SOMMAIRE

Pour convertir une estimation de la production d'oeufs de sprats dans le secteur nord-ouest de la Mer du Nord de manière à obtenir la biomasse de la population de poissons, on a calculé la fécondité des sprats échantillonnés de 1974 à 1976. Du fait que les sprats déposent leur frai sériellement, on a procédé à un examen histologique du cycle de maturation pour établir quelle est l'époque de l'année où il convient de déterminer la fécondité.

Le communiqué décrit les aspects intéressants du cycle de maturation des sprats mâles et femelles, et, sur la base des travaux histologiques, on a estimé la fécondité sur la base du nombre d'oeufs de 144 µm et plus présents dans l'ovaire avant l'époque du frai. En adoptant un régression adaptée de la fécondité logarithmique en fonction de la longueur logarithmique ou et d'un rapport entre le poids et la longueur des sprats à l'époque du frai, a estimé que la biomasse de population de poissons dans le secteur occidental de la Mer du Nord était de 4,1 x 10⁵ tonnes.

Le communiqué considère différents aspects de l'estimation de la fécondité dans les poissons qui déposent leur frai sériellement.

International Council for the Exploration of the Sea

C.M. 1977/ H:32
Pelagic Fish (Northern) Committee

PRELIMINARY OBSERVATIONS ON THE MATURATION CYCLE AND FECUNDITY OF SPRATS IN THE NORTH-WESTERN NORTH SEA

by

R.S. Bailey and R.K. Pipe
Marine Laboratory, Aberdeen, Scotland, UK

SUMMARY

To convert an estimate of sprat egg production in the north-western North Sea to spawning stock biomass, fecundity determinations were made on sprats sampled from 1974-1976. Because sprats are serial spawners, a histological examination was made of the maturation cycle to ascertain the appropriate time of year to determine fecundity.

The paper describes relevant aspects of the maturation cycle of male and female sprats and, on the basis of the histological work, fecundity was estimated as the number of eggs of 144 µm and above present in the ovary before spawning. Using a fitted regression of log fecundity against log length and a weight-length relationship for spawning sprats, the spawning stock biomass in the western part of the North Sea was estimated to be 4.1×10^5 tonnes.

Various aspects of the estimation of fecundity in serial spawners are discussed.

INTRODUCTION

To estimate the size of the spawning stock of sprats Sprattus sprattus in various parts of the western North Sea, Johnson (1970a), Johnson & Dawson (1975) and Bailey & Braes (1976) carried out plankton surveys for sprat eggs and larvae. To convert the estimates of egg production obtained to the weight of spawning stock, these studies used published fecundity estimates obtained from sprats in areas outside the North Sea. It was clearly desirable, therefore, to obtain estimates of the fecundity of North Sea sprats. This paper describes the methods used and the results of fecundity estimates made at the Marine Laboratory, Aberdeen, from 1974 to 1976.

Determination of the fecundity of sprats, defined as the total number of eggs released in one spawning season, is difficult because the oocytes of individual sprats develop in batches over a long but unknown period (Heidrich, 1925). As a result, the ovaries of individual fish contain several size groups of oocytes destined to be released at successive spawnings, the intervals between which are not known. To estimate the total number of oocytes destined to be liberated during one season it is critically important to sample ovaries before the first batch of oocytes has been released, but after all the oocytes due to be shed that season have become distinct from the reserve oocytes. Since the spawning season is later in the northern North Sea than in the south, the maturation cycle is not synchronised throughout the North Sea population, and so the ideal time to collect fecundity material varies geographically.

The appropriate time to estimate fecundity in a given area can only be ascertained by microscopic examination of a series of ovaries collected over the whole period of maturation. As a first step, therefore, a histological examination of sprats at different stages of the maturation cycle was made to assess whether the stages of gonad maturation can be reliably distinguished macroscopically. For completeness the male maturation cycle was also investigated.

The maturation scale used for sprats at the Marine Laboratory is a modified version of that described by Johnson (1970b). For convenience the criteria used are listed in Table 1. In addition to a general comparison of the morphological and histological changes that accompany maturation, answers to a number of specific questions were required:

a. Is there any evidence that male or female sprats spawn at one year of age?

b. Can previous spawners be distinguished from first spawners outside the spawning season? If so, over what period of the year is this possible?

c. Is there any difference in the timing or duration of the maturation cycle of sprats of different sizes and ages?

d. During the spawning season, is it possible to distinguish gonads that have already released some of their spawning products?

Since the maturation cycle of sprats has been described in some detail elsewhere (Heidrich, 1925; Aleev, 1958; de Silva, 1973), only those aspects relevant to the present investigation are described in the present paper. For the purposes of this paper the birthday of sprats is taken to be 1 July. Thus, sprats spawned in the summer are termed 0-group throughout their first winter.

MATERIALS AND METHODS

Histological examination

For histological purposes sprats of a wide length range were sampled within 30 minutes of capture and the ovaries or testes preserved, after macroscopic classification, in Bouin's or Zenker's fixative. Details of samples taken are given in Table 2. Each fish was measured and the otoliths taken for age determination. The gonads were embedded in paraffin wax and sections were cut at 5 µm and stained with Mayer's haemalum and aqueous eosin. Oocyte diameter measurements were made only on those oocytes sectioned through the nucleus.

Fecundity determination

For fecundity determination, ovaries were preserved in 10% formaldehyde. Eggs were removed from the ovaries by pressure using a round-ended glass rod. The eggs were washed out into a vacuum sieve of pore size 115 µm. To break up and remove clumps of small, undeveloped oocytes, the material in the sieve was subjected to a strong jet of water.

After washing into a beaker, water was added to make the volume up to 200 or 400 cm^3 depending on the size of ovary. The contents of the beaker were stirred vigorously using non-rotary motion to disperse the eggs as randomly as possible. A subsample of 1 cm^3 was extracted with a stempel pipette as soon as stirring stopped and before settling occurred. All eggs above 144 µm diameter (5 eyepiece units) were counted under a binocular microscope (see below). Six subsamples were extracted and counted from each ovary.

