are males many of which were running and gave active sperm (see Table III), there can remain no doubt that the ripe male phase is normal in parr of *Salmo salar* at an age mainly of two years in the Cheshire Dee. The 38 fish of doubtful sex are in all probability immature males, as they have a long tubular gonad extending along almost the whole length of the abdominal cavity, whereas all the recognizable females have short gonads not reaching to the middle of this cavity. These are mainly two-

year-old individuals and as some ripe males are three years old, it seems probable that a fairly large proportion of males fail to develop the gonad until the third year.

The evidence given by these samples is therefore not sufficient to permit the statement that *all* male salmon parr pass through a functional sex-phase in fresh water, but there is no doubt that the greater proportion, and possibly all, do so.

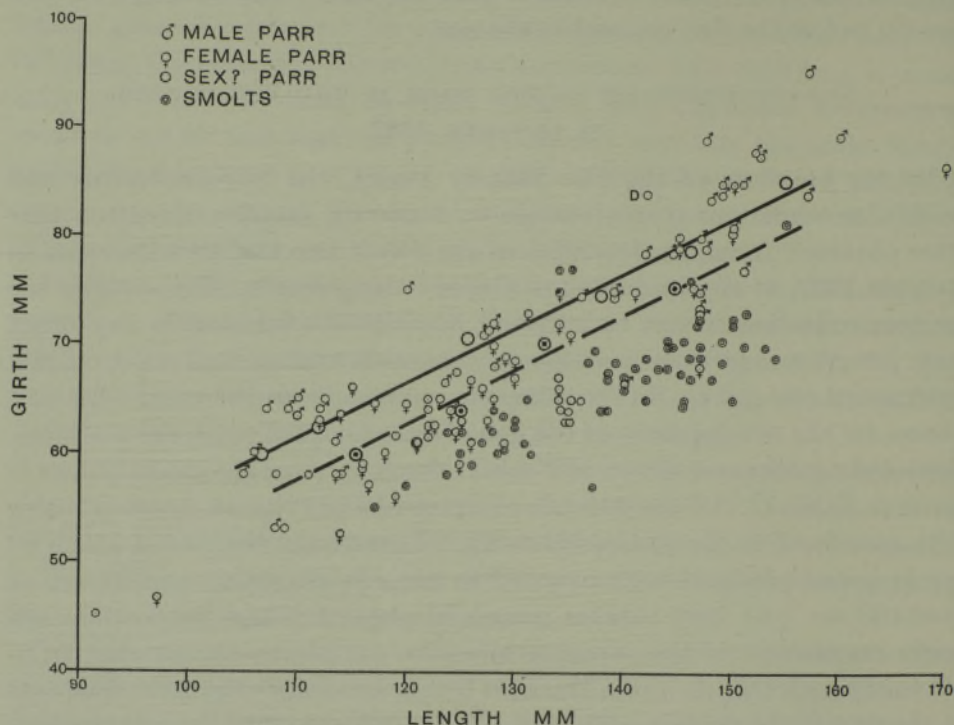


FIG. 1. Distribution of sex and size (= Length/Girth) in 106 salmon parr, *Salmo salar*, from the River Dee, Cheshire, and its tributaries, Hirnant brook, Llandrillo brook and River Ceiriog, October 1937, and size in 69 smolts from the River Dee, May 1937. (See notes on Table VI, p. 113.)

The continuous line gives the average range in size of the males, the discontinuous one that of the females. Length is measured from the tip of the snout to the fork of the tail, and girth immediately in front of the dorsal fin.

The females remain immature in the parr stage, as is reflected in their smaller girth for a given length (see fig. 1). In the sample the largest individuals are mostly males, and it may be that males grow larger than females, but a larger sample of the population is required to obtain satisfactory evidence.

COMPARISON OF SEX-CONDITION IN MATURE PARR AND SMOLTS

As the parr change into smolts which pass down the Dee seawards about May, the condition of the smolts in May will give some clue as to what has happened to the parr in the spawning season.

