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The breeding and growth of whiting, *Merlangius merlangus* in captivity

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Data are presented on the spawning of whiting in captivity. The females were found to have a high fecundity, each shedding numerous batches of eggs over a spawning period that lasted for many weeks. Batch size tended to diminish throughout the spawning season. Measurements of the diameters and dry weights of eggs collected at different times from the commencement of spawning showed that eggs shed at the beginning of the season were both larger and heavier than those shed later. The possible significance of this phenomenon is discussed. It is shown that spawning imposes a greater physiological strain on females than on males. It was estimated that spawning caused losses in the body weight of females that ranged from 0·03% to 0·40% per day.

Introduction

Although several of the commercially important gadoids breed readily in captivity, few studies have been made of the reproduction of these fish. Those papers that have been published refer mainly to rather specialised aspects of the subject. Thus there are good descriptive accounts of the spawning behaviour of cod, *Gadus morhua* (Brawn, 1961), haddock *Melanogrammus aeglefinus* (Hawkins et al. 1967) and whiting (Hawkins, 1970), based on observations of captive fish, but these papers make only passing references to the more quantitative aspects of reproduction. There is still a need to answer such questions as: how many eggs does a female produce in a spawning season; how long does the spawning season of an individual female last; are there changes in either the quality or the quantity of eggs produced as the spawning season progresses. This paper attempts to answer some of these questions using data obtained from whiting that spawned in the aquarium of the Marine Laboratory, Aberdeen, in 1970, 1972 and 1973.

Materials and methods

The whiting were caught by trawl, Danish seine or handline either in the northern North Sea or the Minch, in November or December. They were allowed to acclimatise in the aquarium for two or three weeks and were then weighed, measured and given an identification mark by fin clipping. The fish were housed in glass-fronted concrete tanks, measuring approximately 1·50 m × 1·50 m × 1·50 m which, until spawning began, received a steady supply of filtered, recirculated sea water. Once spawning had begun, it was important that no eggs were lost from the tank outflows and the circulation was discontinued, the tanks being flushed out rapidly with clean sea water for a short time each day. The water temperature usually ranged from 9°C to 12°C but towards the end of the 1972 observations, essential maintenance work in the aquarium resulted in a steady rise of temperature to a peak of 14·5°C. The tanks were lit from above between about 0730 h and 1700 h and were in darkness for the remainder of the 24 h.

The fish were fed on squid. In 1972 they were allowed to feed *ad libitum* but in 1970 and 1973 weighed rations were administered individually, by hand, to each fish.

When a female liberated eggs they floated to the surface of the water, where they formed a thin layer. They were removed with a hand-held net made from 250 μm plankton netting. The efficiency of egg collection was high, at least 95% of the eggs being taken on most occasions. Sometimes a proportion of the eggs were dead or damaged. These tended to sink to the floor of the tank and were more difficult to recover. The eggs were preserved in formaldehyde solution. In 1972 and 1973 this solution was isotonic with sea water and no shrinkage was detected when fresh eggs were transferred to the preservative.

The eggs were counted with a machine of the type described by Parrish et al. (1960). The accuracy of this counter was tested by conducting a series of replicate counts of a sample containing a known number of eggs. The results were found to be consistent to ± 1% but in 1970 the counts were found to underestimate the true value by 5% and all data obtained in that year were adjusted accordingly.

In 1972 and 1973 the diameters and dry weights of samples of eggs were determined. After the diameters had been measured batches of 250 or 500 eggs were dried to constant weight (48 h at 50°C) and weighed to the nearest 0·1 mg on either a Stanton SM 12 or a Mettler H 31 balance.

Brief descriptions of the experiments conducted in the three years are given below.

