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ESTIMATION OF TOTAL POTENTIAL FECUNDITY AND ATRESIA IN THE WESTERN MACKEREL STOCK, 1989

by

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SUMMARY

Total potential fecundity was estimated jointly by the Marine Laboratory Aberdeen and the Fisheries Laboratory Lowestoft as part of a triennial survey to estimate spawning stock biomass of the Western mackerel stock. A value of 1,608 eggs/g of total fish weight was calculated for 1989, representing a 10% increase compared to 1986. Estimates of atresia were made in 1989 in order to convert potential to realised fecundity. The duration of atretic oocytes in mackerel ovaries is not yet known but assumptions of five and 10 days would reduce potential fecundity by 13 and 6% respectively.

INTRODUCTION

The size of the western mackerel spawning stock has been estimated triennially by egg survey, under the auspices of ICES, since 1977. In order to calculate stock size from the egg production, estimates of fecundity are required. Traditionally this has been carried out by counting the number of maturing oocytes in the ovaries of late pre-spawning fish to provide an estimate of the total potential fecundity for the mean size of individual within the stock. Two previous estimates of this kind have been made for the Western mackerel stock, Lockwood *et al.* (1981) - for the egg surveys of 1977, 1980 and 1983 - and Greer-Walker *et al.* (1986) - applied to the survey of 1986. This report gives the results of similar investigations in 1989, undertaken jointly by MAFF and DAFS in conjunction with the University of Aberdeen (AU). The report provides new data on the size threshold at which oocytes mature and on atresia (the resorption of developing oocytes) - both areas identified by a previous ICES workshop (Anon, 1987) as requiring further investigation. Estimates of atresia are required to convert potential fecundity (the maximum number of oocytes which might become fully developed and shed) into realised fecundity (the number of oocytes which are actually shed). These have not been available in the past. A first attempt to quantify atresia is made in this report, but the results must be considered speculative at this stage since they are based on an assumption on the duration of atresia, which at present remains unknown. As in previous investigations the fecundity estimate made for 1989 is based upon the assumption that mackerel is a determinate spawner.

MATERIALS AND METHODS

Ovaries for estimating fecundity, atresia, and the size threshold at which oocytes mature were collected from six different cruises (Table 1). All samples were collected within the main spawning area, near the edge of the continental shelf, between latitudes 46'N and 54'N.

A new simplified maturity scale (Appendix 1) was used to ascribe mackerel to maturity stage. Only stage 3 fish (those with ovaries occupying >3/4 of body cavity and without hydrated oocytes) were selected for fecundity estimation. After histological sectioning and staining any ovaries containing post-ovulatory follicles were rejected. One hundred ovaries in late pre-spawning condition, stratified to cover the size range of spawning fish, were used to determine length-fecundity and weight-fecundity relationships. The sampling work was allocated equally between DAFS and MAFF.

In addition to the sampling of pre-spawning ovaries a further 36 ovaries, mainly from fish in the later stages of spawning, were examined histologically to determine the oocyte size threshold above which maturation of oocytes occurs.

To estimate atresia, the first ten females were collected from a number of hauls covering all but the first of the five mackerel egg survey periods. Length, maturity stage, total weight, ovary weight and age were recorded for each fish. One ovary from all stage 3 fish was placed in Gilson's fluid for volumetric analysis and the other was fixed in 4% buffered formol saline for histological examination. For other maturity stages both ovaries were fixed in formol saline for histological examination.

Egg Counts Using the Volumetric Method

The sampling methods adopted by DAFS and MAFF in 1989 were slightly modified compared to those used in 1986. The latter are described in Greer-Walker *et al.* (1987). Differences in techniques between the two laboratories in 1989 are summarised in Table 2.

As in 1986 ovaries were digested in Gilson's fluid over a period of approximately three months with frequent agitation before counting commenced. Differences in technique compared to 1986 are given in Appendix 2.

In order to compare results in the two laboratories one sample was exchanged in each direction.

Effect of Formalin and Gilson's on Oocyte Diameter

To convert oocyte measurements made from histological section to their equivalent in Gilson's fluid the same factor was used as established by MAFF in 1986:

oocyte diameter in Gilson's = oocyte diameter in histological section x 0.84

Histology

Ovaries were dehydrated in alcohol, embedded in resin, sectioned and stained either with Schiff's or Mallory's trichrome (by MAFF) or with haematoxylin and eosin (by AU) as in 1986 (Greer-Walker *et al.*, 1987).

Estimation of the Size Threshold at which Oocyte Maturation Occurs

Maturation of oocytes is indicated by the onset of vitellogenesis. In histological sections stained with Schiff's reagent (MAFF), the intracellular yolk stains a magenta colour, while in haematoxylin and eosin stained sections (AU) the presence of yolk is indicated by cytoplasmic vacuoles. In order to determine an appropriate size threshold for use in the total fecundity calculations two types of measurement were made:

1. The maximum size of previtellogenic oocytes (pvo's) in recently spent fish.

2. The size at which 50% of oocytes showed signs of vitellogenesis in fish nearing the end of spawning.

Estimation of Atresia

Histological sections were examined to establish the presence or absence of atretic eggs, vitellogenic eggs, hydrated eggs and post-ovulatory follicles. The samples were divided equally between MAFF and AU for analysis. For the purpose of quantifying atresia only those eggs up to the mid α stage were used. The following criteria (all three) were used to define this stage:

1. Disorganised yolk granules with a clear ring just below the zona pellucida.

2. Wrinkled zona pellucida with a convoluted outline.

3. Pits and breakage in the zona pellucida but without breaking down to isolated clumps.

To ensure standardisation of interpretation between MAFF and Aberdeen University, sections of six fish were analysed by both laboratories, a reference set of photographs to identify and stage atretic eggs was prepared and comparative counts were made.

To estimate the number of atretic eggs per fish both laboratories used their own established stereological methods (Emerson *et al.*, 1990 - MAFF; Laird and Priede, 1986, mimeo - AU).

To calculate the effect of atresia on the egg production of the whole spawning stock it is necessary to calculate a production curve for atretic oocytes which, when added to the egg production curve, accounts for the total potential fecundity of the spawning stock (Fig. 1).

In order to calculate a production curve for atretic oocytes it is necessary to estimate the mean prevalence, relative intensity and duration of α atresia. The first two terms are defined below:

Prevalence - the proportion of females in "spawning condition" with α atretic eggs. (Spawning fish are defined as those with migratory nuclei, hydrated eggs, post-ovulatory follicles or α atretic oocytes).