To test the validity of the subsampling method all oocytes over 144 /um in diameter were counted in three ovaries of different sizes. The results given below indicate that the method used provided estimates very close to the true value.

Estimate from six subsamples with 95% confidence limits	Total count
32 200 ± 4 294	31 115
24 700 ± 1 446	24 618
4 160 ± 408	3 910

Sampling for fecundity determination was carried out in May 1974, June 1975 and June and July 1976. Sampling positions and details of the samples are given in Figure 1 and Table 3 respectively. Only fish at maturation stages 3 and 4 in Table 1 were sampled.

THE MATURATION CYCLE

Below, the histological stages are described in turn with an indication of whether they are adequately distinguished by macroscopic examination.

Maturation of the ovary

The immature ovary contains undeveloped primary oocytes ranging in diameter from 12-84 /um. Several ovaries at this stage were macroscopically classified as stage 2D (Table 4).

At histological stage 2 some of the primary oocytes had begun to increase in size, but there was no sign of yolk formation. The largest were 126 /um in the October sample, 156 /um in December and 170 /um subsequently. In May and June the developing oocytes at this stage had a covering of follicle cells which was not present in the winter samples.

Sprats recorded as stage 2 in June were all one year old on the evidence of their otoliths. It is not known whether they would have spawned later the same season.

Recovered spent (2R) ovaries were sometimes distinguishable from 2D ovaries by their thicker, folded wall (up to 200 /um thick) and by the presence of connective tissue among the oocytes. The oocytes of ovaries thought on this basis to be 2R were on average larger than those of 2D ovaries collected at the same time and this may mean that the former tend to develop earlier in the season. The mean oocyte diameter was also greater in December than in October indicating that maturation had begun during the early winter. No distinct 2R ovaries were found in the June sample, so fish which had spawned the previous year had probably by then reached a more advanced stage of maturation.

Macroscopically, discrimination between 2D and 2R ovaries was unreliable, even in the sample taken in October (Table 4). In particular a number of ovaries which histologically showed no evidence of previous spawning were macroscopically classified as 2R. It appears, therefore, that developing fish that did and did not spawn in the previous season cannot be distinguished without histological examination, and even then not with any certainty.

At stage 3 some oocytes contained yolk and the largest were 600 /um in diameter. In both the May and June samples almost all ovaries examined contained collapsed follicles indicating that at least one batch of eggs had already been spawned.

In addition to the largest developing oocytes, the ovary also contained resting oocytes ranging in diameter from 50-100 /um and developing oocytes of an intermediate size. The pooled size composition of oocytes in three stage 3 ovaries that had already spawned and three that had not (Figure 2) shows that three size groups of oocytes were present in the former, and three or possibly four size groups in the latter.

Since the first signs of maturation, ie an increase in mean oocyte diameter, were observed in the December sample it seems likely that oocytes take at least three or four months to develop to full maturity. If so, then it is unlikely that any resting oocytes found in June samples would be released the same season, unless development in the summer is very much more rapid. It may tentatively be inferred, therefore, that oocytes destined to be liberated in the same season can be distinguished by size alone from the late spring onwards.

Figure 2 indicates that resting oocytes range in size up to about 135 /um in mature individuals taken during the spawning season. To avoid including them in the fecundity estimates, only those oocytes larger than 5 eyepiece units (equivalent to 144 /um) were counted. A small proportion of developing oocytes may have been excluded on this basis.

In a number of ovaries preovulatory degeneration was in progress. Usually, only one or two oocytes per section showed signs of degeneration, but in one extreme case there appeared to be mass degeneration of a whole batch of ripening oocytes in about half the ovary. Degeneration on any scale will affect the validity of fecundity estimates. In the present study there was no evidence that it occurred on a significant scale early in the spawning season, ie May or June. No samples, however, were available towards the end of, or shortly after the spawning season in August and September. Consequently no estimate could be made of the percentage of developing oocytes that are not liberated.

From the data shown in Figure 2a an estimate was made of the relative quantity of oocytes in each size group. Excluding the residual oocytes, the groups, from largest to smallest, constituted 23%, 37% and 40% respectively. This may indicate that the first batch of eggs to be released is smaller than subsequent ones, although the proportions were not compared statistically.

At stage 4 the largest oocytes, up to 974 /um in diameter, contain large, faintly staining yolk vesicles dispersed through the cytoplasm. None of the seven fish sampled at this stage in either May, June or July showed any sign of empty follicles, yet these were normally found in stage 3 ovaries. With such a small sample it is difficult to interpret this finding, but it may suggest that empty follicles are resorbed or reorganised before the subsequent batch of oocytes reaches full maturity. If so, then the release of each batch of eggs is likely to be separated by a recuperationperiod, but this is at present of unknown duration. This finding, however, is not in agreement with that of Alеev (1958), who recorded the presence of "resorbing elements" (presumably both unspawned ova and empty follicles) in fish about to spawn their second or third batch of eggs. In only one stage 4 ovary was there any evidence of oocyte degeneration and then of a smaller developing oocyte.

Maturation of the testes

The immature testis is very small and threadlike. It contains primary germ cells amongst a meshwork of connective tissue septa. As development proceeds, the connective tissue forms tubules varying in diameter from 25-75 /um which contain primary germ cells and spermatogonia. In the developing testis, the tubules enlarge and develop lumina which become filled with cells at various

stages of spermatogenesis. Several distinct stages of development are therefore all classified under the macroscopic stage 2. In the most advanced stage 2 testis the lumina contain fully developed spermatozoa.

The testes of recovering spent sprats appear to differ from those of 2D fish for a relatively short period after spawning. Only in the October sample and in two fish in December was it possible to distinguish between stages 2D and 2R. The recovering spent testes in October were characterised by the thicker, folded connective tissue wall. The tubules of the testes at this stage appeared collapsed and, apart from connective tissue cells, the most numerous cells were primary germ cells, spermatids and spermatocytes, with some residual spermatozoa. Some fish classified macroscopically as recovering spents in the December and February samples were histologically indistinguishable from 2D fish.

