

The fecundity of whiting, *Merlangius merlangus* (L.) in the North Sea, the Minch and at Iceland

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Fecundity estimations were made for whiting from the North Sea, the Minch and Iceland. For the Icelandic fish fecundity was related to length in the manner $\text{Fecundity} = a L^{3.72}$ (cm), for all other samples the relationship was found to be $\text{Fecundity} = a L^{3.25}$ (cm). The coefficient a was found to vary both within and between sea areas but in general fecundity at a given length was highest the southern North Sea, intermediate in the Minch and northern North Sea and lowest at Iceland. When regional differences in growth rates were taken into account it was shown that at a given age Iceland whiting had the highest fecundity and those from the southern North Sea the lowest. No evidence was found to suggest that older fish were more or less fecund than younger ones at the same length over the range of ages examined.

Introduction

A biological parameter, needed for the estimation of the absolute size of a spawning population of fish from total egg production data, is the average fecundity of a representative female in the population. Although fecundity may be defined in a number of ways it is common, when dealing with fish, to estimate fecundity as defined by Bagenal (1968), i.e. "the number of ripening eggs in the female just prior to the next spawning period". This paper presents results of investigations of the fecundity of whiting, *Merlangius merlangus* (L.), in the North Sea and neighbouring areas in the north-east Atlantic.

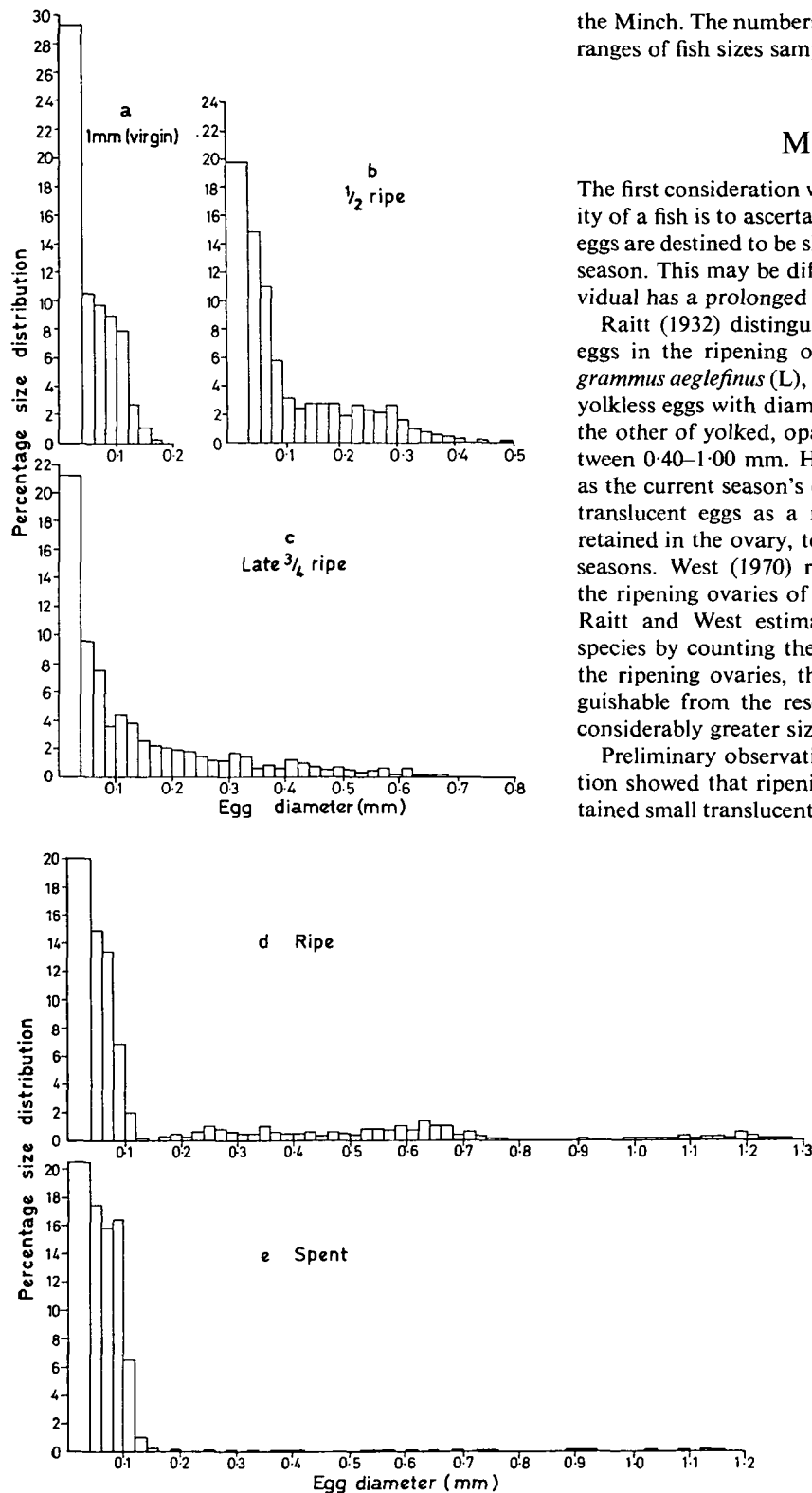
There are few references to the fecundity of whiting in the literature. Fulton (1891), from the examination of a small number of ovaries taken from the Firth of Forth concluded that a whiting produced, on

