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Temporal and Spatial Variation in Fecundity of Atlantic Cod (*Gadus morhua*) in Newfoundland Waters

A. T. Pinhorn
Fisheries Research Branch, Department of Fisheries and Oceans
Northwest Atlantic Fisheries Centre, P. O. Box 5667
St. John's, Newfoundland, Canada A1C 5X1

Abstract

Fecundity of Atlantic cod from inshore bays of Newfoundland and from St. Pierre Bank off the south coast of Newfoundland is described in relation to fish length and age. Fecundity-length relationships are compared to published results for offshore areas. Annual differences were noted within areas in the numbers of eggs produced by length and age but not in the rate of increase in egg production with increase in length or age. Differences were noted among areas in the rate of increase in egg production with increase in length and these are discussed in relation to environmental conditions.

Introduction

For many species of fish, fecundity data are important, in conjunction with egg and larval surveys, for estimating spawning biomass of a given stock. Conversely, if spawning biomass and fecundity by length or age of the fish are known, an estimate of total egg production can be derived and used to calibrate ichthyoplankton sampling gear. Data on fecundity of Atlantic cod are generally scarce, and only two studies are known from Newfoundland waters. May (1967) described the fecundity of cod from offshore Newfoundland waters (NAFO Div. 2J, 3K, 3L, 3N and 3O) in relation to fish length, weight and age, based on 130 ovaries distributed throughout these areas. Postolakii (1967) described the fecundity of cod off central and southern Labrador (Div. 2H and 2J), based on 65 ovaries. Data in the present paper allow comparisons of fecundity of cod from the inshore bays of eastern and southern Newfoundland and St. Pierre Bank (Div. 3L and 3Ps), which were not included in previous studies. Also, data from the same area in more than 1 year allow evaluation of annual variation in cod fecundity.

Materials and Methods

Collection and handling of ovaries

For the reasons outlined by May (1967), collections of materials were made just before and during the spawning season, with only ovaries showing no clear eggs being taken. Areas, dates and sizes of the collections are listed in Table 1. Place names and areas mentioned in the text are shown in Fig. 1.

All ovaries, except those from the St. John's area, were collected at sea aboard research vessels from otter-trawl catches on St. Pierre Bank and from gillnet catches in other areas. The material from the St. John's area was collected onshore from the gillnet catches of inshore boats operating in the area. Otoliths for ageing and fork-length measurements (nearest cm) were obtained from all cod sampled. Procedures for storing the ovaries and cleaning the eggs were identical to those described by May (1967), except that the cleaned eggs were stored in a weak alcohol solution to prevent deterioration of the mirrors in the automatic counting machine from formalin fumes. In all cases, ovaries were stored in Gilson's fluid for periods less than 6 months prior to cleaning.

Sampling and counting

Two methods of estimating fecundity were employed in this study, referred to as the automatic-counting method and the dry-weight method. The

TABLE 1. Numbers of cod ovaries collected for fecundity estimation in eastern and southern Newfoundland waters by area, time of sampling, and range of cod size.

Area	Year	Month of sampling	No. of ovaries	Length range of cod (cm)
Bonavista Bay	1967	May	19	65-109
	1968	May	39	
Trinity Bay	1967	Mar, May	28	60-108
	1968	Apr	50	
St. John's area	1966	Feb	12	61-118
	1968	Mar-Apr	50	
Placentia Bay	1966	Apr-May	96	64-113
St. Pierre Bank	1967	Apr-May	13	51-128
	1968	May	3	
	1969	Mar	43	
	1970	Feb-Mar	45	
Total all areas			398	51-128

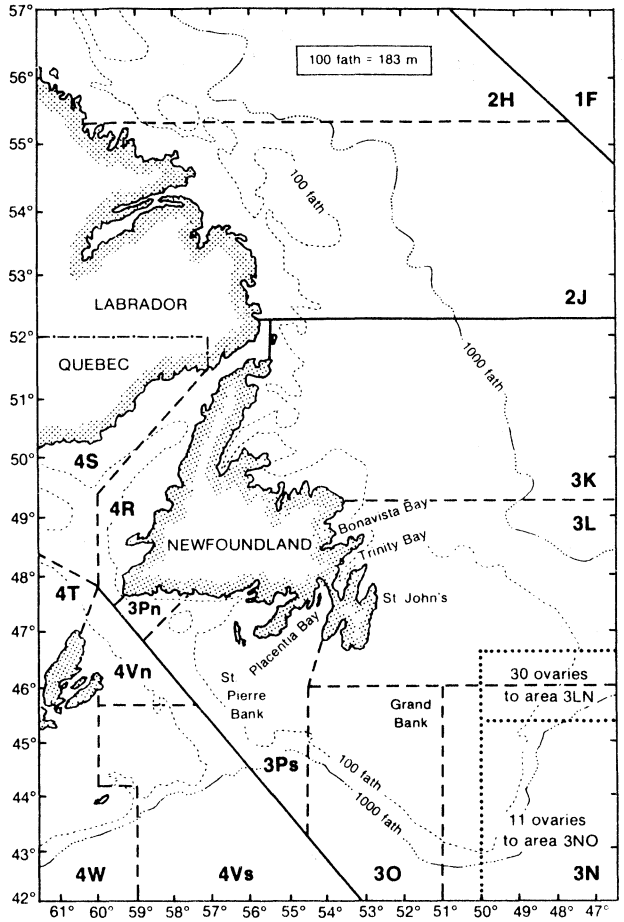

Fig. 1. Place names and NAFO Divisions mentioned in the text. (The areas bounded by dots refer to adjustments in May's (1967) cod fecundity data, which is dealt with in the Discussion.)