Histologically it was possible to distinguish between stage 3 testes that had already released spermatozoa and those which had not. The latter, only recorded in the May and June samples, had large tubules containing many spermatozoa and spermatids, and also large numbers of densely-packed primary and secondary spermatocytes around the periphery. The tunica was very thin (1-2 µm). In testes that had already spawned the tunica was thicker (5-10 µm) and the tubules contained fewer spermatocytes but more primary germ cells and spermatogonia. The lumina still contained numerous spermatids and spermatozoa and each tubule presumably therefore liberates its spermatozoa in batches.

Spawning testes have the sperm duct packed with masses of mature spermatozoa. There was no clear distinction between those which had and those which had not already released spermatozoa.

The relationship between maturation, size and age

The number of sprat gonads sampled for histological examination is too small to quantify the relationship between maturation, size and age with any exactness. Nevertheless, a short analysis is given below for males and females separately. Details are given in Tables 5 and 6.

Males

In the October sample the smallest males showing signs of maturation were 10 cm 1-group fish. None of the 1-group fish sampled showed clear evidence that they had spawned previously and those examined at stage 1 are most unlikely to have done so. In December four 0-group males which were at the upper end of the length range for this age group showed the first indications of maturation, as did all the larger and older sprats. In February a similar pattern occurred. In the May sample most of the 0-group sprats were still at stage 2 whereas all the older sprats were more advanced. In June, however, three 0-group males were at stage 3 or 4 and it is therefore likely that they would have spawned before the end of the season. Following from this it is also probable that some of those 1-group sprats at stage 2 in October had already spawned.

With such a small sample it is not possible to state the length at which maturation first occurs. No stage 3 or 4 males, however, were found at a length of less than 11 cm. It is not known whether the smaller sprats at stage 2 in May would have been able to mature in time to spawn in the same season. Nevertheless, it seems clear that a proportion of male sprats first spawn at one year of age.

Females

In the October, December and February samples, all the 0-group females were immature, and the 1-group and older were at stage 2. In May, however, all the 0-group of 8.5 cm and longer were at least at stage 2 and three 0-group females from 10.5 - 11.5 cm in length were at stage 3. The sample in June was smaller, but the same pattern applied. It therefore seems likely that a proportion of the one year old females spawn.

In both May and June, a high percentage of the ovaries of fish 13 cm and over had empty follicles indicative of an earlier spawning. Since stage 3 females from 10.5 - 12.5 cm in length showed no such evidence, it seems likely that large sprats mature earlier in the season than the smaller fish. The smallest female sprat sampled for histological examination at stage 3 was an 0-group fish of 10.5 cm.

FECUNDITY ESTIMATES

On the basis of the histological work described above fecundity was defined for present purposes as the number of eggs of 144 µm or above in diameter found in stage 3-4 ovaries. Female sprats at these stages of maturation were collected over the length range 86-154 mm.

The estimates of fecundity tended to increase with length of fish and ranged from 1 900 - 51 900. For each sample a regression equation of log fecundity against log length was calculated (Table 7). A scatter diagram showing the individual observations in each sample is shown in Figure 3 together with a regression curve for all samples combined. There were marked differences in the fecundity-length relationship between samples and, to show this more clearly, the mean of the observed values of fecundity for each cm length group are given in Table 8 and regression curves for each sample are plotted in Figure 4.

Although there are considerable differences between the samples in the fecundity-length relationship, there is no simple way of interpreting them. The difference between the results for June and July 1976 (Table 8, Fig 4) may be due to partial spawning in the interim period. On this interpretation, however, the low values in May 1974 might indicate considerable annual variation although geographical variation within the north-western North Sea can also not be excluded (see Fig 1).

Three of the four samples indicate much lower fecundities at length than those published for the west coast of Scotland by de Silva (1973), also summarised in Figure 4. This difference may be due either to the fact that the North Sea ovaries had already released some oocytes, or to a difference in technique, since de Silva used a sieve of pore size 112 µm to separate out reserve oocytes and presumably counted all those retained. Alternatively, there may be regional differences in fecundity-length relationship. The period over which de Silva (1973) took his samples is not stated.

Other fecundity estimations have been made by Andreu (1966) for the sprat population off northwest Spain. A fecundity-length relationship based on his data (Table 7, Figure 4) lies within the range of the present values. Unfortunately the published results of Aslanova (1954) for the Black Sea and of Petrova (1960) for the Baltic do not include data in the form from which a fecundity-length relationship can be calculated. The former author, however, gives values of fecundity from 1 000 - 31 000 in fish ranging in length from 45-116 mm, very much higher values than those recorded for small sprats in the present investigation. Petrova's (1960) estimates appear to be within the range of variation of other estimates.

Further investigation is clearly needed to determine the source of the considerable variation between fecundity estimates made from sprats at different times and in different areas.

Estimation of Spawning Potential in the North-western North Sea

In a previous contribution, Bailey & Braes (1976) estimated the total sprat egg production in an area of the north-western North Sea from June-August 1975 to be 4.8×10^{13}. (Owing to an error in calculation this estimate should have been 2.4×10^{13}; the eggs present in the sea at any moment of time are the result of four, not two days spawning as previously supposed.) This estimate was converted to biomass of spawning stock using de Silva's (1973) published estimate of fecundity-weight relationship. As noted above, his estimates of fecundity at length were consistently higher than those obtained from the North Sea sprat and, consequently, the spawning stock biomass has been recalculated using the fecundity-length relationship obtained from the present data.

Although the estimates of fecundity obtained in the present study are, in general, estimates of "residual" fecundity, ie the number of developing oocytes present in the ovary after t e release of at least one batch, they can be used as an estimate of the numbe: of eggs likely to be liberated during the remainder of the season. Since the estimate of egg production given above was based on surveys carried out during the main spawning season, which, in the north-western North Sea, takes place from mid-June to August (Bailey & Braes 1976), only those fecundity samples taken in late May and the first half of June have been used to estimate a fecundity-length relationship to convert the egg production to number of females (Table 7).