1970 observations

At the end of 1969 a number of whiting were being maintained in two tanks for feeding and growth experiments. Early in February, 1970, three fish in one tank began to show spawning activity and between 10 and 21 February, three batches of unfertilised eggs were found in the tank. On 23 February, a male whiting from another tank was introduced and on the same day was observed to mate with two of the

Table 1. Egg production by captive whiting in spring, 1970. (Three females of 35, 42 and 51 cm, 1 male)

Date	Number of eggs (thousands)	Remarks
Feb		
10	56·5	Unfertilised
11		
12		
13		
14		
15	26·5	Unfertilised
16		
17		
18		
19		
20		
21	28·0	Unfertilised
22		
23	202·5*	Male introduced
23	34·5*	(a.m.)
23	26·0*	Unfertilised
24		
25		
26	41·5	
27		
28		
Mar		
1	80·0	
2		
3	75·0	
4	45·5	
5		
6		
7		
8	36·5	
9		
10	102·0	
11		
12	32·0	
13	41·5	
13	80·5	
14		
15	75·5	
16		
17	56·0	
18	4·5	
19	79·0	
19	39·0	
20	26·5*	
21		
22	45·5	
23	25·5	
23	17·0*	
24		
25	19·0	
25	96·0	Unfertilised
26		
27	110·0	
27	24·0	
28		
29	37·0	
30		
31	49·5	
Apr		
1	25·5*	
2	36·5	
3	12·5	
4	22·5	
5	8·0	
6	60·0	
6	13·5	
7	55·0	
8		
9	67·0	
10	25·5	
11	2·0	
12		
13	50·0	
14	7·0*	
15	20·5	
15	2·5*	
16		
17	42·0	
17	58·0	
18		
19	57·0*	Unfertilised
20		
21		
22	62·0	
22	29·5	
23		
24	11·0	
24	10·5	
25		All fish dead
Total	2 334·0	

* Spawning observed

original occupants, while the third shed eggs spontaneously. Thereafter, all but two of the batches of eggs collected from the tank were found to be fertilised. Spawning continued at frequent intervals until 25 April, when all the fish died due to an overnight failure in the aeration system. The numbers of eggs collected from the tank each time they were shed are shown in Table 1. When more than one batch of eggs was found on a particular day, the numbers of eggs in each batch are shown separately.

1972 observations

Early in 1972 six whiting were held in the tank used for the 1970 observations. It was thought that three or four of these fish were female but it transpired later that there were two females and four males. Spawning began on 28/29 February and continued until 7 May. During this period two males died, and the remaining fish were sacrificed on 10 May. The number of eggs collected on each day are shown in Table 2, together with water temperature and the developmental stages of the eggs at the time of their collection.

Table 2. Egg production by captive whiting in spring, 1972 (2 females, 31 cm, and 32 cm, and 4 males). *E.B. = Early blastodisc