average, 200 000–300 000 eggs per annum. Hoffmeister (given in Kändler (1958)) estimated the fecundities of 37 pre-spawning whiting from the Baltic, ranging in length from 25–39 cm. His estimates of their fecundity ranged between 108 000 and 221 000 eggs, and he expressed the relation between fecundity and fish length in cm (L) in the form $\text{Fecundity} = 72\,000 + 2.404 L^3$. Messtorff (1959) estimated the fecundity of 37 whiting, ranging in length from 23.5–38.5 cm, from the southern North Sea. He reported fecundities ranging between 120 400 and 1 151 000 eggs, and a relationship between fecundity and length as $\text{Fecundity} = 0.0065 \times L^{5.28}$. He also noted a tendency for older whiting to be more fecund than younger ones at the same length.

In the present investigation fecundity estimates were made for whiting from the northern and southern parts of the North Sea, from Iceland and from

Table 1. Numbers of ovaries examined from each area in each year. The length ranges of the samples (cm) are given in parentheses

Area	1964	1965	1966	Year 1967	1968	1969	1970
N. N. Sea	70 (21–42)	126 (26–50)	30 (25–40)	62 (22–40)	–	82 (22–51)	–
S. N. Sea	–	–	52 (22–41)	52 (23–41)	–	–	–
Minch	–	–	–	–	–	–	51 (25–51)
Iceland	–	–	–	–	12 (43–64)	134 (26–69)	–



the Minch. The numbers of ovaries examined and the ranges of fish sizes sampled are given in Table 1.

Material

The first consideration when determining the fecundity of a fish is to ascertain which of the intra-ovarian eggs are destined to be shed during the next spawning season. This may be difficult, particularly if an individual has a prolonged spawning period.

Raitt (1932) distinguished two distinct groups of eggs in the ripening ovaries of haddock, *Melanogrammus aeglefinus* (L), one consisting of translucent, yolkless eggs with diameters less than 0.10 mm, and the other of yolked, opaque eggs with diameters between 0.40–1.00 mm. He identified the opaque eggs as the current season's crop and regarded the small, translucent eggs as a reserve store that would be retained in the ovary, to be shed in future spawning seasons. West (1970) reported similar findings for the ripening ovaries of cod, *Gadus morhua*, L. Both Raitt and West estimated the fecundity of these species by counting the numbers of opaque eggs in the ripening ovaries, these eggs being easily distinguishable from the reserve eggs by virtue of their considerably greater size.