procedures of the automatic-counting method were as follows:

1. Eggs were removed from the alcohol solution, filtered with suction through a Büchner funnel with a double filter of nylon screening (26 meshes/cm) until liquid ceased to pass from the funnel, and left to air-dry for about 12 hours on filter paper.
2. A 1/25 sample was then selected from each air-dried ovary by scooping eggs from the filter paper onto a balance (tared to zero) from the known weight of all eggs in the ovary until the weight of the eggs on the balance was 1/25 of the original weight of all eggs. Each scoop of eggs was taken from a different location on the filter paper to provide "randomness" to the selection.
3. The sample of eggs was then spread on filter paper and rolled gently to break up clusters, and it was then passed rapidly through a Decca Radar Mastercount automatic bath counter to break up any remaining clusters of eggs (Boyar and Clifford, 1967).
4. Before automating counting commenced, the sensitivity control, feed rate control, input voltage and counting channel width of the egg-counter were adjusted according to the diameter of the eggs being counted. This was accomplished by manually counting a batch of approximately 100 eggs under a microscope and running the batch through the machine. The machine controls were then adjusted and the process repeated until a difference of no more than ±5% was obtained between the machine and manual counts.
5. Several manual counts of 100 eggs each were then compared with machine count of the same eggs for calibration calculations.
6. Counting commenced with the machine set to count batches of 9,000 eggs. At about the halfway point, several more subsamples were counted manually and compared with machine counts. If agreement at this point was within ±5%, the remaining eggs were counted, following which several more subsamples were counted manually and compared with machine counts. If, after initial calibration, the halfway or final manual and machine counts varied by more than ±5%, the machine was recalibrated until agreement was within ±5% and counting was repeated from the beginning. If the machine counting was successful, the total number of eggs in the ovary was found by multiplying the machine count by 25.

Except for the Placentia Bay material for which fecundity estimates were done before the acquisition of the automatic egg-counter, the number of eggs in the ovary in the majority of cases (63%) could be estimated by the machine method. However, some ovaries were collected well in advance of the spawning season (Table 1), and the eggs were so small that accurate counts could not be obtained with the egg-counter. In these cases, the number of eggs in the ovary was estimated by the dry-weight method. This involved selecting 1/1000 subsamples, by taking 1/1000 of the total weight of eggs in the ovary or by taking 1/40 of the original 1/25 sample, and by following the dry-weight procedure outlined by May (1967) to obtain fecundity estimates.

In the manual counting of eggs under the microscope, two distinct sizes of eggs were recognizable. The larger first-generation eggs (about 0.5–1.0 mm diameter) are those that would have been released during the impending spawning period (March–May), and the much smaller second-generation eggs (<0.1 mm) are those that were destined for release in a succeeding year. Only the first-generation eggs were counted, and pieces of eggs were counted only if they were larger than half the size of a normal egg. Of course, the small second-generation eggs and pieces of eggs less than half the size of a normal egg would not

be counted by the machine after it had been calibrated to count normal-sized eggs.

Validation tests

Dry-weight method. For each of 10 ovaries, a sample of approximately 50,000 eggs was selected and the eggs were manually counted under a low power microscope. Two smaller samples of 1,000–2,000 eggs were then selected from the remaining portion of the ovary by the same method and counted separately. The three samples were oven-dried and weighed as usual. The relative weights of the two small samples and the "50,000-egg" sample were then used to estimate the number of eggs in a typical 50,000-egg sample. These estimates are compared with the manual counts in Table 2. On the average, the dry-weight method overestimated the number of eggs by 2.8%. Application of the paired-comparison t-test to the 10 pairs of counts showed that the difference was not significant ($P>0.05$), indicating that a small subsample of 1,000–2,000 eggs is just as reliable as a much larger subsample in estimating fecundity by the dry-weight method.

TABLE 2. Validation of dry-weight estimates of eggs in samples of selected cod ovaries from Placentia Bay.

Ovary No.	Number of eggs: Dry-weight estimates	Manual counts	Difference
1	53,481	50,000	3,481
2	51,223	50,000	1,223
3	54,396	50,000	4,396
4	46,279	44,785	1,494
5	48,083	50,100	-2,017
6	51,229	51,000	229
7	52,925	50,000	2,925
8	50,586	50,000	586
9	48,472	50,000	-1,528
10	53,316	50,000	3,316
Average	50,999	49,589	1,410
Excess dry weight over manual (%)			2.8

Automatic-counting method. Before and after counting and at the halfway point during counting with the machine, several batches of about 100 eggs each were counted manually under a microscope and by the machine. Comparisons of these subsample counts by batch type and sampling area with paired-comparison t-tests (Table 3) indicated significant differences ($P<0.05$) in four of the 12 cases, the machine counts being significantly lower than the manual counts in three tests and higher in one test. These differences were not considered to be of practical importance in estimating numbers of eggs in the ovaries. It is interesting to note that all except two of the differences were negative, implying that the automatic egg counter tended to underestimate the numbers of eggs by a very small margin. Apparently, the egg-counter occasionally missed eggs which passed by the light beam in pairs or which were broken into pieces which were too small to interrupt the light beam.