To estimate the weight of female sprats required to produce a given quantity of eggs, a fecundity-weight relationship is required. Since ovaries were sampled for fecundity determination at sea, it was not possible to weigh the sprats sampled. Instead, separate samples were frozen for determination of weight-length relationship in June 1975 and July 1976. In addition numerous samples were taken in the spawning area around the Orkney Islands in June 1975 and July 1976 to obtain a length composition of the spawning population. The length composition of spawning males and females and the weight and estimated fecundity at each $\frac{1}{2}$ cm length interval are given in Table 9. From these and the fecundity-length relationship it was calculated that sprats spawn 970.9 eggs per g body weight. The weight of spawning females in the survey area is thus estimated to have been 24 700 t. Using a length composition for spawning males obtained on the same cruises (Table 9) and assuming an equal sex ratio, the total spawning stock is estimated to have been 46 500 t. This compared with an estimate of 25 500 t using de Silva's (1973) published fecundity-weight relationship based on sprats collected on the west coast of Scotland (cf Bailey & Braes 1976; but note correction of error mentioned above). Since the proportion of one year old sprats that spawn is not known (see Discussion), it is not known what relationship the estimate of spawning stock bears to the total stock including immatures.

The survey area is only a small part of the total spawning area in the North Sea. Using egg densities for the southern and central North Sea published by Johnson & Dawson (1975), the total spawning stock in the western half of the North Sea is tentatively estimated by direct proportionation to be 4.1×10^5 tonnes.

DISCUSSION

The present investigation reinforced the widely held conviction that estimating the fecundity of serial spawners presents special difficulties (Fischer & Balbontin, 1970). In the first place, the total duration of spawning of individual sprats is not known and, in the second, it is not known how many

batches they spawn in a season. Some previous authors have assumed that the number of eggs released at each spawning is the same, but evidence given above supports the earlier conclusion of Aleev (1958) that it may increase; as eggs are liberated, there may be room for a larger number to develop in successive batches. Thus, to estimate the number of batches, it is not appropriate to divide the total number of developing oocytes by the number in the largest group. In the case of sprats, therefore, it is likely that the number of batches is closer to the lower published estimate of three (Aleev, 1958) than to the higher published estimates of about six to nine (Aslanova, 1954; Petrova, 1960; de Silva, 1973). No experimental evidence exists to confirm either view.

Johnson (1970a) and Johnson & Dawson (1975) assumed that the eggs present in the sea during a survey were the result of one batch of spawning in their attempts to estimate spawning stock size in the southern North Sea. This, however, is not a strictly valid approach, partly for the reason given above that the number of batches and therefore their average size is not known, and partly because the period between spawnings and degree of synchronisation throughout the population are not known. To use egg surveys to obtain estimates of spawning stock size, there is thus no alternative to determining the spawning curve, and from this the total number of eggs spawned. The total fecundity must also be known with reasonable accuracy.

In the present investigation, the compromise used was to estimate the number of eggs spawned during the main spawning season and the number of eggs in the ovary immediately beforehand. The fact that some spawning had taken place previously is then irrelevant provided that it was produced by the same population.

To determine the number of eggs actually liberated by a female during the whole season, one requires to know the number of eggs that develop and the number which are resorbed both during development and after spawning has ceased, as pointed out by Macer (1974) in his study of T. trachurus. Aleev (1958) recorded the presence of resorbing oocytes in Black Sea sprats at the end of the spawning season, and MacGregor (1957) even suggested that resorption of the final batch of eggs may be characteristic of serial spawners. In the absence of any evidence, no allowance has been made for egg resorption in the present study.

In a protracted spawner it is not possible to determine the true fecundity, ie the number of eggs actually liberated, from a sample taken just before spawning begins. It is thus essential to carry out histological examination of the ovaries both of fish used for fecundity determination, as advocated by Fischer & Balbontin (1970), and of fish sampled earlier and later in the maturation cycle. Combined with the extensive sampling of larvae required to describe the spawning curve in each area of the North Sea, this would clearly be an enormous undertaking.

In the October sample there was histological evidence that some sprats with one winter ring on their otoliths, and therefore presumed to be one-year-olds, had already spawned. Johnson (1970b) also found evidence for first year spawners in the southern North Sea. In confirmation, some 1-ringed fish were also found at advanced stages of maturation in the summer in the present study. Since small one year old sprats, however, are not present in the spawning area during the spawning season, it is not possible to estimate what proportion of the population spawn in their first year. There is also at present no indication of whether the proportion of one-year-olds spawning varies from year to year, but since age of maturation is partly dependent on size, it may well do so.

ACKNOWLEDGMENTS

We wish to thank the following for their comments on an early draft of this paper: Dr J.R.G. Hislop, Dr J. Richards, Mr A. Saville and Mr M. Walsh.

REFERENCES

Aleev, Y.G. 1958 [On the biology and commercial importance of the Black Sea sprat Sprattus sprattus phalericus (Risso).] Trudy sevastopol. biol. sta. 10: 90-107. (Marine Laboratory, Aberdeen, translation, no 1581, 1970).

Andreu, B. 1966 Fecundidat del espadín atlántico (Sprattus sprattus) del NO de España. Inv. Pesq. 30: 589-602.

Aslanova, N.E. 1954 [The sprat of the Black Sea.] Trudy VNIRO, 28: 75-101. (Fisheries Laboratory, Lowestoft, translation N.S. 10, 1963).

Bailey, R.S. & Braes, A. 1976 Surveys of sprat eggs and larvae to the north and east of Scotland 1973-75. ICES CM 1976/H:29 pp 6. mimeo.

De Silva, S.S. 1973 Aspects of the reproductive biology of the sprat, Sprattus sprattus (L.) in inshore waters of the west coast of Scotland. J. Fish. Biol. 5: 689-705.

Fischer, W. & Balbontin, F. 1970 On the investigation of ovarial cycle and fecundity of fish with special reference to partial spawners. Ber. Dt. Wiss. Komm. Meeresforsch. 21: 56-77.