Relative intensity - the number of atretic oocytes divided by predicted potential fecundity.

The duration is unknown at present. For purposes of calculation assumed values have been used to cover its expected range. The resulting estimate for atresia, therefore, is only as good as the assumption on its duration.

let

P_i = mean prevalence of atresia during period i
R_i = mean relative intensity of atresia during period i
D_i = duration (days) of atresia during period i
f = potential fecundity per gram female

The daily production rate of atretic oocytes per gram female during period i ai is given by

$$a_i = P_i R_i f / D_i$$

let

T_i = duration of period i (days)
E_i = egg production during period i

The biomass of spawning females B_i corresponding to the egg production Ei is given by:

$$B_i = E_i / (f - a_i T_i)$$

The production of atretic oocytes A_i during period i is

$$A_i = a_i T_i B_i$$

Total female SSB is then calculated as $\sum B_i$ or, equivalently, $\sum (A_i + E_i) / f$.

Note that B_i is the biomass of females required to spawn all their eggs during the period i to account for the observed production. In fact, a larger biomass would spawn a proportion of their eggs during this time period. The method must therefore be regarded as an approximation.

The percentage difference between realised and potential egg production (ie assuming no atresia) is

$$100 \times A_i / E_i$$

This is the value by which the biomass estimate needs to be increased to take account of the effect of atresia.

RESULTS

Oocyte Maturation Size Threshold

Figure 2 shows the change in maximum pvo size through spawning. The data indicate a decline in maximum pvo size from the beginning to the end of spawning with a value of 157 μm at the end of spawning.

Appendix 3 gives details of oocyte diameter measurements made on individual fish classified macroscopically as maturity stages 5 (partially spent) and 6 (spent). These data are summarised in the text table below:

Data source	Sample size	Maximum pvo size (μm)		
		Minimum	Maximum	Mean
DAFS/AU	12	134	196	157.0
MAFF	12	145	196	165.5
Combined	24	134	196	161.3

The differences between the two data sets were not significant.

A different approach to determining the size above which oocytes mature is to calculate the diameter at which 50% of oocytes show signs of vitellogenesis in fish close to the end of spawning. This requires an overlap in the size distributions of pvo's and maturing oocytes. In practice it was found that in six out of the 10 fish examined to estimate this threshold there was no overlap in the size range of pvo's and maturing oocytes. In the four individual fish in which there was an overlap the 50% threshold values ranged between 138 and 160 μm. In view of the rather small numbers of oocytes used to calculate the thresholds in individual fish it was decided to pool oocyte measurements from all fish with pvo's and maturing oocytes. These data are shown in Figure 3 and gave a 50% threshold value of 160.5 μm.

Sample Exchange - Volumetric Counts

Results of a comparison between oocyte counts made by DAFS and MAFF on subsamples taken from the same ovary are given in Table 3.

In both samples DAFS gave higher counts than MAFF but the differences were not statistically significant.

Fecundity/Length Relationships

Fecundity/length relationships were calculated separately from the counts made by DAFS and MAFF and for the two data sets combined:

DAFS	Fecundity = $2.845 \times 10^{-5} \times \text{Length (mm)}^{4.03956}$	$r^2 = 0.9616$ n = 50
MAFF	Fecundity = $4.017 \times 10^{-5} \times \text{Length (mm)}^{3.93753}$	$r^2 = 0.9492$ n = 50
DAFS + MAFF	Fecundity = $2.539 \times 10^{-5} \times \text{Length (mm)}^{4.03857}$	$r^2 = 0.9321$ n = 100

The data are plotted in Figure 4. In each data set fecundity is significantly correlated with length. The slopes of the DAFS and MAFF data are not significantly different but the intercepts of log transformed regressions are. For a medium-sized fish (35 cm) the DAFS values are 29% higher than those of MAFF.

The 1989 DAFS and MAFF data are compared with previous fecundity/length data for the western stock in Figure 5.

Fecundity/Weight Relationships

Calculated fecundity/weight relationships were:

DAFS	Fecundity = -79354 + Weight (g) x 1988.5	$r^2 = 0.9667$ n = 47
MAFF	Fecundity = -53834 + Weight (g) x 1559.8	$r^2 = 0.9523$ n = 50
DAFS + MAFF	Fecundity = -67725 + Weight (g) x 1777.3	$r^2 = 0.9342$ n = 97

The data are plotted in Figure 6. In each data set fecundity is significantly correlated with weight. When the DAFS and MAFF data are compared there are significant differences in both the slopes and intercept values. In the MAFF data the 95% confidence limits for the intercept fall on either side of the origin indicating an intercept not significantly different from zero. In the other two data sets the confidence limits fall below the origin but the upper limit lies close to it (DAFS -8197, DAFS + MAFF -6614).

Fecundity/weight relationships for 1989 are compared with the 1986 value in Table 4.

The DAFS 1989 value was 23% higher than that of 1986 while the MAFF value was 4% lower than that of 1986.

Atresia

Data are summarised in Table 5.

The prevalence of α atresia varied between 26% and 50% over the four sampled time periods but with no seasonal trend. Relative atresia in individual fish varied between 0.3% and 59%, mean values per survey period showed no seasonal trend. The lowest value for relative intensity of atresia, however, was associated with the highest value for prevalence and vice versa. The highest numbers of atretic oocytes/gm in the total spawning population were found during periods three and four ie around peak spawning.

The effects of these levels of atresia on estimates of spawning stock biomass are given in Table 6 using two alternative assumed duration periods for α atresia.

The estimates of female SSB are increased by 13% and 6%, assuming durations of α atresia of five and 10 days respectively, compared to the estimate assuming no atresia. These values are equivalent, given the approximations used, to the differences between potential and realised fecundity.

DISCUSSION

Oocyte Maturation Size Threshold

Investigations in 1986 (Greer-Walker *et al.*, 1987) showed that the vitellogenic size threshold in pre-spawning fish was significantly higher than the maximum pvo size in spent fish. This implied that maturation of oocytes takes place below the size threshold measured in pre-spawners and that if the latter were to be used in making fecundity counts it would result in a considerable underestimate of total fecundity. As a result it was decided in 1986 to use the maximum pvo size in spent fish (converted to its equivalent size in Gilson's) as the appropriate size above which to make counts in Gilson's. This approximated to 130 μm the value also used in the only previous Western fecundity estimate (Lockwood *et al.*, 1981).

The 1989 data given in Figure 1 provide the first firm evidence that maximum pvo size decreases as spawning progresses and confirm the supposition made in 1986 that a vitellogenic size threshold measured in pre-spawning fish is inappropriate for fecundity determination. A better approach is to determine this threshold in fish close to the end of spawning.