Date	Time collected	Number of eggs (thousands)	Stage of development	Temperature (°C)	Remarks
March					
1	1100	1·0	Gastrula	10·0	Most eggs lost
2	–	18·0	?	10·0	
3				10·0	
4	0915	32·0	64 cells	9·9	
5	–			9·8	
6	0930	35·0	?	9·5	
7	0900	21·5	32 cells	9·8	
7	1525	26·5	Uncleaved		Spawning observed
8	1930	14.0	2 cells	10·0	
9	0900	30·0	?	10·2	
10	0915	19·0	2 cells	10·5	
11	0915	17·0	?	10·5	
12	0920	18·0	?	10·5	
12	2000	24·0	?		
13				10·3	
14	0855	23·5	?	10·3	
14	1200	20·0	Uncleaved		
15	0845	24·5	?	10·3	
16	0900	26·0	16 cells	10·4	
17				10·4	
18	0900	44·0	4 cells + E.B.*	10·8	Double spawning
19	0930	21·0	64/128 cells	10·8	
20	0830	19·0	?	10·8	
21	0830	21·5	64/128 cells	10·9	
21	1515	18·5	Uncleaved		
22	1515	19·5	Uncleaved	11·0	
23	0830	16·0	64/128 cells	10·6	
24	0830	12·5	?	10·5	One male dead
25	0930	20·0	?	10·5	
26	1030	12·0	?	10·6	
26	2200	19·5	2 cells		
27				10·5	
28	0845	14·0	Uncleaved	10·5	
28	1445	14·5	2 cells		
29	0900	17·5	32/64 cells	10·5	One male dead
30	0845	20·0	Uncleaved	10·3	
31	0730	12·0	?	10·5	
April					
1	0715	17·0	?	10·6	
	1700	16·0	2 cells		
2	1000	4·5	?	11·0	
3	1000	29·5	?	11·0	
4	0900	22·0	?	11·0	
5	0845	18·0	32/64 cells	10·7	
6	0850	29.0	16 cells + E.B.*	10·7	Double spawning
7	0845	17·0	2 cells	10·9	
8	0930	12·5	E.B.*	11·0	
9	1000	15·5	2/4 cells	11·2	
9	1630	13·0	Uncleaved		
10	0830	17·5	?	11·0	
11	0830	14·0	E.B.*	11·0	
12	0830	11·0	64/128 cells	11·0	
13	0850	16·0	E.B.*	11·0	
13	1640	15·0	Uncleaved		
14	0915	15·5	8 cells	11·1	
15	0820	11·0	64/128 cells	11·3	
16	1030	12·0	E.B.*	11·3	
17	0845	28·0	2 cells + E.B.*	11·4	Double spawning
18	0830	12.0	2 cells	11·3	
19	0850	11·5	E.B.*	11·2	
20	0855	18·5	8 cells + uncleaved	11·2	Double spawning
21				11·4	
22	0935	17·5	2/4 cells + E.B.*	11·5	Double spawning
23	1000	10.0	?	11·5	
24				11·5	
25	0850	13·5	8/16 cells	11·5	
26	0845	11·0	2/4 cells	11·5	
27				12·5	
28	0900	27·5	2/4 cells + E.B.*	13·5	Double spawning
29	1030	3·0	64/128 cells	14·0	
30	1100	10·5	E.B.*	14·0	
May					
1			20% 2 cells +	14·0	
2	0900	14·5	80% infertile	14·0	
3				14·0	
4	0850	3·5	Infertile	14·1	
5				14·2	
6				14·2	
7	0945	2·0	Infertile	14·5	
8				14·3	
9				14·4	
10	Fish killed			14·2	
Total:		1 140.5			

1973 observations

In 1973 an attempt was made to establish three breeding pairs of whiting, in separate tanks. Unfortunately there was high mortality, and observations were restricted to one male and two females, which shared the same tank for most of the experimental period. Spawning began on 9 January and continued until 29 March.

Results

Total egg production (1970 and 1972)

The fecundity of marine fish is usually estimated by counting the numbers of ripening eggs in the ovaries. Messtorff (1959) and Hislop and Hall (1974), have shown that the fecundity of whiting estimated in this way is very high. Aquarium observations on the actual numbers of eggs liberated provide a direct check on these estimations.

In the 1970 experiment the three females shed a total of 2 334 000 eggs. The fish died before the completion of spawning and the numbers of ripening eggs still in their ovaries were estimated, using the volumetric method described by Hislop and Hall (1974). The total number of residual eggs was estimated to be 1 356 000, giving a grand total of 3 690 000 eggs. Hislop and Hall give regression equations which describe the relationship between fecundity and fish length, L, (cm) for northern North Sea whiting. Applying a mean equation $\text{Log } F = 0{\cdot}77 + 3{\cdot}25 \text{ Log } L$ (cm) to the aquarium fish, predicted fecundities were: female A (51 cm): 2 089 000, B (42 cm): 1 107 000, C (35 cm): 673 000. The predicted total fecundity for the three fish was therefore 3 869 000 eggs.

In the 1972 experiment the predicted fecundities were: female C (31 cm) 414 000 and female D (32 cm) 459 000 eggs, giving a predicted combined egg production of 873 000. The observed total number of eggs shed by the fish was approximately 1 140 500. Thus in both years the aquarium observations supported the conclusions of Messtorff (1959) and Hislop and Hall that the fecundity of whiting is high.