Heidrich, H. 1925 Ueber die Fortpflanzung von Clupea sprattus in der Kieler Bucht. Wiss. Meeresunters. Abt., Kiel. N.F. 20: 1-48.

Johnson, P.O. 1970a Sprat spawning surveys off the British Isles in 1959-67. Papers presented to Sprat symposium, Lysekil 1968. (Second Part) In medde. Havsfisk. Lysekil No 88. pp 21.

Johnson, P.O. 1970b The Wash sprat fishery. Fishery Invest. Lond., Ser. 2, 26, no 4, pp 88.

Johnson, P.O. & Dawson, W.A. 1975 The distribution of eggs and larvae of some pelagic fish species in the central and southern North Sea during June 1972. ICES CM 1975/H:13 pp 10. mimeo.

Macer, C.T. 1974 The reproductive biology of the horse mackerel Trachurus trachurus (L.) in the North Sea and English Channel. J. Fish. Biol. 6: 415-438.

MacGregor, J.S. 1957 Fecundity of the Pacific sardine (Sardinops caerulea). Fishery Bull. Fish Wildl. Serv. US 57: 427-449.

Petrova, E.G. 1960 [On the fecundity and maturation of the Baltic sprat.] Trudy VNIRO 42: 99-108. (Fishery Laboratory, Lowestoft, Translation, N.S. 20. 1963).

Table 1 Sprat Maturity Scale in use at Aberdeen

Scale		Description
1	Immature	Organs very small, (threadlike), and transparent.
2D	Developing virgin fish	Males partially transparent, females a transparent pink colour; organs approximately $\frac{1}{2}$ length of the body cavity.
2R	Recovering spent	Distinct red colouration with numerous blood vessels in females; males creamy-pink in colour; organs approximately $\frac{3}{4}$ length of the body cavity.
3	Ripening	Organs beginning to fill body cavity; ovaries yellowish-orange; testes white; opaque and transparent eggs visible.
4	Spawning	Eggs transparent; testes a milky white; both eggs and sperm flow freely.
5	Spent	Follicle bloodshot, baggy and empty, but may contain a few residual eggs and sperm.

Table 2 Details of gonad samples for histological examination

Date	Area	Testes			Ovaries		
		Number	Length range (mm)	Maturation stages	Number	Length range (mm)	Maturation stages
31 Oct 1973	Moray Firth	20	93–127	1, 2D, 2R	26	88–143	1, 2D, 2R
18 Dec 1973	Moray Firth	12	83–145	2D, 2R	15	49–150	1, 2D, 2R
5 Feb 1974	Moray Firth	6	96–146	2D, 2R, 3	7	82–150	1, 2R
28 May 1974	Moray Firth	20	82–152	1, 2D, 3, 4	21	82–164	2D, 2R, 3, 4
Jun-Jul 1975	Orkney area	24	85–150	1, 2D, 3, 4	24	91–153	2D, 3, 4

Table 3 Numbers of sprats sampled for fecundity determination

Length to ½cm below	28-30 May 1974 "Mara"	5-25 June 1975 "Clupea"	17-18 June 1976 "Explorer"	12-13 July 1976 "Clupea"	Total
8					
.5		1			1
9					
.5			1		1
10	1		4		5
.5	1		6	4	11
11	3		3	3	9
.5	1	2		5	8
12	1	1	1	4	7
.5	1	2	2	3	8
13	4	4	3	2	13
.5	6	8	7	1	22
14	3	5	3	1	12
.5	5	6			11
15	4	4			8
.5					
Total	30	33	30	23	116

Table 4 Comparison of histological and macroscopic classification of sprat ovaries at early stages of maturation

Classification		Month of sampling				
Histological	Macroscopic	October	December	February	May	June
		Numbers of fish sampled				
1.	1	1	3	1	0	-
	2D	1	1	0	1	-
	2R	0	0	0	0	-
2D	1	1	0	-	0	0
	2D	2	1	-	6	4
	2R	7	0	-	0	0
2R	1	0	0	0	0	0
	2D	1	0	0	1	1
	2R	11	7	6	1	0

Table 5 The ages of individual male sprats sampled at each length and stage of maturation in each month

Month of sampling	OCTOBER		DECEMBER		FEBRUARY		MAY			JUNE		
Maturation stage	1	2	1	2	1	2	1	2	3/4	1	2	3/4
Length												
8				0			0					
.5				0				0				
9	0			0			0,0				0	
.5	1,1,1			0		0	0,0					
10	1	1					0,0					
.5	1	1		1			0					
11	1	1,1		1		1					0	0
.5		1,1,1		1					1			0
12		1,1,1		1		1			1,1			0
.5		1,1,1							1,2			1,1
13						1			1,2			1,1
.5				1		2			1			1
14				2					2			
.5				2		3			2			
15									2			1

Table 6 The ages of individual female sprats sampled at each length and stage of maturation in each month

Month of sampling	OCTOBER		DECEMBER		FEBRUARY		MAY					JUNE				
Maturation stage	1	2	1	2	1	2	1	2	3	PS*	4	1	2	3	PS*	4
Length																
6																
.5			0													
7																
.5			0,0													
8			0		0		0									
.5	0							0								
9	0,0		0					0,0				0				
.5		1						0					0			
10		1,1,1		1				0,0								
.5		1,1,1				1		0,0	0				0,0			
11		1,1,1		1					0							
.5		1,1,1							0					0		
12		1,1,1		1		1					1					
.5		1,1,1		1		1					1					
13		1		1		1				1,2					1	
.5		2				2				1,3					1,1	
14		1,2		2						1					1	1
.5				2										1	1,1,2	1
15				3		2			3							2
.5																
16										3						

PS* denotes gonads with empty follicles which had therefore already spawned at least one batch of oocytes.