Three different values were calculated from the 1989 data:

	Histological section	Gilson's equivalent
Maximum pvo size in spent fish as estimated by regression	157.0	132
Maximum pvo size in mat stage 5 and 6 fish	161.3	135
50% vitellogenesis size threshold in stage 5 and 6 fish	160.5	135

These values are all very similar and indicate that the value of 130 μm used in the past is not inconsistent with the data collected in 1989. Maximum pvo size appears to give a very close approximation to the 50% vitellogenic size threshold and has the advantage of being much quicker and easier to measure, it can also be measured in fish where there is no overlap in size between pvo's and maturing oocytes. In the light of the above results, and for consistency with previous estimates, a size threshold of 130 μm was used in calculating total potential fecundity (use of a 135 μm threshold would lower fecundity by about 1%).

Differences Between DAFS and MAFF Fecundity Estimates in 1989

The cause of the differences between the 1989 MAFF and DAFS fecundity estimates is not at all clear. The sample exchange indicated a relatively small and non significant difference between counts made on the same fish whereas the total data sets indicate much larger differences. The most likely source of the difference was thought to lie in the alternative volumetric techniques. These were subsequently rechecked by subsampling a known quantity of eggs (23,700). DAFS took 50 subsamples which gave an estimate of fecundity 0.7% higher than predicted while MAFF took 30 subsamples giving a value 2.4% lower than predicted. Both methods therefore indicated an acceptable level of precision and the source of the difference remains unexplained. The DAFS results appear to deviate more from previous estimates than those of MAFF. However ovary weights for fish of comparable length were higher in 1989 than in 1986 (Fig. 7). A comparison between mean fecundity per gram of ovary from the different data sets is given below:

		Sample size	Nos maturing oocytes/g ovary
1986	DAFS + MAFF	53	20,944
1989	DAFS	50	21,484
1989	MAFF	50	17,096

The DAFS 1989 value is 3% higher than that of 1986 while the MAFF value is 19% lower. In the absence of further information the data were therefore pooled for the purpose of stock size estimation.

Atresia

The data presented represent the first systematic attempt to quantify the effect of atresia on the spawning population as a whole. At present the duration of α atresia remains unknown and experiments on captive mackerel are required to quantify this. The estimates given must therefore still be considered speculative.

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TABLE 1

Details of samples analysed for fecundity, atresia and oocyte maturation size threshold

Research vessel	Cruise	Dates	No fish analysed for		
			Total fecundity	Oocyte maturation size threshold	Atresia
Cirolana	3/89	07/3-03/4	86	-	-
Scotia	4/89	22/4-16/5	6	7	26
King's Cross	-	23/5-12/6	-	16	42
Cirolana	5/89	19/5-12/6	8	-	-
Lough Foyle	-	12/6-30/6	-	-	35
Tridens	-	10/7-19/7	-	13	45

TABLE 2

Differences in volumetric methods of fecundity determination used by MAFF and DAFS

	DAFS	MAFF
Minimum mesh-size in sieves used to filter samples	106 μm	100 μm
Total volume or weight of sampling medium	1,500 ml (sucrose + water mixture 1:1 by weight)	1,150 g (sucrose + water mixture 1:1.3 by weight)
Subsample volume	1 ml (nominal)	0.663 g
Stempel pipette type	Electrically operated	Manually operated
Mixer type	12 volt motor driving vertical action perforated disc stirrer	Domestic electric mixer
Oocyte measurement	binocular microscope with graduated eyepiece	VIDS analyser consisting of colour camera, digitising tablet, colour monitor and computer
No and size of subsample	As 1986 no of samples determined from table in Hislop and Hall (1974). In practice between 2 and 10 samples according to counts eg >300 take 2, <80 take 9	Enough replicates to give about 250 eggs >130 um

TABLE 3

A comparison between oocyte counts made by DAFS and MAFF on subsamples taken from the same ovary

Sample No	Sampler	Oocyte counts (1)				Percentage significance (2)	Significance
		No	Range	Mean	s.e.		
1	DAFS	10	65-81	73.8	1.77	5.8	not significant
	MAFF	10	54-84	69.7	3.03		
2	DAFS	5	160-252	216.4	15.2	10.8	not significant
	MAFF	4	170-215	195.3	9.5		

Notes

(1) Counts adjusted to take account of different fractions sampled

(2) Calculated from ratio 100 x (DAFS - MAFF)/MAFF

TABLE 4

A comparison between 1989 and 1986 fecundity/weight relationships

1	1986	DAFS + MAFF	Fec = 1457 x wt (g)	
2	1989	DAFS	Fec = 1796 x wt (g)	(forced through origin)
3	1989	MAFF	Fec = 1396 x wt (g)	
4	1989	DAFS + MAFF	Fec = 1,608 x wt (g)	(forced through origin)

TABLE 5

Prevalence and relative intensity of α atresia and mean number of α atretic oocytes per gm of fish

Egg survey period	2	3	4	5
Egg survey dates	23/4-20/5	21/5-6/6	7-29/6	30/6-17/7
No of fish examined	26	42	35	45
Prevalence (%)	50.0	38.1	25.7	35.5
Relative atresia (no fish/category)				
0	13	26	26	29
0.1-9.9%	11	7	3	7
10-19.9%	2	6	4	3
20-29.9%	-	1	1	3
30-39.9%	-	-	1	1
40-49.9%	-	-	-	1
50-59.9%	-	2	-	-
60-69.9%	-	-	-	-
Geometric mean % relative atresia (excluding fish without atresia) - (1)	3.90	7.35	12.43	5.87
Mean no. atretic oocytes/gm of fish with atresia - (2)	63	118	200	94
Mean no atretic oocytes/gm of all fish (with or without atresia)	32	45	51	33

Notes:

(1) Geometric mean used because of non normal distribution of relative intensity of atresia.