Comparison of dry-weight and automatic-counting methods. For a selected number of ovaries (18), the 1/25 fractions of the machine-counted eggs were also oven-dried, together with the remaining 24/25 fractions. The number of eggs in the ovary was then estimated from the relative dry weights of the fractional components. These estimates were compared to the numbers estimated from the automatic-

TABLE 3. Comparison of machine counts with manual counts of eggs, in batches of 100, before, during and after the sampled eggs were counted for fecundity estimation. (* and ** indicate significance at P = 0.05 and P = 0.01 respectively.)

Area	Number of ovaries	Number of eggs: Machine counts	Manual counts	Percent difference	t for paired comparison test
Initial batch counts					
Bonavista Bay	38	17,067	17,112	-0.26	1.06
Trinity Bay	54	22,991	23,261	-1.16	2.28*
St. John's area	36	16,832	16,840	-0.05	0.25
St. Pierre Bank	55	21,214	21,193	0.10	0.26
Halfway batch counts					
Bonavista Bay	21	6,183	6,433	-3.89	2.88**
Trinity Bay	32	12,415	12,674	-2.04	2.03
St. John's area	7	1,962	1,999	-1.85	1.00
St. Pierre Bank	7	2,429	2,473	-1.78	1.35
Final batch counts					
Bonavista Bay	25	8,128	8,228	-1.22	1.93
Trinity Bay	24	8,205	8,324	-1.43	1.83
St. John's area	45	9,048	9,003	0.50	2.98**
St. Pierre Bank	33	9,056	9,147	-0.99	2.14*

counting method by the paired-comparison t-test (Table 4). Relative to the automatic-counting method, the dry-weight method overestimated the number of eggs in the ovary by a small margin (1.34%), but the difference was not significant. This implies that the weight ratio of oven-dried eggs differed slightly from that of air-dired eggs. This may have resulted from a small loss of eggs from the 1/25 samples during repeated handling.

For 12 of the ovaries, a much smaller fraction of approximately 1/1000 of the total number of eggs was selected by taking 1/40 of the original 1/25 fraction of air-dried eggs. These subsamples were oven-dried, counted manually and used to estimate the numbers of eggs in the ovaries. These dry-weight estimates were compared with the corresponding machine-count estimates by the paired-comparison t-test (Table 4). Compared to the automatic-counting method, the dry-weight method overestimated the number of eggs in the ovary by 5.2%, the difference being significant at P = 0.05 but not at P = 0.01. For practical purposes, the bias was not considered serious and no adjustments were made to the estimate. The difference is larger in this case than in the immediately preceding comparison because of additional handling as well as fewer ovaries and different methods of prorating.

TABLE 4. Comparisons of fecundity estimates for selected ovaries by the automatic-counting method with dry-weight estimates based on two different sample sizes. (The machine counts were based on 1/25 samples of air-dryed eggs.)

	Estimated number of eggs		
Ovary No.	Machine count	Dry weight (1/25)	Dry weight (1/1000)
1	717,907	725,089	—
2	823,184	832,956	—
3	1,757,275	1,692,723	—
4	2,789,700	2,837,152	—
5	937,721	957,867	—
6	1,323,125	1,315,788	—
7	2,818,245	2,800,375	—
8	2,754,019	2,772,463	3,069,350
9	972,211	970,931	1,030,417
10	4,921,941	5,181,364	4,780,018
11	3,366,138	3,392,867	3,712,375
12	905,450	952,407	1,055,738
13	1,016,698	1,032,361	1,097,776
14	2,036,551	2,061,185	2,121,057
15	2,259,672	2,259,238	2,128,523
16	1,768,585	1,798,895	1,897,499
17	2,197,527	2,227,496	2,239,308
18	2,963,538	3,013,340	3,170,255
19	2,103,000	—	2,381,528
Mean (1-18)	2,018,305	2,045,306	
Difference		1.34%	
Mean (8-19)	2,272,111		2,390,320
Difference			5.20%

As a further comparison, the fecundity-length relationships of those specimens for which fecundity estimates were based on both the automatic-counting method and the dry-weight method were compared by area. Analysis of covariance (Table 5) indicated no significant difference between methods for the slopes of the regression lines and a significant difference for only one set of elevations (St. John's) at P = 0.05 but not at P = 0.01. This implies that fecundities calculated by these two methods may be combined for the calculation of slopes of regressions of fecundity versus length by area.

Although it is shown later in the paper that there were significant area and time differences in the fecundity-length and fecundity-age relationships, the data were pooled initially to determine the overall general type of relationship between these variables. Arithmetic regressions of pooled fecundity-length and fecundity-age data resulted in correlation coefficients (r) of 0.75 and 0.64 respectively, compared with values of 0.79 and 0.68 for the corresponding log-log regressions. Although the correlation coefficients of the arithmetic and log-log regressions are not significantly different for either the fecundity-length or the fecundity-age relationship (P>0.05), such relationships have been described traditionally in terms of

TABLE 5. Analysis of covariance of log-log fecundity-length regression lines for number of eggs estimated by dry-weight (DW) and machine (MC) methods, and comparative fecundity estimates for three lengths of cod. (Number of specimens in parentheses.)