Table 7 Regression equations of fecundity F against length of fish in mm (L) using the relationship

$$F = aL^b$$

	a	b
May 1974	6.229×10^{-5}	3.9413
June 1975	7.404×10^{-6}	6.3101
June 1976	4.464×10^{-10}	6.5412
July 1976	3.314×10^{-15}	8.8700
Overall	2.072×10^{-6}	4.6734
May and early June samples only	1.959×10^{-8}	5.6000
de Silva (1973) West coast Scotland 1971-72	2.366×10^{-4}	3.8131
Andrew (1966) N.W. Spain 1955	2.005×10^{-2}	2.7857

Table 8 Mean fecundity at each cm length

Length group (cm)		May 1974	June 1975	June 1976	July 1976
8–9	mean		1 900		
	n		1		
9–10	mean			5 100	
	n			1	
10–11	mean	4 950		8 290	5 225
	n	2		10	4
11–12	mean	7 225	6 300	9 033	7 600
	n	2	2	3	8
12–13	mean	12 500	13 933	29 300	11 543
	n	2	3	3	7
13–14	mean	16 070	20 808	30 260	16 667
	n	10	12	10	3
14–15	mean	20 125	30 991	38 300	21 300
	n	8	11	3	1
15–16	mean	19 350	36 150		
	n	4	4		

Table 9 Length compositions of male and female spawning sprats, with mean weight and mean fecundity at each ½ cm length interval (Pooled data from June 1975 and July 1976)

Length to ½ cm below	‰ length composition of Ripe females	Ripe males	Mean[1] fecundity	Mean[2] weight in g
8				
.5	7.3	7.3	1 470	4.8
9				5.7
.5		2.2		6.7
10		3.4		7.8
.5		1.5		9.0
11	6.2	18.4	6 004	10.4
.5	13.3	19.8	7 660	11.9
12	13.4	75.7	9 673	13.5
.5	120.7	293.4	12 102	15.3
13	261.4	315.0	15 011	17.2
.5	281.8	173.4	18 471	19.3
14	177.5	71.9	22 561	21.5
.5	49.1	7.7	27 368	24.0
15	69.2	10.2	32 985	26.6
.5	0.1		39 516	29.4

Notes 1) Fecundity-length relationship

$\log F = -7.708 + 5.6 \log L$, where L is length in millimetres

2) weight-length relationship

$\log W = -5.325 + 3.0913 \log L$, where W=weight in g; L=length in millimetres

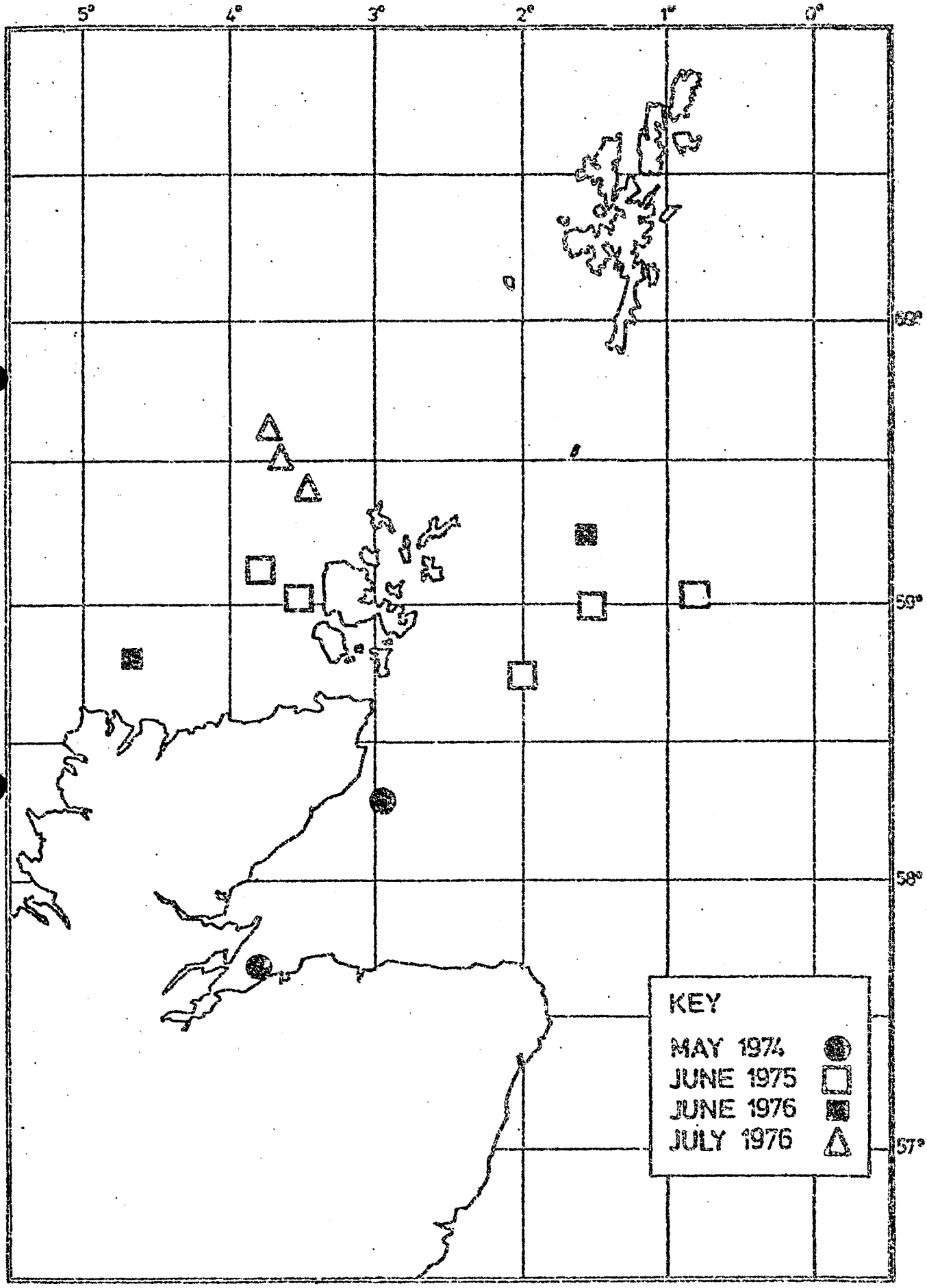

Figure 1 Sampling positions for sprat fecundity determinations.