Duration of spawning period

Fulton (1891) noted that the ripe ovaries of whiting contained maturing eggs of a very wide range of sizes and concluded that an individual probably had a prolonged spawning season, lasting perhaps from six weeks to two months. The aquarium observations support this conclusion. The group of whiting described by Hawkins (1970) spawned over a period of 90 days. In the present experiments the fish spawned for 69 days (1972), 80 days (1973) and, in 1970 they had been spawning for 74 days before their death. These are probably slight over-estimates of the length of the spawning period of an individual, as they are based upon the dates when the first and last batches of eggs were collected from the tanks and thus apply more properly to the length of the spawning season of the whole group. However, there was no evidence in the experiments that one fish had started to spawn, or had finished spawning many days before the other, or others, in its group.

Number of eggs shed per spawning

The numbers of eggs shed in a single liberation varied greatly. Not only did different females tend to produce different sized batches but the batches shed by each female were very variable. The largest number of eggs shed at one time was just over 200 000 (female A, 1970), but this was probably atypical. It occurred a short time after the male had been introduced and many of the eggs were opaque and mis-shaped. Batch size appeared to be related to the size of the fish. In the 1970 experiment the females were considerably

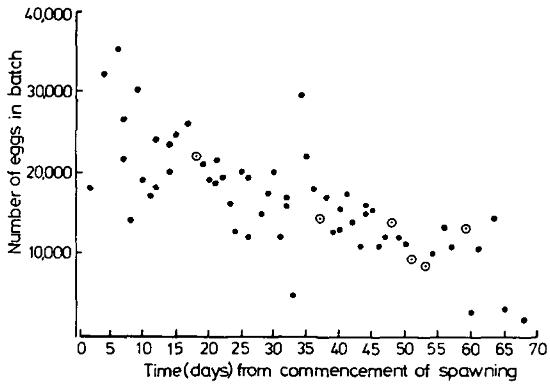

Figure 1. Numbers of eggs in batch related to time (days) from the commencement of spawning, 1972 observations. A double symbol represents spawning by both fish, where half the total egg count has been recorded.

larger than those used in 1972, and the batches tended to be larger. There was a marked tendency for fewer eggs to be shed per liberation as the season progressed. In Figure 1, the numbers of eggs in each batch shed in 1972 have been plotted against the time that had elapsed since the commencement of spawning. At the beginning of the season the fish liberated batches of 20 000 to 30 000 eggs but towards the end the numbers were of the order of 10 000 to 15 000.

Changes in the size and weight of eggs with time

No egg measurements were made in 1970 but in 1972 and 1973 it was decided to find out whether the mean size and dry weight of the eggs varied during the long spawning season. The diameters were measured of samples of 100–150 eggs collected at intervals during the total spawning period, using a calibrated scale mounted in the microscope eyepiece. Dry weights were taken of samples of 250 or 500 eggs from the same batches used for the diameter measurements. Mean diameters and dry weights per 500 eggs are given in Tables 3 and 4, for the two years separately. The mean diameters and dry weights have been plotted against the time (days) from the commencement of spawning in Figures 2 and 3 respectively.

Changes in egg size

Figure 2 shows that in both years there was a tendency for the size of the eggs to decrease as the spawning season progressed. Initially, mean diameters ranged between 1·15–1·22 mm but the end of the season they had decreased to 1·05–1·12 mm. The diameters of the eggs shed in 1973 were, on average, slightly larger than those in 1972.