		Regression parameters		Covariance P-values		Fecundity (000 eggs) at		
Location	Method	Slope	Intercept	Slope	Intercept	50 cm	80 cm	100 cm
Bonavista Bay	DW	3.73 (33)	-0.85			307.0	1,772.3	4,073.8
	MC	3.52 (45)	-0.49	0.77	0.43	309.3	1,617.6	3,548.1
Trinity Bay	DW	2.71 (39)	1.09			494.5	1,767.6	3,235.9
	MC	3.55 (54)	-0.55	0.09	0.09	302.9	1,606.8	3,548.1
St. John's	DW	1.27 (26)	3.75			808.5	1,468.7	1,949.8
	MC	1.65 (36)	2.92	0.66	0.02*	528.8	1,148.4	1,659.6
St. Pierre Bank	DW	3.36 (53)	-0.38			213.1	1,033.7	2,187.8
	MC	3.47 (55)	-0.57	0.82	0.74	211.6	1,080.7	2,344.2

* Significant at 5% level.

general allometry equations (Bagenal, 1957a; Nagasaki, 1958; Hodder, 1963; Pitt, 1964; May, 1967). Therefore, in subsequent analyses, the data were transformed to base 10 logarithms for the regression analyses.

Results

Fecundity-length

For each area except Placentia Bay, data were available for more than one year, and analysis of fecundity *versus* length among years was possible (Fig. 2, A–D). The analysis of covariance indicated that the slopes of the regression lines were not significantly different among years ($P>0.05$) for any area except Trinity Bay (Fig. 2B) where the difference was significant at the 5% but not at the 1% level. On the other hand, the elevations were significantly different ($P<0.01$) for all areas except St. John's. Although the slopes and intercepts of the regression lines for St. John's appear to be different (Fig. 2C), the scatter of points was so great in the 1968 sample ($r^2 = 0.12$) that neither the slopes nor the intercepts were significantly different.

Since only one of the areas showed a significant inter-year difference in slopes and then only at the 5% level, data for the different years were combined for each area, and analysis of covariance was used to test the differences in slopes among the resulting regression lines (Fig. 2E, Table 6). Since all except one set of intercepts (St. John's data) were significantly different among years within areas, it was not valid to test for differences in elevations among areas. With reference to the slopes of the regression lines, the tests (Table 7) showed that the slope for St. John's was significantly different from those for Bonavista Bay and Trinity Bay, the slope for Placentia Bay differed significantly from those for Bonavista Bay and St. John's, and the slope for St. Pierre Bank differed from those for St. John's and Placentia Bay.

Fecundity-age

For the regressions of fecundity *versus* age (Fig. 3, A–D), analysis of covariance indicated that the slopes were not significantly different among years for any of the areas. However, the elevations of these regression lines were significantly different among years for all areas except St. John's (Fig. 3C). Again the explanation for this area is the wide scatter of points in the 1968 sample.

Since none of the areas showed significant difference in slopes among years, data for the different years were combined for each area (Fig. 3E, Table 6), and analysis of covariance was used to test for differences in slopes among areas (Table 7). The slopes of the regression lines for St. John's and Placentia Bay differed significantly from that for Trinity Bay, and the slope for St. Pierre Bank differed significantly from those for St. John's and Placentia Bay.