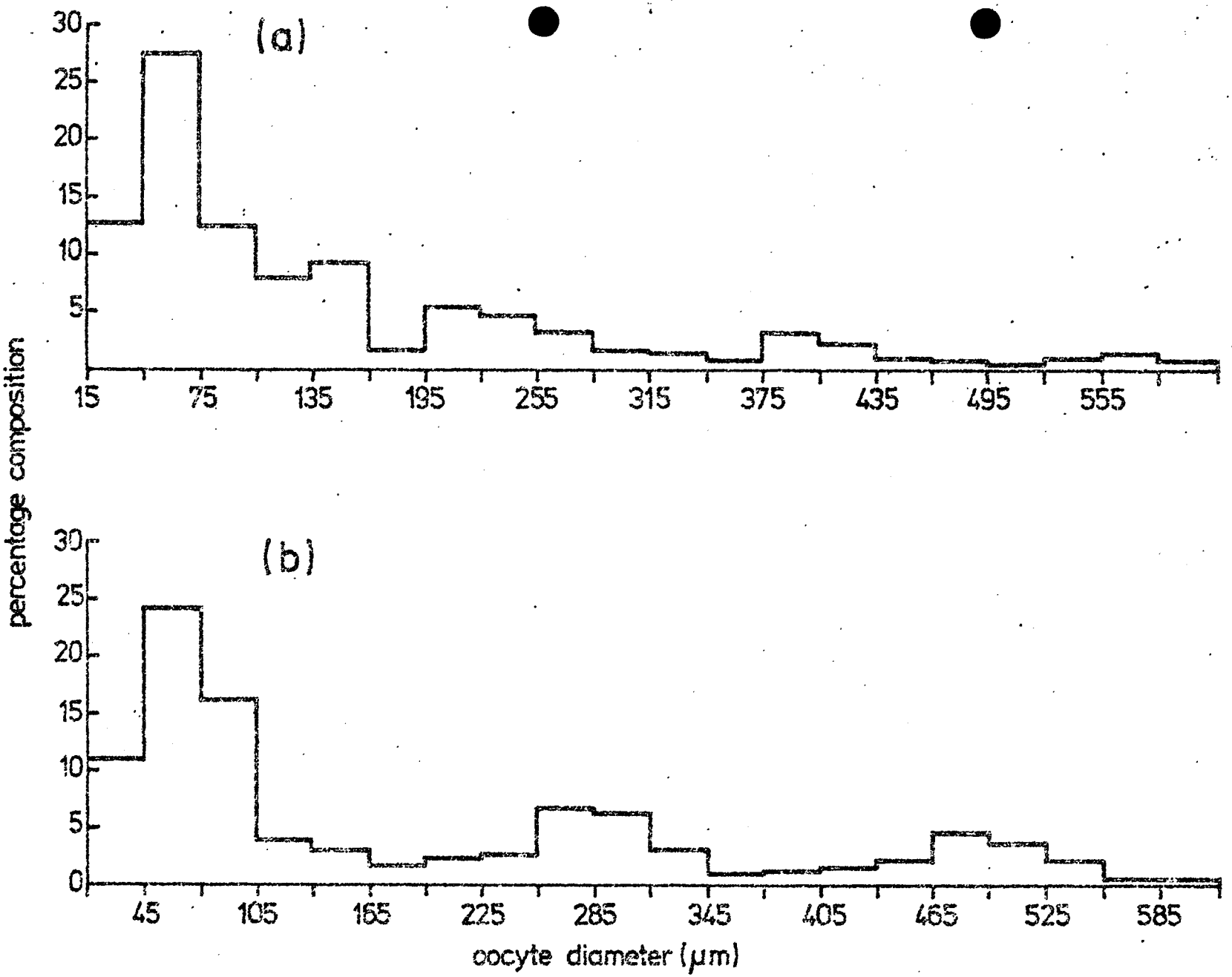

Figure 2 Pooled size composition of oocytes in
a. three ovaries which have not already spawned, and
b. in three ovaries which have already spawned a batch of oocytes.