Fortunately samples of smolts had been collected for the study of their scales in May 1937 and a small sample was available for May 1936. These were examined for sex-condition and size. The size is plotted in fig. 1 and shown in Table V along with that of the parr; the range in length is about

TABLE I. ARBITRARY STAGES IN THE DEVELOPMENT OF THE GONAD IN SALMON PARR, *SALMO SALAR*

Stage 0.	No gonadial tube visible to the naked eye.
Stage I.	Gonadial tube present about 1 mm. wide.
Stage II.	Gonad about 5 mm. wide.
Stage III.	Gonad filling about half the abdominal cavity.
Stage IV.	Gonad filling rather more than half the body cavity.
Stage V.	Gonad full grown, filling the whole of the available space in the abdominal cavity.
Stage VI.	Gonad full grown and ripe gonadial elements oozing to the exterior, that is, the animal is either spawning or ready to spawn.
Stage VII.	Gonad spent.

Notes on Table I

Stage I. A definite visible small gonoduct is present in some individuals extending the length of the body cavity; in some cases this is enlarged and vascular in the anterior half.

Stage II. In the recognizable female salmon parr the gonad is developed anteriorly only with no visible oviduct in the hinder $\frac{3}{4}$ to $\frac{4}{5}$ of the abdominal cavity. No larger stages than II have been seen. In the recognizable male in stage II the gonad extends the whole length of the body cavity.

Stage VII represents the final stage in spawning; intermediate stages of gonads diminishing from full are sometimes recognizable during the spawning season, and their grade size may be noted by that of the corresponding stage.

the same as that of the parr and the girth is shown as rather less, but as the smolts had shrunk from preservation in formalin the girth measurements are unreliable and the length is probably a little less than in the living fish. Nevertheless the smolts are about the same size as the parr, and it is reasonable to conclude that little if any growth occurs after the mature

parr stage, even though the parr were taken in October and the smolt in May of 1937.

TABLE II. DISTRIBUTION OF SEX AND SEX-PHASES IN SAMPLES OF PARR OF *SALMO SALAR*, RIVER DEE (CHESHIRE), OCTOBER 1937

Sample no.	Locality	Sex	Stages of gonad development							Totals		
			0	I	II	III	IV	V	VI	♂	♀	+♀
1	R. Ceiriog 53	♂	—	—	—	5+2	9+5	3+2	?	26	—	—
		♀	—	1	22	—	—	—	—	—	23	—
		+♀	2	2	—	—	—	—	—	—	—	4
2	Llandrillo brook 50	♂	—	—	—	4+3	5+3	5+1	?	21	—	—
		♀	—	—	18	—	—	—	—	—	18	—
		+♀	—	11	—	—	—	—	—	—	—	11
3	R. Dee 50	♂	—	1	—	2+2	4+1	10+1	?	21	—	—
		♀	—	0+1	25	—	—	—	—	—	26	—
		+♀	—	3	—	—	—	—	—	—	—	3
4	R. Alwyn 62	♂	—	—	—	2	8+2	8	6	26	—	—
		♀	—	—	20	—	—	—	—	—	20	—
		+♀	—	16	—	—	—	—	—	—	—	16
5	Hirnant brook 11	♂	—	—	—	—	—	—	—	0	—	—
		♀	—	—	7	—	—	—	—	—	7	—
		+♀	1	3	—	—	—	—	—	—	—	4
Totals												
226		♂	—	1	—	13+7	26+11	26+4	6+?	94	—	—
		♀	—	1+1	92	—	—	—	—	—	94	—
		+♀	3	35	—	—	—	—	—	—	—	38

Notes on Table II

- (1) The sign + indicates gonads larger than the average for the group.
- (2) As the samples were all examined at Liverpool, except one, the total males taken running is not known; the bailiffs reported running males in most samples.
- (3) In sample 5. The high proportion of neuter individuals and absence of males from the Hirnant brook is associated with very low water, the brook being nearly dry; it seems possible that the males may have deserted the drying stream.
- (4) In samples 2 and 4. The relatively high proportion of neuter individuals in these samples is interesting; it is correlated with mature males.

The sex-condition is given in Table IV; 55 out of the sample of 87 smolts were female, 16 were identified as spent males and 16 were of the type regarded as immature males, but none was found with such well-developed testes as the parr showed in October. It is possible that some of the immature gonads were of the spent male type; in the fresh condition it would probably be easier to identify these with certainty.