(2) Derived from product of mean relative intensity of atresia and mean potential fecundity (1,608 eggs/gm of fish)

TABLE 6

Estimates of female spawning stock biomass corrected for atresia

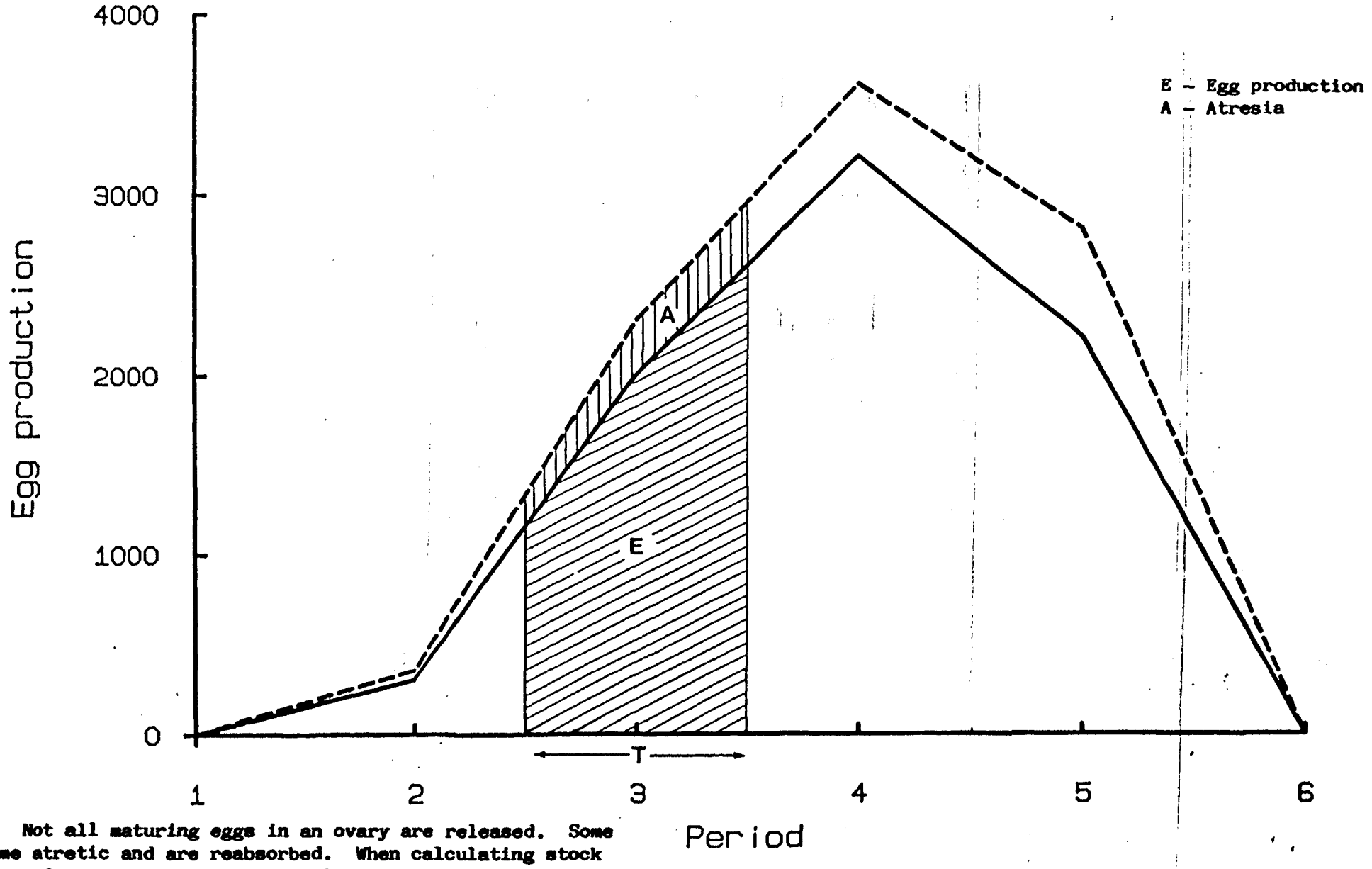
E_i = egg production during period i (x 10^{15})
T_i = duration of period i in days
a_i = daily egg production of atretic oocytes per gram female
B_i = corresponding female SSB for period i (x 10^3 tonnes)

Period of egg production				Assuming no atresia	Assuming duration of atresia of			
					5 days		10 days	
		T_i	E_i	B_i	a_i	B_i	a_i	Bi
1	21/03-22/04	33	19.2	119.2	(6.300)*	136.9	(3.150)	127.4
2	23/04-20/05	28	44.4	276.5	6.300	310.6	3.150	292.5
3	21/05-06/06	17	35.2	218.9	8.992	241.9	4.496	229.8
4	07/06-29/06	23	34.2	212.8	10.280	249.5	5.140	229.7
5	30/06-17/07	18	7.9	49.5	6.674	53.5	3.337	51.4
Totals			140.9	876.9		992.4 +13.2%		930.8 +6.1%

Notes:

*no data on atresia for first survey period, therefore assumed to be the same as period 2. Values for T_i and E_i are taken from Anon (1990)

Figure 1. Schematic representation of realised and atretic egg production curves



Note Not all maturing eggs in an ovary are released. Some become atretic and are reabsorbed. When calculating stock biomass from egg surveys and total fecundity data it is therefore necessary to estimate the seasonal production of atretic eggs.