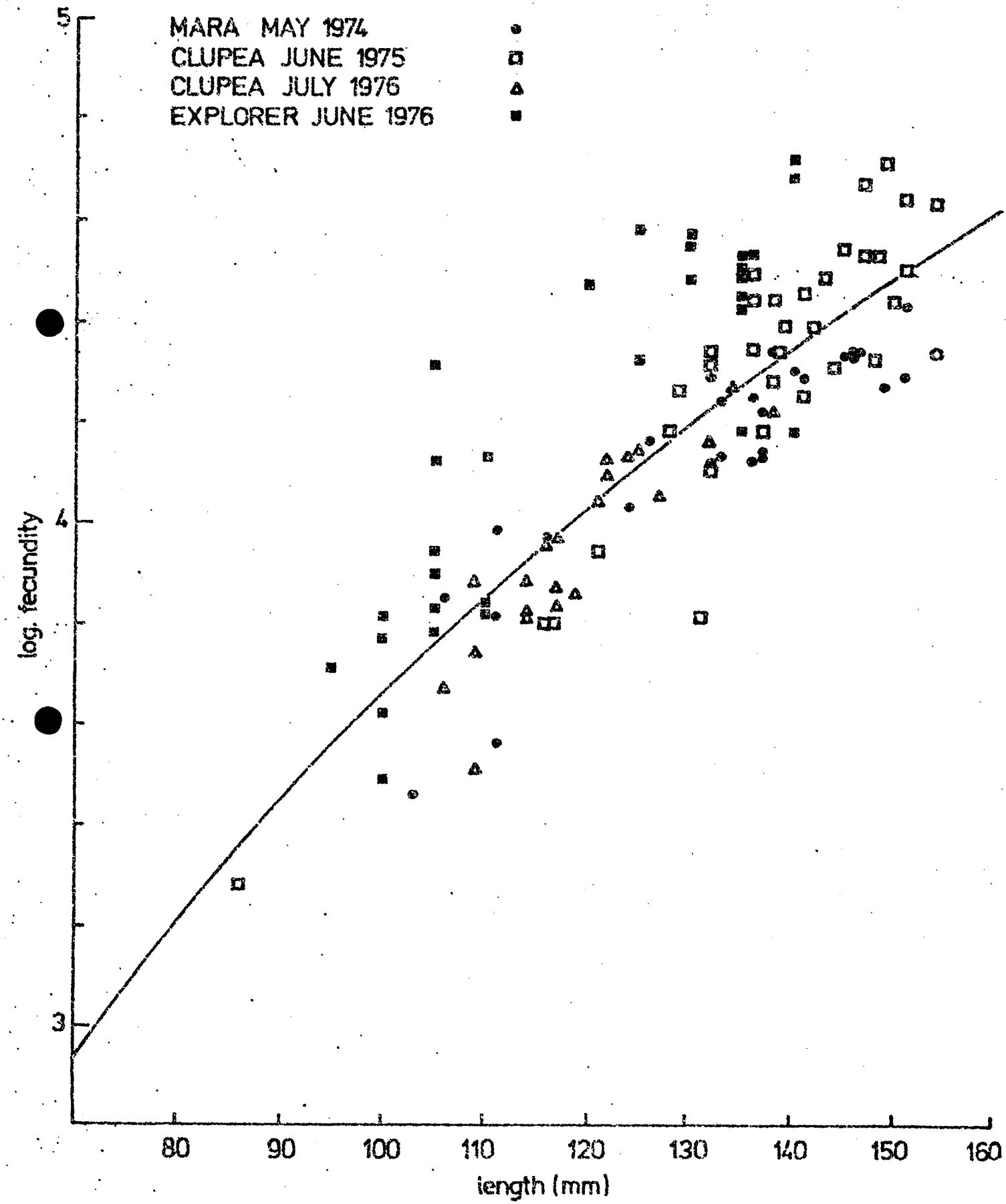

Figure 3 Estimates of log fecundity plotted against length of fish (mm), with fitted regression curve.

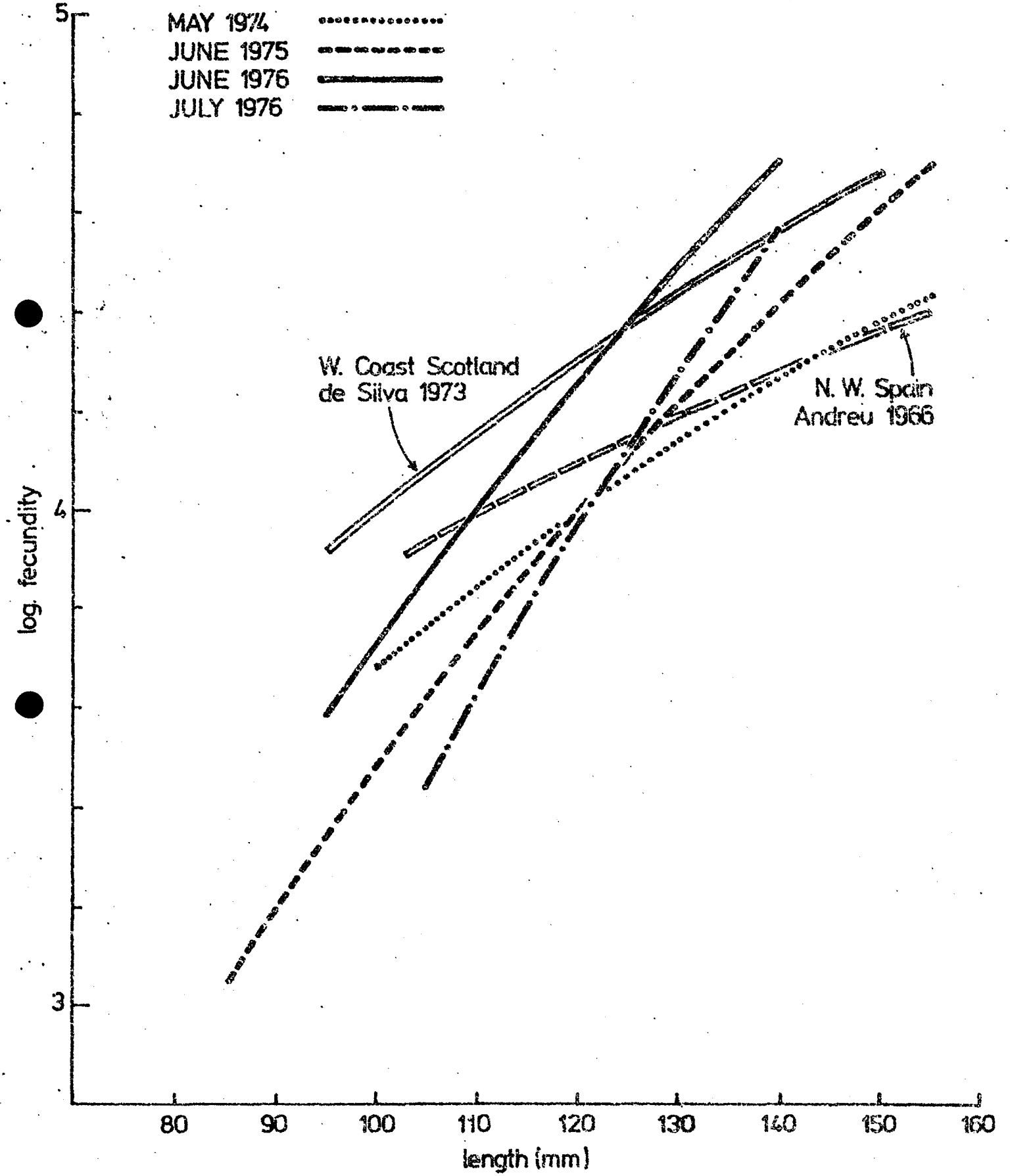

Figure 4 Fitted regression curves of log fecundity against length of fish (mm) on each survey and from published data.