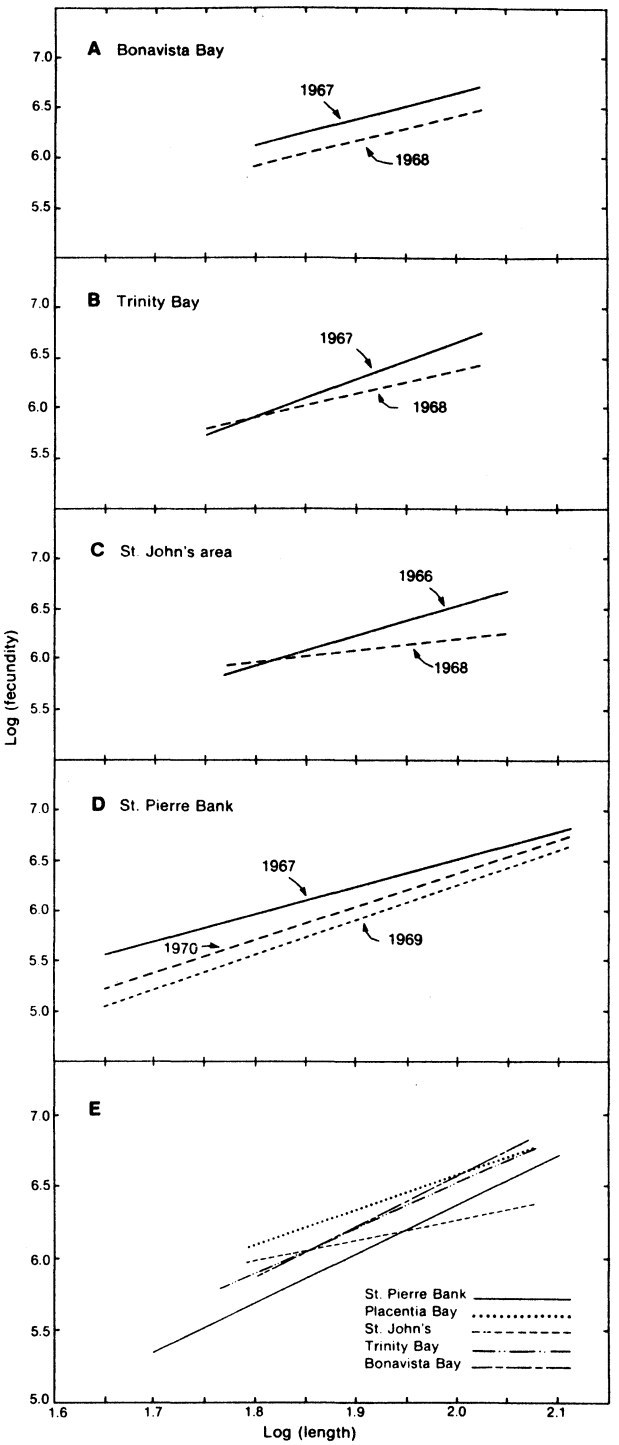

Fig. 2. Log-log regressions of fecundity on length for four inshore Newfoundland areas (**A–D**) by year for each area, and (**E**) by area for years combined.

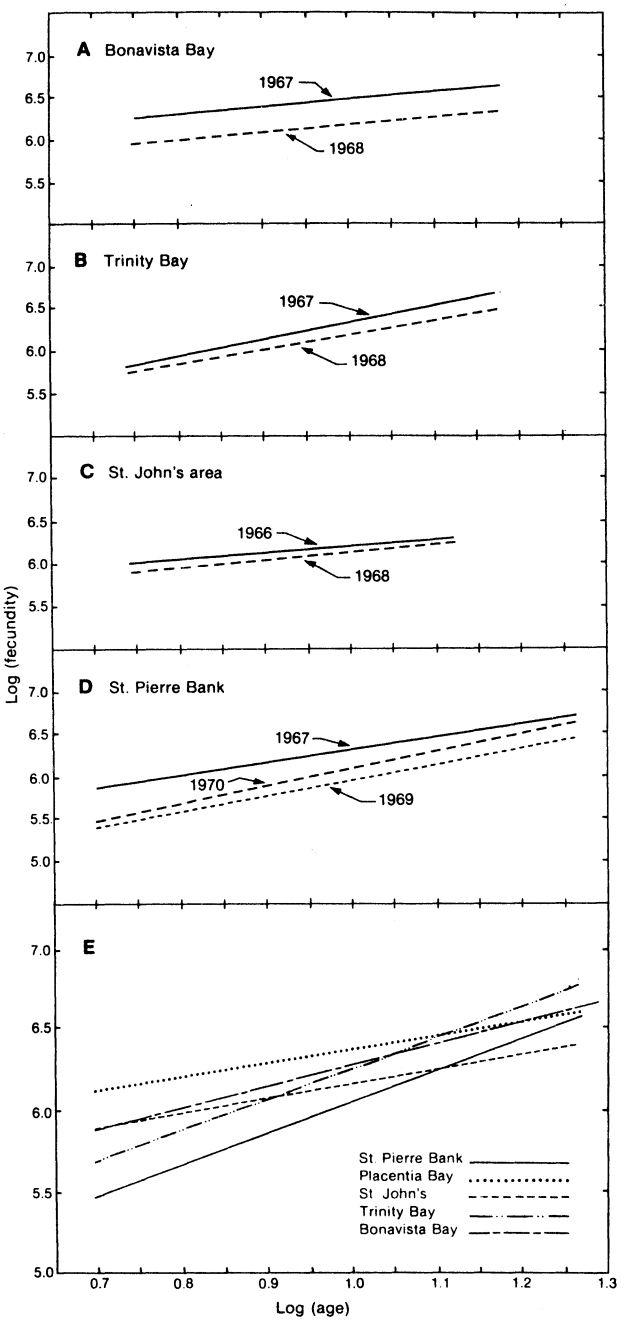

Fig. 3. Log-log regressions of fecundity on age for four inshore Newfoundland areas (**A-D**) by year for each area, and (**E**) by area for years combined.

Discussion and Conclusions

Results of the present study indicate significant inter-year differences in elevations (numbers of eggs produced at a given length or age) but not in slopes (rate of increase in egg production with increase in length or age) of the fecundity-length and fecundity-age regression lines for the various areas. The numbers of years in which fecundity observations were made for the same area were too few to allow correlation of the data with environmental factors, but Hodder (1963) suggested, for Grand Bank haddock, that the environment influenced the number of eggs produced each year by fish of a given length. He also noted that the rate of increase in egg production with increase in length was not different among years. Other authors (e.g. Bagenal, 1957b) have reported similar results. Since the rate of increase in egg production with length and age evidently does not vary annually but the number of eggs produced at a given length or age does vary significantly from year to year, caution must be exercised in using fecundity estimates for a particular year to generalize about egg production of the population.

TABLE 6. Log-log regression parameters of fecundity-length and fecundity-age relationships and correlation coefficients (r) for cod from various Newfoundland areas. (Adjusted data from May (1967) are dealt with in the Discussion.)