Figure 2. Reduction in the maximum PVO diameter during spawning

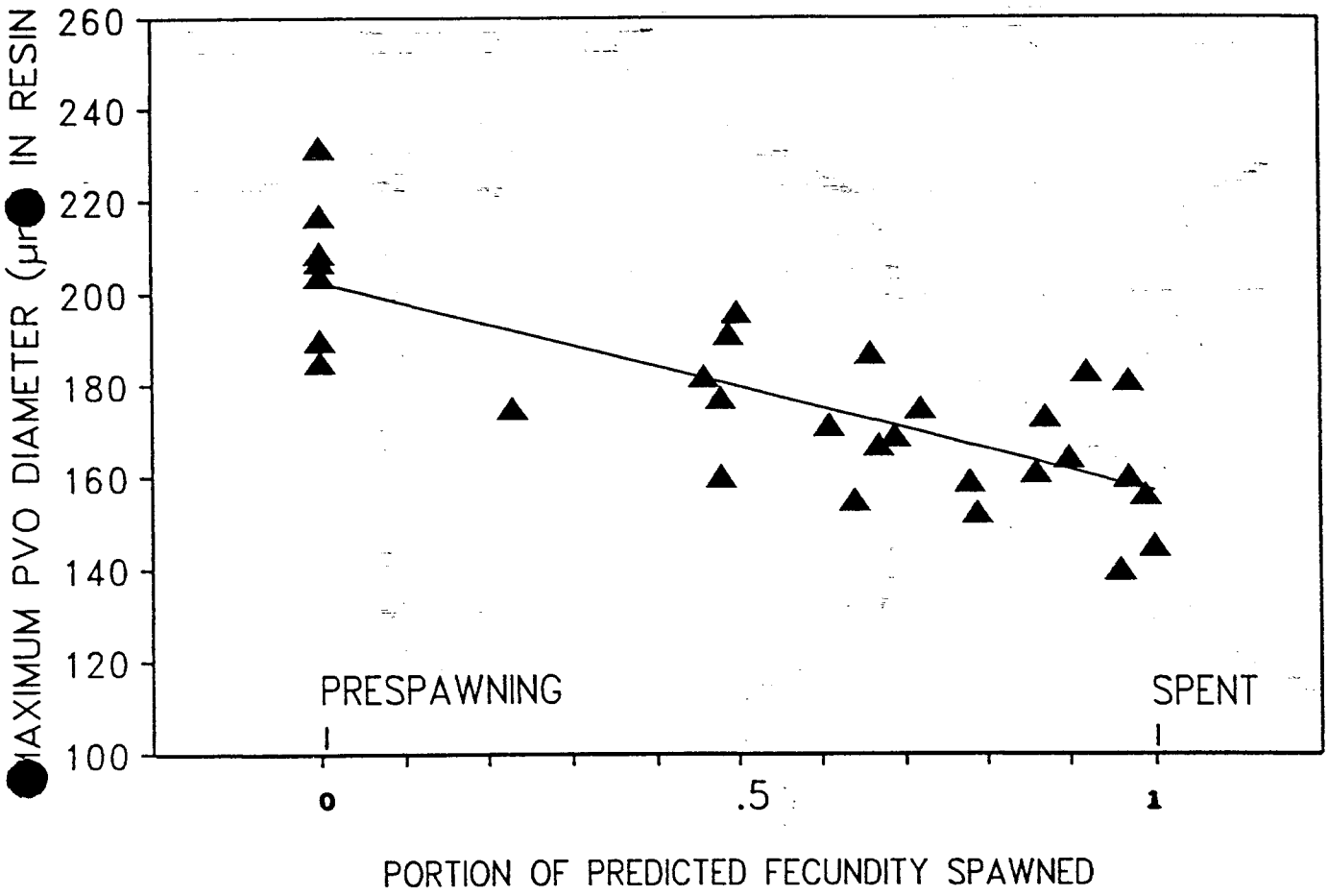


Figure 3. *Vitellogenesis size threshold in nearly spent fish*