Preliminary observations in the present investigation showed that ripening whiting ovaries also contained small translucent eggs and larger opaque eggs,

Figure 1. The size distribution of whiting eggs taken from ovaries at successive stages of maturity (material preserved in Gilson's fluid).

but the difference in size between the two groups was much less pronounced than in haddock and cod. In order to determine which eggs represented the current season's crop the approach described by Messtorff (1959) was followed. Samples were taken from ovaries at successive stages of maturity that had been fixed and preserved in modified Gilson's fluid (Simpson, 1951). The diameters of all the eggs in these samples were measured, and their size-frequencies were plotted, as shown in Figure 1. This shows that at all stages of ovarian maturity the greatest proportion of the eggs had diameters of less than 0.10 mm. At successively later stages of maturation the proportion of larger eggs increased, but even when the ovary was $\frac{3}{4}$ ripe (Figure 1c) there was still no marked discontinuity in the size-frequency distribution. It was only when an ovary had reached the "ripe" stage (defined here by the presence of large, mature translucent eggs) that there was a clear size distinction between the smallest ripening eggs of the current season and the largest reserve eggs. The measurements illustrated in Figure 1d showed that at that stage there were in fact three distinct size groups of eggs:

- a) small, translucent eggs, diameters less than 0.12 mm;
- b) maturing, opaque, yolked eggs, diameters 0.16–0.80 mm; and
- c) mature, translucent eggs, diameters 0.90–1.29 mm.

Observations on "spent" ovaries (Figure 1e) showed that virtually all of the remaining eggs were of group (a). It was therefore concluded, that for the estimation of the fecundity of whiting, ovaries that were just "ripe" should be used, and that all eggs with diameters greater than 0.12 mm represented the current season's crop. This size criterion is in close agreement with that given by Messtorff (1959) who counted all eggs larger than 0.11 mm.

As indicated by Raitt (1932), in using fully "ripe" ovaries containing translucent eggs for fecundity estimation, there is a chance that some of the eggs might have been shed already, and the estimated fecundity would therefore be lower than the true value. In view of this any ovaries which extruded mature eggs when they were subjected to pressure were discarded from the analysis, as were ovaries which, when opened, were found to contain large numbers of such eggs. The stage considered most suitable can best be described as "early ripe". Such ovaries were swollen, creamy in colour and very few, if any, translucent eggs could be seen through the ovary wall.

The ovaries were stored in modified Gilson's fluid which broke down the connective tissue and helped

to separate the eggs from one another. All the fish from which ovaries were taken were measured either to the nearest centimetre or to the centimetre below. A sagittal otolith was taken from most of the fish for age determination.

Sampling methods

As whiting ovaries contain a large number of eggs the fecundity was estimated, using sampling methods. Two methods were used, as follows:

Volumetric sampling method

The 1964, 1967 (northern North Sea), 1968, 1969 and 1970 ovaries were sampled volumetrically. The ovaries from each fish were shaken vigorously in their storage jars until the eggs were separate and then they were poured into a large, flat-bottomed glass tray where all large pieces of ovary wall and strands of connective tissue were removed with forceps. The eggs were then placed in a graduated glass cylinder and water was added to make up a suspension of known volume. The suspension was agitated, using a non-rotary action, until the eggs appeared to be distributed uniformly and, while the eggs were still dispersed, a sample of known volume was extracted with a Stempel pipette. This process was repeated several times. The eggs in each sample were counted and the mean value was calculated. The fecundity estimate was made by multiplying the mean value by the factor V/v , where V is the volume of the suspension and v is the sample volume.

Whirling vessel method

This method was used for the 1965, 1966 and 1967 (southern North Sea) samples. The method was similar in principle to that used by Hodder (1964) for estimating haddock fecundity, involving the use of a rotating circular, flat-bottomed perspex vessel, 178 mm in diameter, mounted on a central spindle. The floor of the vessel was divided into ten shallow numbered compartments of equal capacity which were used to obtain 10% samples or subsamples.

For both sampling methods investigations were undertaken to determine the optimum numbers of samples that should be taken from each ovary.

In the first place, replicate samples were taken from the ovaries of several fish, using both sampling methods. The counts were tested, for each fish separately, to determine whether their distributions were of a random (Poisson) type. It was found that in

general the distributions of the sample values obtained by both methods were of the Poisson type and subsequent argument was based on this assumption.

The next consideration was that the numbers of eggs in each sample should be kept fairly small, to minimise counting errors, and it was thought desirable that the number of eggs in a sample should not normally exceed 300. In the case of the volumetric method of sampling this was accomplished by the use of two different suspension volumes. Small ovaries were diluted to 2000 ml, and the large ones to 4000 ml. Sample volumes were between 0.90 and 1.00 ml in both cases. In the case of the whirling vessel method samples of 0.01% were used and the numbers of eggs were always less than 300.