Although the numbers of apparently spent males are few, they afford a valuable indication that the ripe parr may actually spawn during the winter season. The high proportion of females in two of the samples suggests the possibility that the sexes may migrate separately in shoals. Sampling of shoals would give useful information.

With the help of Fishery Boards it is hoped to examine large numbers of at least post-spawning parr in the winter and smolts in the spring to obtain further information regarding changes in sex-condition during and after the spawning season.

DISCUSSION

The occurrence of a high percentage of ripe male parr at the beginning of the breeding season on the Dee leaves no doubt that the male sexual phase of parr in fresh water is normal and typical in this locality, while the occurrence of numerous ripe or ripening males on the Wye as shown by Carr, in the Norwegian and Finlandian waters by Dahl, and the prevalence of ripe males in other parts of Great Britain, virtually proves that this sex phase is normal and typical for *Salmo salar* throughout its geographical distribution. Sexual maturity is attained in the Cheshire Dee mainly at an age of two years.

Young parr are recorded by many observers as consorting in numbers up to a dozen with adult female salmon in the redd (Shaw *loc. cit.*; King 1930), and the suggestion has been made that they might be there to fertilize the ova. That this is possible can no longer be doubted. The abundance of young male parr in most rivers may be ample to fertilize the eggs of all the adult females, so that the role of the adult male salmon may not be simple. New critical observations on the relations of young male parr and large male salmon to the spawning female may disclose entirely new information regarding their behaviour. The condition of the gonad in smolts is not well known and is apparently generally considered to be undeveloped, (as shown in Table IV) but Dahl (1910) and Pentelow with his co-workers (1933) record the occurrence of males with well-developed testes in their samples. The spawning of the male parr in the rivers in which they are born cannot therefore be regarded as proved. It is hoped, however, to examine in detail large samples of smolts from the Cheshire Dee next year to determine whether the male parr spawned this season.

Early sexual maturity in males in the invertebrata is well known; it occurs in the common rock limpet, *Patella vulgata* (Orton 1928), the Gephyrean, *Bonellia viridis* (Baltzer 1914), the European oyster, *Ostrea*

TABLE III. ANALYSIS OF A SAMPLE OF SALMON PARR, *SALMO SALAR*, FROM THE RIVER ALWYN, CHESHIRE DEE, 22 OCTOBER 1937

No.	Gonad phase	Gonadal elements		Sex	Length in mm.	Age ¹ in years
		Ova	Ripe sperm			
1	III R.l. running ²	—	∞ active	♂	142.5	2
2	IV R.l. ³ running	—	„	♂	lost	
3	IV R.l. running	—	„	♂	149	2
4	I	—	—	—?	125	2
5	I	—	—	—?	123	2
6	I	—	—	—?	115	3
7	IV+ R.l.	—	∞ active	♂	163	2
8	II	∞ 200μ ⁴	—	♀	125	2
9	III	—	∞ not active	♂	127	2
10	V eq. running	—	„	♂	119	2
11	IV R.l.	—	∞ some active	♂	150.5	3
12	V R.l. running	—	„	♂	147	3
13	I	—	—	—?	lost	
14	II	200μ	—	♀	115	2
15	I	—	—	—?	lost	
16	I	—	—	—?	123	2
17	VI L.l. running	—	∞ active	♂	lost	
18	I	—	—	—?	131	2
19	V R.l. running	—	∞ active	♂	112	2
20	I	—	—	—?	112	2
21	I	—	—	—?	114	2
22	II	∞	—	♀	130	2
23	VI R.l. running	—	∞ active	♂	133	3
24	V R.l. running	—	∞ some active	♂	137	3
25	VI sub-eq. running	—	∞ active	♂	114	2
26	I	—	—	—?	107	2
27	II	∞	—	♀	113.5	2
28	V R.l. running	—	∞ active	♂	126	2?
29	IV eq. running	—	„	♂	145	2?
30	II	∞	—	♀	130	3
31	VI R.l. running	—	∞ not active	♂	150	3
32	V R.l. running	—	„	♂	137	3
33	II	∞	—	♀	123	2
34	II	∞	—	♀	114	2
35	II	∞	—	♀	130.5	3
36	II	∞	—	♀	120	2
37	I	—	—	—?	110	2
38	I	—	—	—?	121	2
39	I	—	—	—?	114	2
40	II	∞	—	♀	109.5	2
41	II	∞	—	♀	113	2
42	II	∞	—	♀	97.5	2
43	II	∞	—	♀	117	2
44	II	∞	—	♀	99.5	2
45	IV-V R.l. running	—	∞ not active	♂	116	2