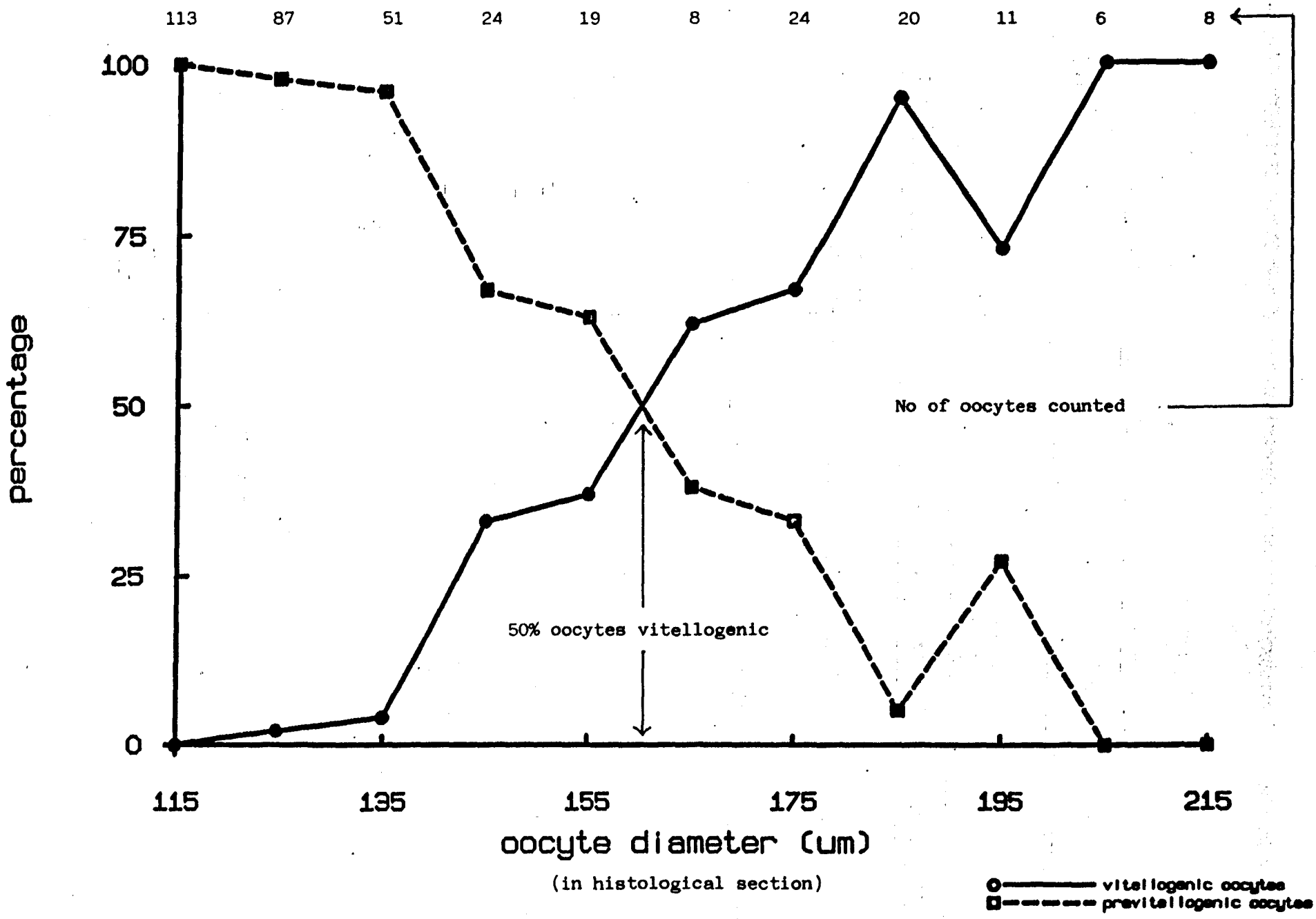


Figure 4. Fecundity/Length relationships - Western stock - 1989

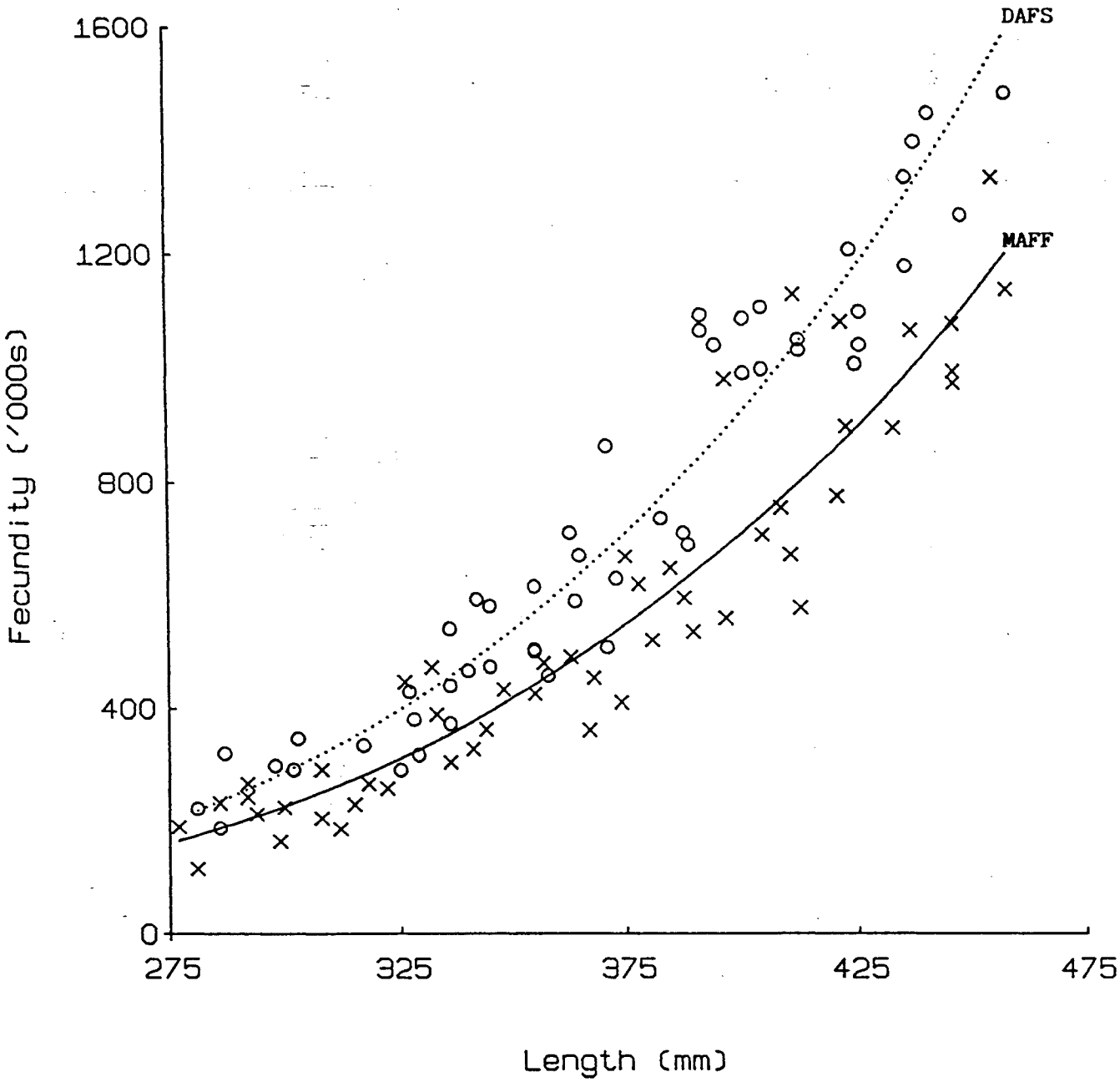


Fig.5 Western mackerel

Fecundity/length relationships