Area	No. of fish	Regression parameters Slope	Intercept	r*
Fecundity-length				
Bonavista Bay	58	3.50	-0.45	0.77
Trinity Bay	78	3.13	0.25	0.78
St. John's	62	1.41	3.42	0.38
Placentia Bay	96	2.42	1.73	0.72
St. Pierre Bank	103	3.37	-0.38	0.82
2J+3K (May, 1967)	28	3.63	-0.64	0.93
3LN (May, 1967)	51	2.90	0.73	0.79
3NO (May, 1967)	51	3.97	-1.45	0.83
Fecundity-age				
Bonavista Bay	57	1.34	4.92	0.56
Trinity Bay	78	1.91	4.34	0.72
St. John's	62	0.92	5.23	0.37
Placentia Bay	96	0.84	5.52	0.54
St. Pierre Bank	104	1.94	4.10	0.68
2J+3K (May, 1967)	26	2.26	3.84	0.70
3LN (May, 1967)	51	1.34	-1.01	0.71
3NO (May, 1967)	51	2.61	-2.28	0.79

* All values significant at 1% level.

TABLE 7. Significance tests (P-values) of slopes of log-log regressions of fecundity on length and age of cod from four Newfoundland areas. (* and ** indicate significance at P = 0.05 and P = 0.01 respectively.)

Area	Trinity Bay	St. John's	Placentia Bay	St. Pierre Bank
Fecundity-length				
Bonavista Bay	0.44	<0.01**	0.01**	0.79
Trinity Bay		<0.01**	0.06	0.57
St. John's			0.03*	<0.01**
Placentia Bay				0.02*
Fecundity-age				
Bonavista Bay	0.10	0.30	0.07	0.11
Trinity Bay		<0.01**	<0.01**	0.93
St. John's			0.80	0.02*
Placentia Bay				<0.01**

TABLE 8. Comparison of incremental increase in fecundity of cod from ages 10 to 11 and of increase with length based on mean lengths corresponding to age 10 and 11 cod from four Newfoundland areas.

Area	Age (yr)	Calculated number of eggs (000)	(A) Increase age 10 to age 11	Mean length (cm)	Length increase (cm)	Calculated number of eggs (000)	(L) Increase with length	A–L / L (%)
Placentia Bay	10	2,291		83.02		2,368		
	11	2,481	0.190	85.94	2.92	2,575	0.207	-8
Trinity Bay	10	1,778		82.12		1,747		
	11	2,133	0.355	86.06	3.94	2,023	0.276	+29
Bonavista Bay	10	1,820		83.54		1,890		
	11	2,068	0.248	86.97	3.43	2,177	0.287	-14
St. John's	10	1,412		83.73		1,353		
	11	1,542	0.130	87.40	3.67	1,437	0.084	+55

When the slopes of the fecundity-length regression lines are significantly or non-significantly different among areas, one might also expect the slopes of the fecundity-age regression lines to follow the same pattern. Such was not the case in 4 of the 10 comparisons (Table 7). In particular, for the Placentia Bay and Trinity Bay comparisons, the slopes of the fecundity-age regression lines differed significantly, whereas those of the fecundity-length regression lines did not, although the P-value (0.06) was close to the 0.05 level. Also, in the case of the Placentia Bay and Bonavista Bay comparisons, the slopes of the fecundity-length regression lines differed significantly but those of the fecundity-age regression lines did not, although the latter were barely so (P = 0.07). In these two cases, because of the proximity of the P-values to 0.05, differences in slopes of the regression lines for length and age were considered to correspond. However, in comparing the St. John's results with those for Placentia Bay and Bonavista Bay, the slopes of the fecundity-length regression lines differed significantly (P = 0.03 and P<0.01 respectively) but the slopes of the fecundity-age regression lines clearly did not (P=0.80 and 0.30 respectively). In the St. John's data, the increase in average number of eggs produced between adjacent ages (e.g. ages 10 and 11) was 55% higher than the increase in the average number of eggs corresponding to the length interval between these adjacent ages calculated from the growth curve (Table 8), whereas the changes ranged from -8% to +29% for the other areas. This is because of the low correlation for the St. John's data (r^2 = 0.14) caused by the broad scatter of points, with resulting lack of correspondence between the fecundity-length, fecundity-age and length-age regressions.

For comparison of data in the present paper with those of May (1967), the latter were recombined for areas 2J+3K, 3LN and 3NO instead of the original 2J+3K, 3L, 3N and 3O. This was to facilitate comparisons of the fecundity data for the various areas in relation to bottom temperatures, because reexamination of the collection sites of May's data revealed that 30 of the ovaries from Div. 3N were actually collected in the northern part of this area (see fig. 1 of May, 1967), which is characterized by bottom temperatures close to those found in Div. 3L, both areas being under the influence of the Labrador Current (May *et al.*, 1965). Consequently, fecundity estimates for 30 ovaries from the northern part of Div. 3N were combined with those from Div. 3L, representing a total of 51 ovaries from area "3LN" (Fig. 1). Fecundity estimates for the remaining 11 ovaries collected by May (1967) in the southern part of Div. 3N, where bottom temperatures were similar to those found in Div. 3O, were combined with estimates for 40 ovaries taken in Div. 3O (a total of 51 ovaries for area "3NO"), both areas being under the influence of the Gulf Stream (May *et al.*, 1965). No adjustments were made to May's (1967) data for area "2J+3K". The recalculated regression parameters for the three areas are given in Table 6.

TABLE 9. Significance tests (P-values) of slopes of log-log regression of fecundity on length, in comparing data for five areas in the present paper with May's (1967) adjusted data for three offshore areas.