It was necessary to ensure that the fecundities of ovaries containing different numbers of eggs were estimated with equal precision. Knowing that the sample values would normally lie within certain limits, it was possible to determine how many samples should be taken, for ovaries containing different numbers of eggs, to ensure that a particular level of percentage accuracy ($100 \times \text{s.e.}/\text{mean}$) of estimation would be maintained. Table 2 shows, for a range of sample values, the numbers of samples needed to maintain three different levels of percentage accuracy of estimation.

In this investigation it was decided that a percentage accuracy of estimation of 3.75% (corresponding to 95% confidence limits of $\pm 7.5\%$) would be acceptable. The sampling scheme shown in the middle column of Table 2 was therefore used for both sampling methods. In practice, the number of eggs

in the first sample from each fish was taken to represent the mean sample value of that fish.

When both methods were used on the same fish the results were consistent. The use of the whirling vessel was discontinued after a relatively short time, however, because the volumetric method was much faster, allowing 3–4 times as many estimates of fecundity to be made in the same time.

Results

Relationship between fecundity and length

The first stage in the analysis was to draw scatter diagrams of fecundity against length for each sample of ovaries (the two samples from Iceland were combined, as only 12 pairs of ovaries were obtained from this area in 1968). The scatter diagrams indicated that, in general, larger fish had higher fecundities, although there was considerable variation in fecundity at any length and the relationship was obviously non-linear.

A curvilinear relationship between fecundity and length has been demonstrated frequently for many species of fish, and it has been found that the most suitable way of expressing the regression of fecundity on length is by an equation of the type $\text{Fecundity} = a \times L^b$.

The fecundity estimates were therefore transformed into logarithmic form, and regression equations of the type $\log \text{Fecundity} = \log a + b \log \text{Length (cm)}$ were calculated for each sample, where a and b are constants. The use of logarithmic values gave linear relationships and tended to stabilise variance over the whole range of fish sizes.

The individual regressions were then compared to see whether their slopes differed significantly. It was found that a common slope ($b = 3.25 \pm 0.084$) could be fitted to the regressions of the five samples from the northern North Sea, the two samples from the southern North Sea and the sample from the Minch. The slope for the Iceland data was found to have a higher value ($b = 3.72 \pm 0.156$), which differed significantly from that of the other samples at the 5% level of probability.

New regression equations were then calculated for all samples, excluding those from Iceland, this time using the common slope value. The logarithmic values of the intercepts, a , obtained are given in ranked order in Table 3. Significant differences were found between the intercepts, those intercepts that did not differ statistically from one another being shown bracketed together. On the basis of their intercept values the samples fall into three overlapping groups. The Minch sample together with the northern

Table 2. Theoretical numbers of samples required to be taken, for different mean sample values, to maintain three levels of percentage accuracy, when using either volumetric or whirling vessel sampling method

Mean sample value	Numbers of samples required to maintain percentage accuracy at the levels		
	2.5%	3.75%	5.0%
20.....	80	36	20
40.....	40	18	10
60.....	27	12	7
80.....	20	9	5
100.....	16	8	4
125.....	13	6	3
150.....	11	5	3
175.....	9	4	2
200.....	8	4	2
225...	7	3	2
250.....	6	3	2
275.....	5	3	1
300.....	5	2	1

Table 3. Relationship between fecundity and length of fish. Intercepts on logarithmic scale for areas with a common slope ($b = 3.25$) (not adjusted to correct for bias introduced by logarithmic transformation).