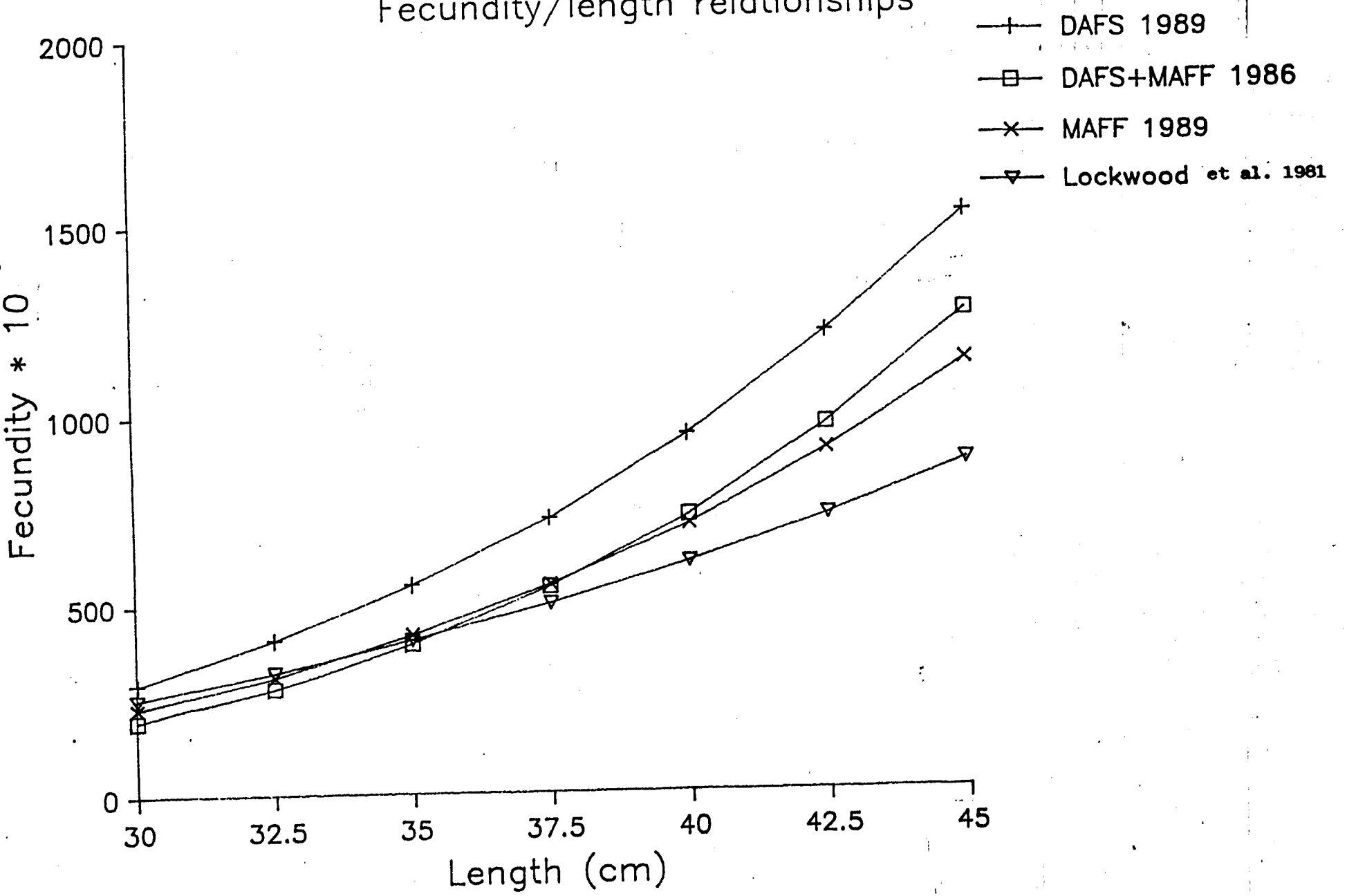


Figure 6. Fecundity/Weight relationships - Western stock - 1989

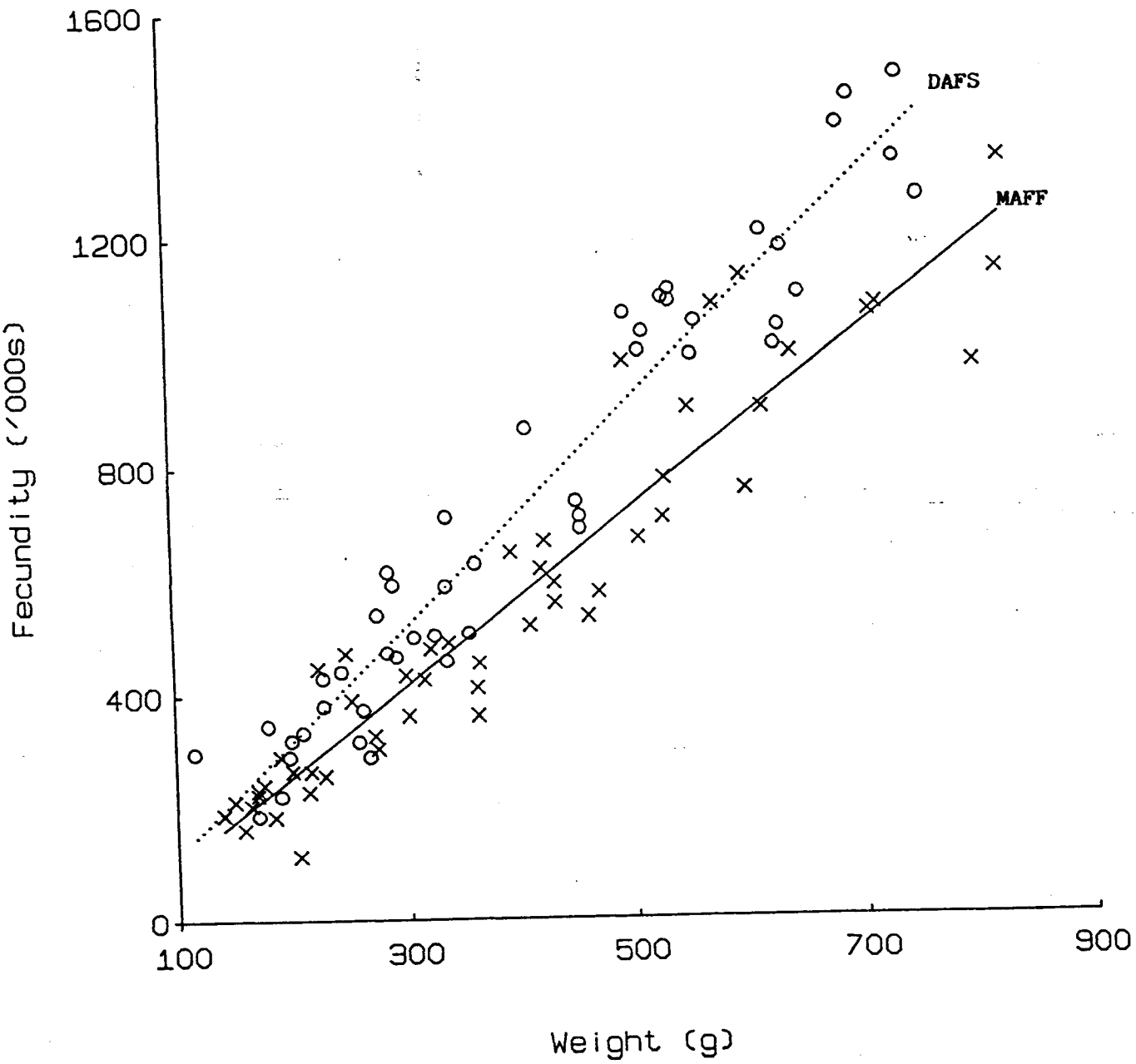
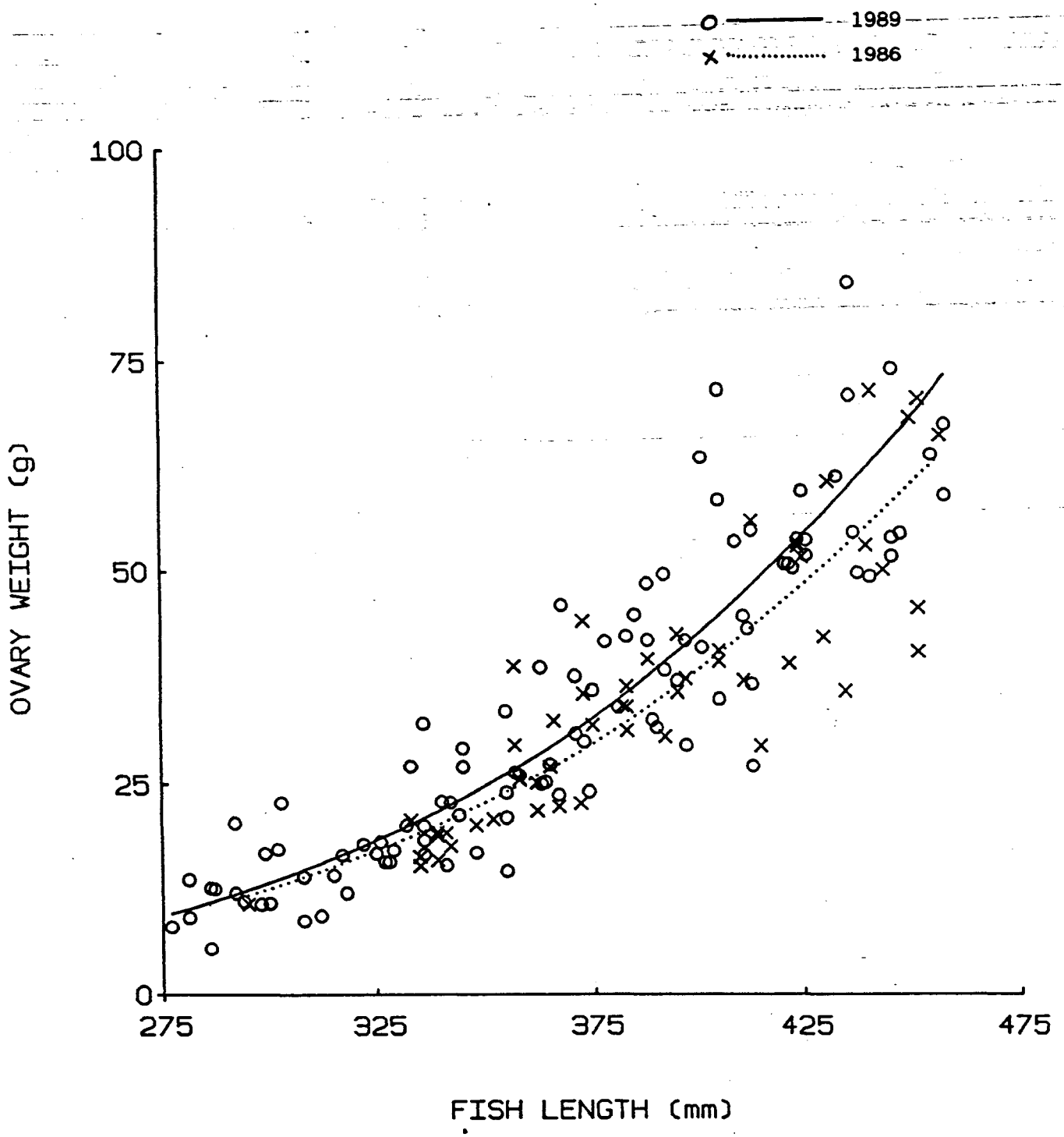