Area	2J+3K	3LN	3NO
Bonavista Bay	0.93	0.24	0.39
Trinity Bay	0.30	0.60	0.07
St. John's	<0.01*	<0.01*	<0.01*
Placentia Bay	<0.01*	0.22	<0.01*
St. Pierre Bank	0.69	0.35	0.18

* Significant at 1% level.

In comparing the fecundity-length relationships from the present data with regression lines recalculated from May's (1967) data (Table 9), the slope for St. John's data differed significantly from those for the three offshore areas and the slope for Placentia Bay data differed from those for two of the areas, the exception being 3LN. On the other hand, the comparisons involving Trinity Bay, Bonavista Bay and St. Pierre Bank indicated a high degree of similarity (P>0.05).

The explanation for the observed differences in rate of egg production with length among areas is likely found in variations in environmental factors. There is sufficient evidence in the literature to indicate that fecundity of a number of species is influenced by environmental variability, particularly water temperature (Hempel, 1965; Nikolskii, 1965). This aspect was investigated by examining variability in temperature among the areas where the samples were taken in the present and May's (1967) study. For St. Pierre Bank, Bonavista Bay, Trinity Bay, Placentia Bay, and areas 2J +3K, 3NO and 3LN (except for 15 ovaries), the temperatures used were mean bottom temperatures at the time of capture of the fish from which the ovaries were taken. Where more than one sampling site existed for an area, the mean bottom temperature was derived by weighting the bottom temperatures by the numbers of ovaries taken at the various sites.

For area 3LN, 15 ovaries were collected from catches of fishing vessels in 1964 at two sites (5 ovaries at one and 10 at another) where no bottom temperatures were available. There were even no research vessel observations in 1964 or preceding years in the vicinity of these sites at the time of year when the ovaries were collected. However, bottom temperatures near the 5-ovary collection site in 1967-68, 1970-72 and 1974 ranged from -1.20 to 0.05° C (average -0.64° C), and those near the 10-ovary collection site in 1968, 1971-72 and 1974 ranged from - 1.41° to 0.02° C (average -0.77° C). These averages were used in conjunction with 1964 bottom temperatures for other collection sites to derive a weighted mean for area 3LN. Although detailed hydrographic observations were not available for the northeastern Grand Bank during the winter-spring period, these average temperatures should be representative of bottom temperatures in the vicinity of the collection sites in 1964 because the temperature over the shallow portion of northeastern Grand Bank is typically 0° C or lower even in summer due to the influence of the cold Labrador Current (May *et al.*, 1965).

In the St. John's area, ovaries were collected from commercial gillnet catches at sites where bottom temperatures and depths of catches were not available. However, gillnet fishermen in this area generally fish in depths of 90-180 m, and these were assumed to define the likely range of depths from which the ovaries were taken. Temperature observations at Station 27, located about 5 nautical miles off St. John's and occupied at least once monthly (Templeman, 1969), were used to derive average temperatures which were considered representative of those at the ovary collection sites. Temperatures at standard depths of 100, 125, 150 and 170 m in the same year and on a date nearest that of each ovary collection were averaged from the temperature sections, and these averages were weighted by the numbers of ovaries in the yearly collections to derive an overall mean bottom temperature for the St. John's area.

These mean bottom temperatures at or near the sites and dates of collection of the ovaries appear to have a systematic relationship with the slopes of the fecundity-length and fecundity-age regression lines for the inshore and offshore areas (Fig. 4). The slopes (representing rates of increase in egg production with length or age) decrease sharply at temperatures below 2° C, and there is some indication of a decline in slopes at higher temperatures, particularly for the fecundity-age relationships. The sharp decrease, at low temperatures, in the rate at which egg production increases as the fish grow larger and older is probably related to their ability to feed and digest food at these low

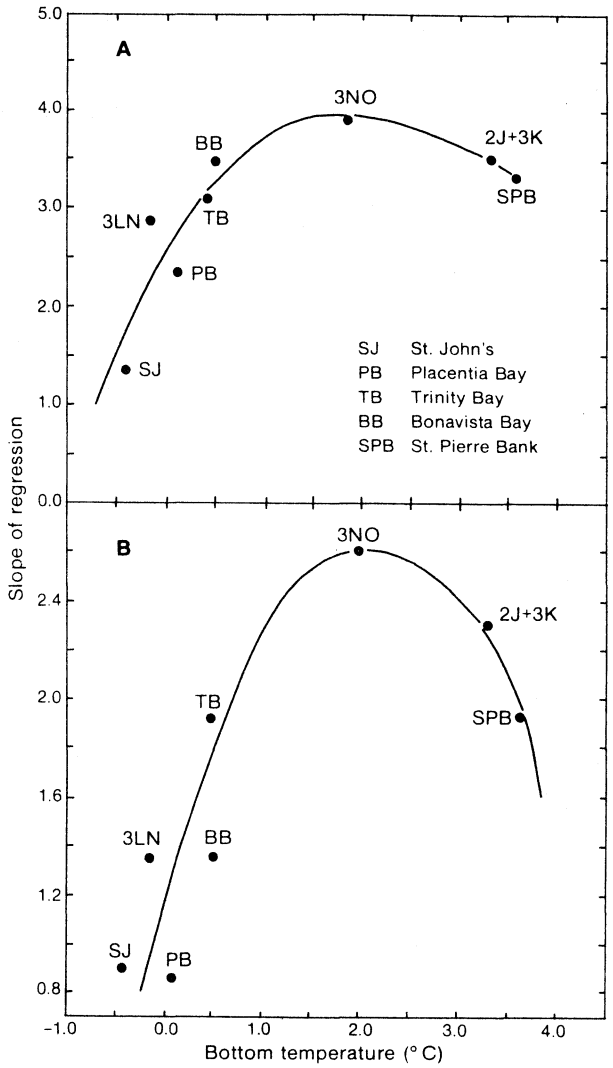

Fig. 4. Plots of slopes of log-log regression lines (Table 6) for (**A**) fecundity-length and (**B**) fecundity-age relationships against mean bottom temperatures at the ovary collection sites. (Curves are free hand drawn to reflect the trends.)