Area	Rank	Year	Intercept (a) mean	s.e.	Ratio of each intercept to minimum value
N. N. Sea	1	1969	0.665	±0.126	1.00
Minch	2	1970	0.675		1.02
N. N. Sea	3	1967	0.749	±0.126	1.21
N. N. Sea	4	1966	0.767		1.27
N. N. Sea	5	1964	0.773	±0.122	1.28
N. N. Sea	6	1965	0.789		1.33
S. N. Sea	7	1967	0.811	±0.130	1.41
S. N. Sea	8	1966	0.839		1.49

Table 4. Relationship between fecundity and length of fish. Final regression equations for each sample (adjusted to correct for bias introduced by logarithmic transformation)

Sea area	Year of sampling	Log fecundity = $\log a + b \log L$			
		$\log a$	s.e. $\log a$	a	b
Northern North Sea	1964	0.79	±0.122	6.179	3.25
	1965	0.81	±0.126	6.415	3.25
	1966	0.79	±0.130	6.098	3.25
	1967	0.77	±0.130	5.843	3.25
	1969	0.68	±0.126	4.816	3.25
Southern North Sea	1966	0.86	±0.126	7.190	3.25
	1967	0.83	±0.130	6.784	3.25
Minch	1970	0.69	±0.130	4.933	3.25
Iceland	1968 & 1969	0.18	±0.256	0.662	3.72

North Sea sample taken in 1969 make up a group with the lowest values: the northern North Sea samples for 1964–1967 form an intermediate group and the two samples from the southern North Sea together with the northern North Sea sample for 1965 form the third and highest group. While it would be possible to fit common regression lines to each of the groups it was decided that as the groups contained data from different sea areas this would not be very meaningful. The individual regressions have therefore been presented, fitted with a common slope where appropriate. The last column in Table 3 indicates the fecundity level of each sample relative to the lowest observed value (that of the northern North Sea, 1969, sample).

The final stage in the analysis was to calculate an individual regression equation of the form $\text{Fecundity} = a \text{Length}^b$ (cm) for each sample. These equations, shown in Table 4, were adjusted for bias introduced

by the logarithmic transformation. These equations were used to predict, for selected lengths, the mean fecundities of fish in each sample. These predictions, together with their 95% confidence limits, are given in Table 5. Extrapolated figures are shown in parentheses.

It is of interest that, although there was no statistically significant difference between the estimated fecundities of whiting from the northern and southern parts of the North Sea, the two samples from the southern North Sea were found to have the two highest levels of fecundity at length. The fecundity level of the fish from Iceland differed from those in the North Sea and the Minch; over the range of fish lengths most commonly encountered in near waters (25–45 cm), the Iceland fish had a relatively low level of fecundity but the rate of increase in fecundity with length was more rapid.

Table 5. Predicted number of eggs (thousands), at selected fish lengths, with 95% confidence limits. Extrapolated figures shown in parentheses

Sea area	Year of sampling	Predicted number of eggs (thousands)					
		$L = 25$ cm		$L = 35$ cm		$L = 45$ cm	
		Mean	95% limits	Mean	95% limits	Mean	95% limits
Northern North Sea	1964	219	203–235	653	606–704	(1480)	(1340–1634)
	1965	(227)	(212–243)	678	644–715	1540	1430–1650
	1966	216	193–242	645	582–715	(1460)	(1302–1638)
	1967	207	191–223	618	572–668	(1400)	(1266–1547)
	1969	170	159–182	509	475–546	1153	1049–1268
Southern North Sea	1966	254	233–278	760	702–824	(1722)	(1562–1899)
	1967	240	219–263	717	663–776	(1624)	(1479–1784)
Minch	1970	175	159–191	522	482–565	1181	1075–1298
Iceland	1968 & 1969	(105)	(88–126)	368	336–402	937	884–992

Relationship between fecundity and age

Because older fish are usually larger than younger ones, and there is a positive correlation between fecundity and length, fecundity tends to increase with age. There is also the question whether older fish are more or less fecund than younger ones at the same length.

This was investigated in two ways. In the first the relationships between fecundity and length of fish were compared for a particular year-class at different ages in the northern North Sea. Figure 2 shows the relationship between log fecundity and log length for whiting of the 1961 year-class in this area at 3 and 4 years of age. Figure 3 gives similar data for whiting of the 1962 year-class, at 2, 3, 4, 5 and 7 years of age. It is clear from the figures that, at least for the younger fish (ages 2–5) fecundity is related to length rather than to age.