Table 3. Diameters and dry weights of eggs spawned in 1972

Date	Days from beginning of spawning	t°C	Dry weight (mg) × 500	n	Range of diameters (mm)	Mean diameter (mm)
Mar						
2	2	10·0	20·3	108	1·09–1·28	1·19
4	4	9·9	21·0	121	1·02–1·22	1·16
6	6	9·5	19·7	121	1·02–1·28	1·18
7 (a.m.)	7	9·8	18·3	117	1·02–1·28	1·16
7 (p.m.)	7	9·8	20·9	116	1·02–1·22	1·15
8	8	10·0	18·6	127	1·02–1·22	1·15
9	9	10·2	19·8	124	1·02–1·28	1·17
14 (a.m.)	14	10·3	15·9	107	0·96–1·15	1·09
14 (p.m.)	14	10·3	18·4	100	1·02–1·22	1·14
21	21	10·9	19·0	109	1·02–1.28	1·16
22	22	11·0	16·9	104	0·96–1·22	1·13
Apr						
1 (a.m.)	32	10·6	18·8	113	0·90–1·34	1·16
1 (p.m.)	32	10·6	18·1	103	0·96–1·22	1·11
7	38	10·9	18·0	121	0·96–1·22	1·13
8	39	11·0	15·8	118	0·96–1·28	1·13
14	45	11·1	17·7	118	0·96–1·28	1·11
15	46	11·3	17·5	127	0·96–1·22	1·13
20	51	11·2	15·8	129	0·90–1·15	1·07
22	53	11·5	16·6	117	0·96–1·15	1·09
23	54	11·5	16·6	117	0·90–1·15	1·08
25	56	11·5	17·2	120	0·90–1·22	1·09
26	57	11·5	17·4	106	0·96–1·15	1·09
28	59	13·5	–	115	0·96–1·15	1·05
28	59	13·5	–	128	0·96–1·15	1·08

Table 4. Diameters and dry weights of eggs spawned in 1973

Date	Days from beginning of spawning	t°C	Dry weight (mg) × 500	n	Range of diameters (mm)	Mean diameter (mm)
Jan						
9	0	10·6	22·2	120	0·84–1·32	1·17
14	7	10·5	24·8	105	1·09–1·28	1·19
15	8	10·5	22·6	115	1·05–1·32	1·18
16	9	11·1	24·0	120	1·01–1·28	1·17
20	13	10·8	28·2	100	1·13–1·28	1·23
24	17	10·3	26·2	125	1·09–1·32	1·23
26	19	11·7	28·2	125	1·01–1·28	1·15
26	19	11·7	22·6	110	1·05–1·32	1·21
28	21	11·7	25·2	115	1·05–1·28	1·20
29	22	11·8	25·6	110	1·09–1·32	1·18
30	23	11·9	25·2	110	1·09–1·32	1·19
Feb						
1	25	12·1	27·2	110	1·09–1·32	1·22
20	44	12·5	21·8	105	1·09–1·32	1·18
22	46	11·8	21·4	105	0·92–1·32	1·14
23	47	10·7	23·6	115	1·05–1·28	1·17
24	48	10·8	27·0	110	1·01–1·28	1·16
26	50	10·8	17·0	105	0·97–1·32	1·13
Mar						
8	60	11·3	24·6	100	1·01–1·37	1·15
10	62	11·2	25·6	125	1·05–1·32	1·16
13	65	11·1	23·6	105	1·01–1·28	1·11
18	70	11·7	20·6	105	1·01–1·15	1·09
27	79	13·0	26·0	120	1·01–1·23	1·12
29	81	13·7	22·4	115	1·01–1·32	1·12

Changes in dry weights of eggs

Figure 3 shows that although there was a difference between the egg dry weights in the two years, the 1973 eggs being generally heavier than those spawned in 1972, in both years there was a tendency for dry weights to decline with time. In 1972 the initial weights were about 20 mg/500, falling to roughly 17 mg/500 by the end of spawning. In 1973 the average value during the first three weeks was approximately 25 mg/500 whereas during the last three weeks the mean weight was 23 mg/500.

The dry weights of whiting eggs are considerably less than those of haddock. In 1972 the dry weight of a sample of 500 haddock eggs taken from the aquarium was found to be 38·0 mg.

Discussion of changes in egg "quality"

It has long been known that the sizes of the eggs produced by many marine fish, including whiting, tend to diminish as the spawning season progresses. An explanation that has been put forward to account for this is that the larger females of the species spawn earlier, and shed larger eggs than the smaller ones. Although there is evidence that large female whiting ripen and spawn earlier than the smaller ones (Des-