TABLE III (continued)

No.	Gonad phase	Gonadal elements		Sex	Length in mm.	Age ¹ in years
		Ova	Ripe sperm			
46	I	—	—	—?	115	2
47	I	—	—	—?	100	2
48	II	∞	—	♀	107	2
49	II	∞	—	♀	123	2
50	V R.l. running	—	∞ some active	♂	128	3
51	VI L.l. running	—	∞ n.s. ⁵ active	♂	118	2
52	IV L.l. running	—	„	♂	108	2
53	IV eq. running	—	„	♂	97	2
54	II	∞	—	♀	129	2
55	VI eq. running	—	∞ n.s. active	♂	109	2
56	II	∞	—	♀	118	2
57	I	—	—	—?	116.5	2
58	II	∞	—	♀	114	2
59	V eq.	—	∞ n.o.	♂	114	2
60	II	∞	—	♀	91	2
61	IV-V R.l. running	—	∞ n.o.	♂	147.5	3?
62	V eq. running	—	„	♂	108	2

¹ Estimated from scales.

² Individuals extruding milt from the sperm duct.

³ R.l. = right gonad larger; L.l. = left gonad larger. The right is mostly the larger but is occasionally shorter than the left, and sometimes the two are about equal = eq.

⁴ The ova varied in diameter from about 180 to 250 μ in all the samples.

⁵ n.s. = none seen; n.o. = not observed.

Note. The average number of rows of scales from the mid-dorsal line to the lateral line immediately posterior to the adipose fin is 11.3. The average number of pyloric caeca is 56.3, of which 9.4 form a separate proximal group, while that of rays in the dorsal fin is 1 spine + 12.7 branched rays, of which the last two are almost always joined at the base.

edulis (Orton 1921), the American slipper limpet, *Crepidula fornicata* (Orton 1909), and many others.

Among fishes it would seem that in current knowledge the salmon is unique in maturing as a male at a size which is insignificant in comparison to what is usually termed the adult. The phenomenon is comparable with late paedogenesis. This may occur however in other Salmonidae and notably in rainbow trout.

SUMMARY

A high proportion, about 40 %, of the population of two- and three-year-old salmon parr became sexually mature in October 1937 in the River

TABLE IV. SEX-PHASES AND GONAD DEVELOPMENT IN SALMON SMOLTS FROM THE RIVER DEE, CHESHIRE

Sample no.	Date	Sex	Stages of gonad development								Totals		
			0	I	II	III	IV	V	VI	♂	♀	♂	
1	15. iii. 37 (39)	♂	—	7?	—	—	—	—	—	7?	—	—	
		♀	—	—	27	—	—	—	—	—	27	—	
		♂+♀	—	5	—	—	—	—	—	—	—	5	
2	11. v. 37 (30)	♂	—	—	5?	—	—	—	—	5?	—	—	
		♀	—	—	21	—	—	—	—	—	21	—	
		♂+♀	2	2	—	—	—	—	—	—	—	4	
3	6-18. v. 36 (18)	♂	—	—	4?	—	—	—	—	4?	—	—	
		♀	—	—	7	—	—	—	—	—	7	—	
		♂+♀	—	6	1	—	—	—	—	—	—	7	
Totals													
		♂	—	7	9	—	—	—	—	16?	—	—	
	(87)	♀	—	—	55	—	—	—	—	—	55	—	
		♂+♀	2	13	1	—	—	—	—	—	—	16	

TABLE V. SIZE DISTRIBUTION (LENGTH/GIRTH) OF SMOLTS (MAY 1937) AND OF MALE, FEMALE AND NEUTER PARR (OCTOBER 1937) OF *SALMO SALAR*, CHESHIRE DEE