temperatures. It is known that cod feed less at lower temperatures (McKenzie, 1938) and digest food at a much slower rate (Tyler, 1970). Also, the abundance and variety of prey items are likely to be less at lower temperatures. Taken together, these factors would result in less food being utilized in cold water for production of both somatic and gonadal products. Fish which live in very cold water are known to utilize their body protein for production of sexual products. In American plaice, as body protein declines, water replaces it, giving rise to a jellied condition (Templeman and Andrews, 1956), but no fecundity estimates are available for jellied American plaice to enable a comparison with those of young fish and fish living in warmer water. Conversely, the cod in the present study were not examined for jellied condition. However, the hypothesis is advanced that, because of low food utilization, the cod in colder water were not only unable to produce as much body protein as fish living in warmer water but were unable to increase their egg production with increased length to the same extent. This would be more evident in the larger and older cod which feed less and especially do not take advantage of the abundant supply of capelin in early summer (Lilly and Fleming, 1981) to recover quickly from spawning as do the younger fish, thus causing the decline in slopes of the fecundity-length and fecundity-age relationships with decrease in temperature.

In regard to the specific period when these low temperatures might affect fecundity, Hodder (1963) considered three possible critical periods for production of eggs by haddock on the Grand Bank: (i) time of formation of oocytes 2 years prior to spawning, (ii) the few months immediately preceding spawning, and (iii) the summer immediately preceding spawning. In relation to (i), the time of formation of oocytes for cod 2 years before spawning would be during the spring period, and, although detailed temperature observations by season are not available, it is well established generally that the deepwater slopes of the offshore banks, where the majority of the ovaries were taken in areas 2J +3K, 3NO and St. Pierre Bank (areas with higher fecundity-length slopes), are washed by relatively warm water for almost the entire year, whereas the inshore areas of Bonavista Bay, Trinity Bay, St. John's and Placentiia Bay and the shallow bank area 3LN (areas with lower fecundity-length slopes) are covered by relatively cold water throughout the winter, spring and early summer periods (Fleming, 1960; May *et al*., 1965; Templeman, 1962, 1965b, 1966; Templeman and Hodder, 1965a, 1965b; Templeman and May, 1965). Thus, the bottom temperatures at the sites and times of ovary collection are probably representative of the temperatures in these areas during each spring period when oocytes are being formed, and this could have produced the results observed in this study.

By the same argument, for critical period (ii) above, these bottom temperatures are probably representative of the temperatures in the areas for the winter months immediately preceding the time of ovary collecton. As well, it is known that, although cod undergo inshore migrations to shallow areas in late spring-early summer and offshore migrations to deep water in late autumn-early winter, very little migration takes place during the winter-early spring period (Templeman and Fleming, 1956; Hodder, 1965; Templeman, 1962, 1965a, 1966, 1979; Lear, 1984). Thus, cod which are in a particular area by early winter are likely to remain there until late spring, and those that were captured at the sites of ovary collection were likely to have been there for several months before being caught. Therefore, environmental factors in the months immediately before spawning could also explain the observed results, the lower temperatures and attendant food restrictions probably inducing some reabsorption of ova (Hodder, 1963).

With regard to critical period (iii), cod which overwinter in warm water on the slopes of the banks in areas 2J+3K, 3NO and St. Pierre Bank do not remain there throughout the year but migrate to inshore shallow waters of different temperatures in summer and mix with other cod populations at the same time. Also, cod which inhabit the inshore areas in winter would experience temperatures considerably different from those prevalent in summer in the same areas. Therefore, it is unlikely that the differences observed in the slopes of the fecundity-length and fecundity-age relationships were caused by environmental factors operating during the summer preceding spawning. In summary, therefore, it appears likely that the observed differences were caused by environmental factors which influenced the ability of cod to utilize food either at the time of oocyte formation or in the months immediately before spawning when the eggs are increasing in size very rapidly.

In conclusion, the numbers of eggs produced at each length and age varied considerably among years within an area, whereas the rate of increase in numbers of eggs produced with increase in length or age did not. In the area comparisons, cod from the St. John's area had a different fecundity-length relationship (lower slope) than those from other inshore and offshore areas, and cod from Placentia Bay had a different relationship (lower slope) than those from all areas studied except area 3LN. On the other hand, the relationships for cod in Bonavista Bay and Trinity Bay and in all offshore areas were similar. This variation among areas in rate of increase in egg production with length appears to be related to the temperature conditions in the areas where the cod lived either during the period immediately prior to spawning or

during the period of oocyte formation 2 years prior to spawning.

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