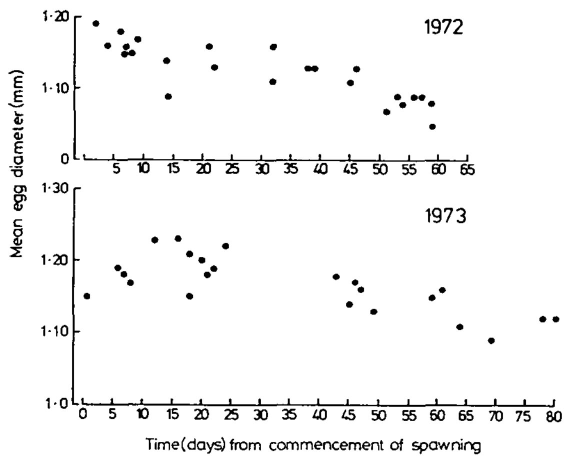

Figure 2. Mean diameters of whiting eggs shed at varying times after the commencement of spawning. 1972 and 1973 observations.

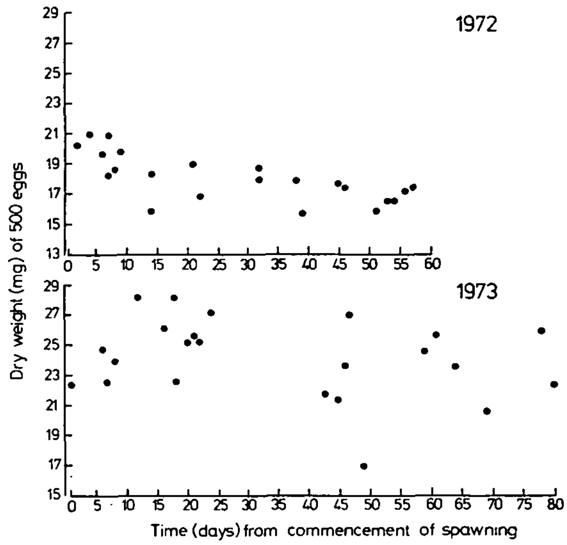

Figure 3. Dry weights of samples of 500 whiting eggs shed at varying times after the commencement of spawning. 1972 and 1973 observations.

brosses, 1945; Bowers 1954), which may partly account for the decrease in eggs sizes throughout the spawning season, the above data demonstrate that the eggs produced by individual females also decline in size with time. Bagenal (1971) reviewed the subject of seasonal changes in the size of marine fish eggs and concluded that they are linked with changes in the availability of larval food. In the northern North Sea, productivity follows a well-defined seasonal cycle (Colebrook and Robinson, 1965). The numbers of larval copepods, the main food of gadoid larvae, are at a relatively low level during the period November–March, increase rapidly in April and May, remain high until September/October and then decline quickly to the winter level. Thus during the period January–May, food organisms suitable for larvae tend to increase in abundance. A species with a spawning season that lasts for several weeks, in this period of the year when the numbers of food organisms for larvae are changing rapidly, is faced with changing conditions for the survival of its larvae. At the beginning, larvae should be less likely to encounter food organisms, by random search methods, than later on when productivity has increased. If larvae produced at the beginning of the season are to have a chance of survival equal to those produced later, when prey species are more abundant, they ought to benefit by being larger. Increased size ought to convey several advantages; the larger larvae ought to have greater searching powers, they ought to be better able to withstand periods of starvation, and they ought to be able to utilise prey over a larger range of sizes than their smaller siblings (Jones and Hall, 1974). Thus from the point of view of larval survival it would seem to be desirable if those fish that spawn early in the season produce larger, heavier eggs or, when the individual has a long spawning season, as with whiting, if each fish sheds large eggs at the beginning rather than at the end of the season.

Feeding and growth during the spawning period

Table 5 gives the initial and final weights and lengths of the experimental fish, together with the changes in length and weight, the initial and final values of the condition factor K ($K = 100 \cdot W \cdot L^{-3}$ where W = weight in g and L = length in cm) and the average daily intake of food over the experimental period.

All the fish for which complete records are available increased in length during the spawning season, although mostly only by a small amount. Changes in total weight were very variable. In the 1970 and 1972 experiments the males grew appreciably heavier (+ 48g, + 26g) but in 1973 the male showed a loss in weight of 27g. Two of the females gained slightly in weight (+ 12g, + 3g) but others experienced losses in weight that were very considerable in some instances (−18g, −36g, −144g, −237g).