	Average size (Length/Girth) in cm. length-groups									
	90-99.5		100-109.5		110-119.5		120-129.5		130-139.5	
	No.	L./G.	No.	L./G.	No.	L./G.	No.	L./G.	No.	L./G.
Male parr	—	—	5	1.78	5	1.80	6	1.78	3	1.85
Female parr	1	2.09	—	—	10	1.93	16	1.95	7	1.88
Neuter parr	1	2.03	2	1.95	4	1.88	5	1.94	2	2.03
Smolts	—	—	—	—	1	2.13	12	2.07	22	1.97
	140-149.5		150-159.5		160-169.5		170-179.5			
	No.	L./G.	No.	L./G.	No.	L./G.	No.	L./G.		
	No.	L./G.	No.	L./G.	No.	L./G.	No.	L./G.		
Male parr	12	1.85	7	1.79	1	1.79	—	—		
Female parr	5	1.91	2	1.81	—	—	1	1.95		
Neuter parr	1	1.69	—	—	—	—	—	—		
Smolts	26	2.11	8	2.12	—	—	—	—		



FIG. 2. Salmon parr, River Dee, October 1937, showing three males with full development of testes and ripe sperm and one female with normal parr type of ovary. In the uppermost fish the testis is shown on the right side only; in the next below the hinder parts of the testes are shown upon a background of black paper; the third one has testes of equal size; the lowest one is a female, the ovary of which is shown alongside on a black ground. Photograph by P. Bond.

TABLE VI. LENGTH AND SEX-CHARACTERS OF SMOLTS
(*SALMO SALAR*) TAKEN AT CHESTER WEIR, 16 MAY 1936

No.	Length in mm.	Gonad phase	Remarks on gonad	Ova	Sperm	Sex	Remarks on sex
1	130	I	Length of body cavity	—	—	♀	Sex indeter- minate
2	144	II	Less than $\frac{1}{2}$ length of b.c.	∞ 200 μ	—	♀	Young female
3	134	II	Length of b.c., yellow	—	n.s.	♂?	Recovering spent male?
4	114.5	II	Less than $\frac{1}{2}$ length of b.c.	∞ 150 μ	—	♀	Young female
5	131.0	I	Length of b.c.	—	—	♀	Sex indeter- minate
6	149	II	Length of b.c., yellow	—	n.s.	♂?	Recovering spent male?
7	123	II	$\frac{1}{2}$ length of b.c.	∞ 150 μ	—	♀	Young female
8	146	II	Less than $\frac{1}{2}$ length of b.c.	∞ 180 μ	—	♀	„
9	137	II	Length of b.c., white	—	n.s.	♂?	Recovering spent male?
10	141	I	Length of b.c.	—	—	♀	Sex indeter- minate
11	143	II	Less than $\frac{1}{2}$ length of b.c.	∞ 160 μ	—	♀	Young female
12	137	II	Length of b.c., yellow	—	n.s.	♂?	Recovering spent male?
13	110	II	Less than $\frac{1}{2}$ length of b.c.	∞ 100 μ	—	♀	Young female
14	114	I	Length of b.c.	—	—	♀	Sex indeter- minate
15	120	I	Length of b.c.	—	—	♀	„
16	118	II	Less than $\frac{1}{2}$ length of b.c.	∞ 120 μ	—	♀	Young female

Notes on Table VI

The fish were held up at the weir on their way to the sea and were too much shrunken for reliable girth measurements, and lengths are only approximately those in the living fish. The diameter of the largest eggs seen is given and is much less than that of the fresh eggs.

The female gonad is always short and differs from that of the male and the indeterminate gonad in this respect.

Dee, Wales and Cheshire. There is some indication that they may spawn on the immigrating adult female salmon redds before migrating to the sea as smolts. Mature and maturing male parr have been observed, in some cases constituting a large proportion of the population, in other rivers in Great

Britain, Norway and Finland, whence it is highly probable that most or all of the males of *Salmo salar* normally attain their first sexual maturity in the river in which they are reared before migrating to the sea. The phenomenon of early sexual maturity in the salmon is comparable with late paedogenesis.

[*Note added in Proof*, 16 February 1938. A number of experiments in fertilizing adult female salmon ova with milt from male parr were made in November. Some made by adding parr milt to ova *in water* were unsuccessful or only partially successful; others made in the usual way by adding excess of milt to the freshly extruded ova were highly successful, yielding a high percentage of larvae (alevins). The work of Shaw and others is thus confirmed and the maturity of parr sperm proved.]

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