Figure 7. MACKEREL OVARY WEIGHT/FISH LENGTH RELATIONSHIPS



APPENDIX 1

Mackerel maturity key

Stage	State	External appearance
1	Immature	Gonads small. Ovaries wine red and clear, torpedo-shaped. Males pale, flattened and transparent
2	Early ripening	Gonads occupying 1/4 to 3/4 body cavity. Opaque eggs visible in ovaries giving pale pink to yellowish colouration, largest eggs without oil globule. Testes off-white, milt not running
3	Late ripening/ partly spent (early)	Gonads occupying 3/4 to almost filling body cavity. Ovaries yellow to orange. Largest eggs may have oil globules. Testes creamy white
4	Ripe	Testes filling body cavity, milt freely running. Ovaries characterised by externally visible hyaline eggs no matter how few or how early the stage of hydration. Ovaries with hyaline eggs only in the lumen are not included. Ovary size variable from full to 1/4
5	Partly spent (late)	Gonads occupying 3/4 to <1/4 body cavity. Ovaries slacker than in stage 3 and often bloodshot. Testes with free running milt and shrivelled at anus end
6	Spent/recovering spent	Gonads occupying 1/4 or less of body cavity. Ovaries reddish and often murky in appearance, sometimes with a scattering or patch of opaque eggs. Testes opaque with brownish tint and no trace of milt

APPENDIX 2

Changes in volumetric technique in 1989 compared to 1986

- DAFS changed from using water to a sucrose solution as the suspension medium and from a hand-held to an electrically-operated Stempel pipette. Ten replicate samples of water were weighed giving a mean subsample weight of 1.02 g (s dev 0.01), the equivalent volume (1.02 ml) was used in calculations of fecundity. The advantage of the electrically operated system over a manual one is that it eliminates differences in speed, angle and position of sampling between different subsamples and operators.

- MAFF continued to use a volumetric method as before but changed from measuring volume to weighing the suspension medium and each subsample. They established that the actual volume of their standard Stempel pipette (nominal vol 0.5 ml) was some 9% higher than the nominal volume. Seven replicate samples of sucrose solution were taken giving a mean weight of 0.6636 g (s dev 0.0037 cv 0.5%), this value was used in their calculations. In 1989 a VIDS V system was used in conjunction with the binocular microscope used previously.

APPENDIX 3

Data used to determine oocyte diameter (um) above which to make fecundity counts

Sample code	Fish length cm	Ovary weight g	Mat stage (macro)	Oocyte diam		pvo/vit overlap gap threshold		
				max pvo	min vit			
S/H12/10	40	26.4	5	139	214	no	75	-
KC/23/81	34	10.2	5	162	197	no	35	-
KC/24/12	41	32.4	5	120	240	no	120	-
KC/23/86	36	10.0	5	148	131	17	-	ID
S/112/3	39	37.5	5	196	212	no	16	-
KC/27/29	35	4.1	6	195	nv	-	-	-
KC/25/18	36	5.9	6	156	264	no	108	-
S/112/2	33	5.7	6	172	124	48	-	144
KC/27/52	40	7.3	6	164	nv	-	-	-
KC/25/8	30	2.1	6	134	145	no	11	-
S/H12/18	43	9.4	6	142	138	4	-	138
KC/26/7	31	2.0	6	156	152	4	-	160
S/112/11	37	24.4	5	185	nm	-	-	-
KC/10/4	31	11.9	5	196	nm	-	-	-
KC/23/3	37	6.4	5	164	nm	-	-	-
S/112/7	37	9.8	5	187	nm	-	-	-
KC/11/17	37	11.0	5	169	nm	-	-	-
S/H12/7	39	10.6	5	152	nm	-	-	-
KC/38/10	40	12.4	5	173	nm	-	-	-
KC/38/6	31	6.2	5	159	nm	-	-	-
KC/23/15	34	4.3	5	160	nm	-	-	-
KC/11/8	40	13.4	5	140	nm	-	-	-
KC/10/15	38	5.4	5	156	nm	-	-	-

Key:

no none present
ID insufficient data
nv no vitellogenic oocytes
nm no measurements