The condition factors provide a guide to the physiological state of the fish both before and after spawning. Three measurements were obtained for most of the fish; a pre-spawning and post-spawning value of K (ungutted) and a post spawning value

Table 5. Initial and final measurements of spawning fish in 1970, 1972, and 1973, together with the total and daily changes in length and weight

Year	Fish	Date	L(cm)	W(g)	K (total)	Estimated gonad weight (g)	Date	L(cm)	Total W(g)	Gonad weight (g)	Gutted W(g)	K (total)	K (gutted)	Change in total W (g)	Change in L (cm)	Squid eaten per day (g)
1970	♀A	19 Jan	50·9	1106	0·84	20·0	25 Apr	51·0	869	50·3	648	0·65	0·49	−237	+0·1	11·2
1970	♀B	19 Jan	41·7	593	0·82	15·0	25 Apr	42·2	596	52·2	496	0·79	0·66	+3	+0·5	8·3
1970	♀C	19 Jan	35·2	372	0·85	7·0	25 Apr	36·1	354	18·8	307	0·75	0·65	−18	+0·2	2·6
1972	♀A	1 Feb	31·0	245	0·82	10·0	10 May	32·7	257	6·6	221	0·74	0·63	+12	+1·7	?
1972	♀B	1 Feb	–*	–*	–*	10·0	10 May	31·9	249	7·1	215	0·77	0·66	?	?	?
1973	♀A	12 Dec	–*	742	0·82	5·0	8 Apr	43·6	598	30·5	521	0·72	0·63	−144	?	7·7
1973	♀B	12 Dec	35·3	446	1·01	5·0	17 Apr	35·8	410	48·6	328	0·89	0·71	−36	+0·5	3·1
1970	♂A	19 Jan	33·4	327	0·88	6·0	25 Apr	34·9	375	2·8	331	0·88	0·78	+48	+1·5	4·2
1972	♂A	1 Feb	–*	–*	–*	12·0	10 May	33·4	355	2·2	312	0·95	0·84	?	?	?
1972	♂B	1 Feb	32·7	333	0·95	12·0	10 May	33·8	359	8·8	317	0·93	0·82	+26	+1·1	?
1973	♂A	12 Dec	32·5	304	0·89	3·5	17 Apr	33·0	276	0·5	255	0·77	0·71	−27	+0·5	2·5

* Data not available.

Table 6. Pre- and post-spawning values of the condition factor, K

Type of Measurement	Males Values of K				Mean	Females Values of K							Mean
Prespawning (total weight)	0·88	0·95	0·89	–	0·91	0·84	0·82	0·85	0·82	0·82	1·01	–	0·86
Post-spawning (total weight)	0·88	0·95	0·93	0·77	0·88	0·65	0·79	0·75	0·74	0·77	0·72	0·89	0·76
Post-spawning (gutted weight)	0·78	0·84	0·82	0·71	0·79	0·49	0·66	0·65	0·63	0·66	0·63	0·71	0·63

Table 7. Predicted and observed daily changes in weight of spawning whiting in 1970 and 1972

	Fish	Mean body weight (g)	A Daily food intake (squid) (g)	B Predicted change in weight per day (g)	C Observed change in weight per day[1] (g)	D Weight loss per day attributable to spawning (B-C)	E Total daily weight loss as % of mean body weight
♀A	1970	987	11·2	1·03	−2·84	3·87	0·39
♀B	1970	594	8·3	0·97	−0·36	1·33	0·22
♀C	1970	363	2·6	−0·20	−0·31	0·11	0·03
♂	1970	351	4·2	0·31	+0·54	−0·23	−0·07
♀A	1973	670	7·7	0·66	−1·45	2·11	0·31
♀B	1973	428	3·1	−0·18	−0·64	0·46	0·11
♂	1973	290	2·5	−0·07	−0·20	0·13	0·04

[1] Adjusted so as to exclude the effects of changes in the gonad weights.

based on gutted weights. These values, together with their means, are shown in Table 6, for the two sexes separately.