The second approach involved the examination of a sample from one area, in one year, of fish of a wide range of ages. None of the samples from British waters contained fish of many age groups but the Iceland data were more suitable. Figure 4 shows the relationship between log fecundity and log length for the 1969 sample from Iceland, each age group being identified by a different symbol. These data again suggest that it is the size of a whiting rather than its age, that governs its fecundity. This finding agrees with that of West (1970) for cod but differs from those of Raitt (1932) for haddock and Messtorff (1959) for whiting. The latter authors noted a tendency for older fish to be relatively more fecund at a given length (although Raitt found that in the oldest haddock that he examined there was a tendency for fecundity to decline).

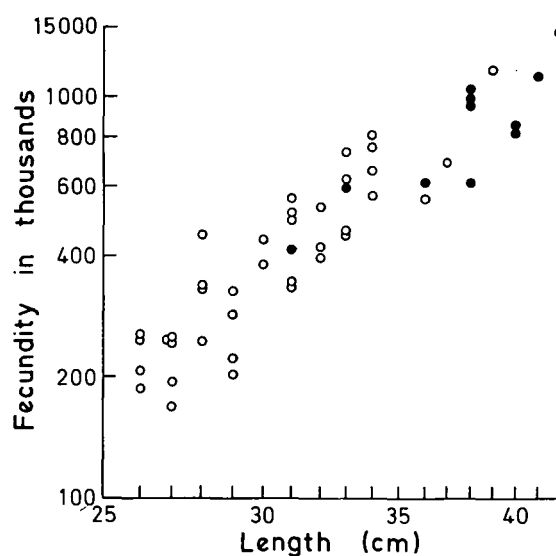


Figure 2. Relationship between log fecundity and log length for whiting of the 1961 year class in the northern North Sea, at different ages. ○, 3 years old; ●, 4 years old.

Regional differences in fecundity at age

When growth rates are taken into account some marked differences in fecundity at age between different areas are evident. Table 6 shows the mean lengths of three and four-year-old whiting, and their estimated fecundities, for fish from Iceland, the northern North Sea and the southern North Sea. The mean lengths of the Iceland whiting are from Saemundsson (1925), and those of the North Sea from Messtorff (1959). The Iceland whiting, by virtue of their rapid growth rate, have the highest

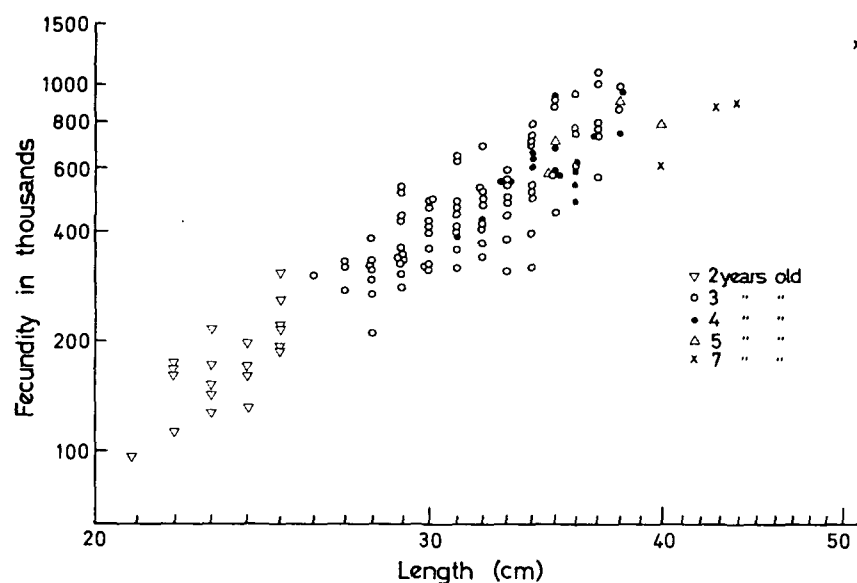


Figure 3. Relationship between log fecundity and log length for whiting of the 1962 year class in the northern North Sea at different ages.