For both sexes, the mean value of K (ungutted) was lower than the corresponding pre-spawning value. The condition factors of the males were usually higher than those of the females; this was particularly so in the case of the post-spawning values. This suggests that although spawning affected both sexes to a certain extent, the physiological strain imposed on the females was greater than that on the males.

The demands imposed on the fish by spawning can be investigated in another way. The fish continued to feed during the experiments and in 1970 and 1972, the average intake of squid (g per day) by each of the fish was calculated. A considerable number of feeding and growth experiments have been carried out at Aberdeen and from these, Jones (personal communication) has determined that during the non-spawning period the daily gain in weight (ΔG) can be related to daily food intake (ΔF) empirically by the relationship:

$$\Delta G = 0{\cdot}73\,[\Delta FW - 0{\cdot}15 - (0{\cdot}018)\,10^{0.035T}\,W^{0.65}]$$

where: ΔG = g (wet weight) day

ΔF = kcal/day (≡ g squid (wet weight)day)/

T = temperature in °C

As the amount of food ingested by each fish is known, it is possible to apply the equation given above and to calculate the theoretical daily change in weight that would be expected for each fish had spawning not occurred. These data are given in Table 7. The observed daily changes in weight are also given in Table 7. These have been adjusted to exclude the effects of changes in gonad weight during the experimental period. This was done by subtracting the gonad weights from both the initial and final total weights. The weights of the gonads at the beginning of the experiment were estimated from the mean gonad weights of whiting of similar sizes killed at the beginning of each experimental period. By subtracting the observed daily change in weight from that predicted using Jones' equation, an estimate is obtained of the daily change in weight that can be attributed to spawning. All of the females and one of the two males gained less in weight than would have been expected had spawning not taken place. This weight change is expressed as a percentage of the mean body weight of each fish in Table 7. There was a marked tendency for the percentage weight lost by the females to increase with the weight of the fish as shown in Figure 4. For the smaller fish, spawning caused a loss of 0·03% of the body weight per day, rising to about 0·40% /day for the largest female.

The suggestion that reproduction may impose a relatively greater physiological strain on larger fish is not new. Russell (1914) showed that seasonal changes in the gutted weights of haddock, associated with the annual cycle of maturation, spawning and recovery, became progressively greater as the size of fish increased. He suggested that in larger haddock, the gonad probably forms a relatively greater proportion of the total body weight than in smaller fish. Orton (1929) pointed out that if this tendency continued unchecked, reproduction might eventually "overbalance normal metabolism and result in death". At present there is insufficient evidence to tell whether fish do die from this cause or whether contro-mechanisms operate to prevent this from happening.

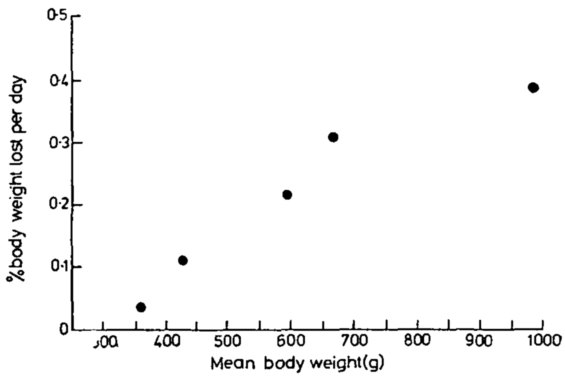

Figure 4. Percentage of body weight lost per day by females due to spawning plotted against mean body weight. 1970 and 1973 observations.

Summary

Observations were made on whiting that spawned in captivity in 1970, 1972, and 1973. The fecundity of the fish was found to be very high, in accordance with predictions based on estimating the numbers of developing eggs in maturing ovaries. The spawning season of an individual female was long, probably lasting for at least ten weeks. During this time each fish shed a large number of batches of eggs, the numbers of eggs per batch tending to decline throughout the season. The mean diameters and dry weights of the eggs also decreased as the spawning season progressed. It was shown that spawning exacted a considerable toll from the fish, and the effect of spawning appeared to be relatively greater for the larger fish.

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