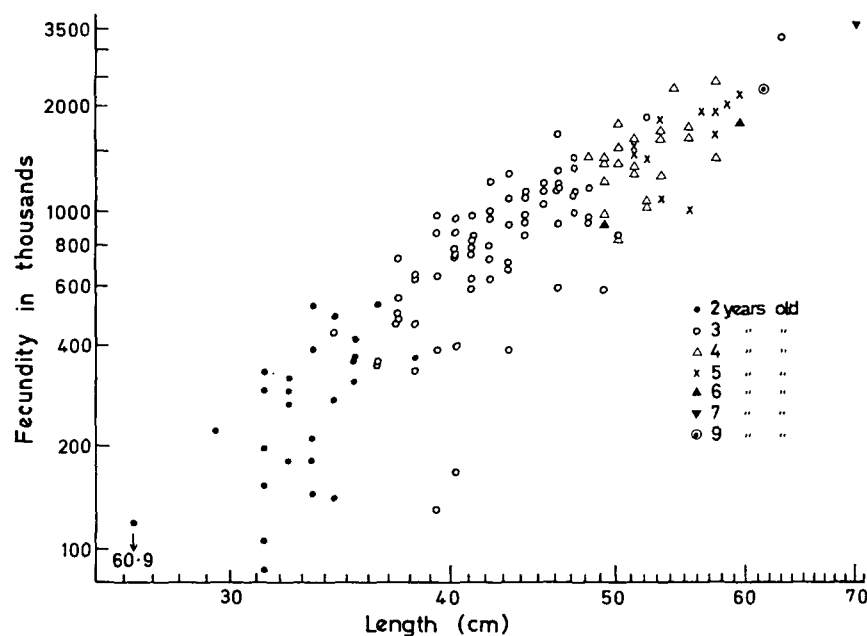


Figure 4. Relationship between log fecundity and log length for whiting of different ages obtained from Icelandic waters in 1969.

fecundity at age and the slow-growing fish of the southern North Sea, although they have the highest fecundity at length, actually have the lowest fecundity at age.

Discussion

The results of this investigation show that the whiting is a very fecund fish, in accordance with Messtorff's (1959) results for southern North Sea whiting. How-

ever, the observed relationship between fecundity and length differs from that obtained by Messtorff. Whereas his results indicated that fecundity increased with length to the power $L^{5.28}$ the present investigation gave values of $L^{3.25}$ and $L^{3.72}$ for whiting in the North Sea and at Iceland respectively. This large difference is probably due to the small number of fish examined by Messtorff over a rather restricted range of fish lengths. In fact, Messtorff's individual estimates of fecundity did not differ greatly from the

Table 6. Estimated fecundities of three and four-year-old whiting from different areas

Area	Age	Mean length (cm)	Estimated fecundity in thousands
Iceland.....	3+	40.2*	613
	4+	47.6*	1115
Northern North Sea	3+	28.1+	301
	4+	31.3+	427
Southern North Sea	3+	25.4+	254
	4+	28.3+	362

* July mean length

+ March/April mean length

present observations at the same lengths. Although the regression equation given by Messtorff may describe his data adequately, it does not give realistic predictions of the fecundities of whiting outside the range of sizes that he examined. For instance, his equation predicts a fecundity of approximately six million eggs for a 50 cm whiting. The highest fecundity found for a fish of this size during the present investigations was 3.1 million eggs.

The high fecundity of whiting, together with the fact that there is such a large range of sizes of maturing eggs in a ripe ovary, suggests that the spawning period of an individual fish may be very long. This has been confirmed by observations on whiting that spawned in captivity in the aquarium at the Marine Laboratory, Aberdeen (Hawkins, 1970; Hislop, unpublished data) during which individual females spawned at regular intervals for ten to fourteen weeks. A prolonged spawning season might be expected to reduce the extent of annual fluctuations in the year class strength of a species as the chances of a large proportion of the spawning products of a population being liberated during a particularly favourable or unfavourable period of environmental conditions should be less than when spawning is restricted to a short period.

Although the fecundity/length relationship of the whiting from Iceland differed significantly from those of the other areas studied, it seems unlikely that the study of fecundity could be used to distinguish be-

tween stocks of whiting in British waters as is possible for herring (e.g. Baxter, 1959). It is of interest, though, that in the two samples from the southern North Sea, the fish were found to be more fecund, at length, than those from the samples from the northern North Sea.

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