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REPORT OF THE MACKEREL EGG AND RECRUITMENT WORKSHOP

25-29 January 1988, Aberdeen

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1. INTRODUCTION

1.1 Terms of Reference

At the 75th Statutory Meeting in Santander it was decided (C. Res. 1987/2:9) that a Mackerel Egg and Recruitment Workshop (Chairman: Mr A. Eltink) will be held in Aberdeen for five days in January 1988 to:

a) coordinate the timing and planning of the Mackerel Egg Surveys to estimate the total egg production of mackerel and horse mackerel;

b) discuss problems in mackerel and horse mackerel fecundity estimation and to review the basis for estimating spawning stock biomass from egg surveys;

c) evaluate the methodology and results of recruitment surveys for 0- and 1-group mackerel and horse mackerel.

In addition, information was required by the Mackerel Working Group on the percentage mature at age in relation to the egg production estimates (Anon., 1987b: Section 9.2). Further information was also needed about the mean weights and length distributions by age and maturity stage during the spawning season for both North Sea and western mackerel stocks (Anon., 1987b: Section 9.2) for both these purposes an agreed maturity scale is essential and this was considered in this report in addition to the main terms of reference.

The chairman of the Mackerel Egg and Recruitment Workshop (A. Eltink) asked J. Roe Hunter (Southwest Fisheries Center, La Jolla, California, USA), who is an expert on the "Egg Production Method", to prepare a working document on the subject, since he was not able to attend the workshop in person. The working document, however, did not reach the workshop in time. In view of its importance and because no other workshop participants had practical experience of the "batch fecundity method" this working document is included as an Appendix. It contains the authors opinions on a number of matters related to fecundity and its estimation in Scomber scombrus and Trachurus trachurus.

1.2 Participation

The workshop met in Aberdeen from 25-29 January 1988 with the following participants:

R S Bailey	UK (Scotland)
E Barnwall	Ireland
P Berrien	USA
W A Dawson	UK (England and Wales)
A Eltink (Chairman)	Netherlands
A Garcia	Spain
P Hopkins	UK (Scotland)
S A Iversen	Norway
E Kirkegaard	Denmark
L M Laird	UK (Scotland)
J Molloy	Ireland
J H Nichols	UK (England and Wales)
C Porteiro	Spain
I G Priede	UK (Scotland)
J Santiago	Spain
M G Walker	UK (England and Wales)
M Walsh	UK (Scotland)

2. NORTH SEA MACKEREL EGG SURVEY 1988

The last egg survey in the North Sea was carried out in 1986 (Iversen, Kirkegaard and Westgaard, 1987). This survey gave the lowest egg production ever estimated since these investigations started in 1980. The spawning stock was estimated at 50,000 tonnes. The surveys in the North Sea have been carried out on a yearly basis during the period 1980-1984 and since then every second year.

In 1988 the Netherlands, Denmark and Norway will carry out the investigations according to a time schedule given in Table 2.1. The investigations will cover both the egg production of mackerel and horse mackerel. The Dutch survey will cover the area and season of the main sole egg production. Horse mackerel spawn mainly in the southern and south-eastern parts of the North Sea. This part will be covered by three Dutch vessels (Tridens, Isis and a chartered vessel) during the period April to late July (Fig. 2.1). The first survey in April is assigned to sole because mackerel usually start spawning a month later with a peak in the second half of June. Usually spawning is over towards the end of July. The rest of the mackerel spawning area will be covered by the Danish ("Dana") and the Norwegian ("Michael Sars") vessels. The spawning season for horse mackerel is not totally known, but is probably similar to that of mackerel.

The main spawning area of mackerel is usually located between 55° and 58°N and between 1° and 5°E. This part will be covered more extensively than the rest of the area. Plankton samples will be sorted onboard and the surveyed area will be adjusted according to these results. However, the area most likely to be sampled are located south of 59°30'N and east of 0° (Fig. 2.1).

Usually the Skagerak has not been included in the investigations. Earlier studies have indicated that the egg production in this area might contribute about 5% of the total production (Iversen, 1977). The western part of the Skagerak will be checked once by "Dana" in June, close to the peak of the spawning season.

An interesting aspect of the surveys this year is that they will verify whether the abundant 1984 year class has recruited to the North Sea stock. If this year class which has been observed in considerable quantities in the North Sea each year since 1985 also spawns there, then this will result in a considerable increase in egg production compared to the production in 1986. In 1986 only very few mature fish of that year class were observed in the western spawning area and in the North Sea. However, the 1984 year class were represented in the spawning concentrations (22%) taken during the Irish Egg Surveys in 1987 (Molloy and Barnwall, WD 1988).

The 1988 mackerel egg survey in the North Sea should be carried out following the standard procedure described in Iversen and Westgard (1984) and Iversen et al. (1985).

The Danish and Dutch vessels will use a modified Gulf III type sampler while the Norwegian vessel uses a Bongo net. From previous surveys there are no indication of any difference in the catch efficiency between the two samplers and the choice of gear type is not expected to have any effect on the results.

A mesh size of 500 µm is suitable for sampling mackerel, horse mackerel and sole eggs and is recommended.

For the purpose of sampling sole eggs the Dutch ships should tow the Gulf III sampler in oblique hauls at a speed of 5 knots to as close to the bottom as possible. For mackerel and horse mackerel the Danish and Norwegian vessels should operate the samplers stepwise in depths of 0.5, 5, 10, 15 and 20 m. The Gulf III sampler should be towed at a speed of 5 knots, 2½ minute at each depth and the Bongo net at 2.5 knots, 5 minutes at each depth.

The standard fixative should be 4% buffered formaldehyde in distilled or fresh water.

At all plankton stations the temperature in the surface layer (approximately 5 m) is required. It is recommended that a temperature depth profile be recorded at each station.

Coordination of the 1988 North Sea mackerel egg survey will be through S.A. Iversen.

When two ships are at sea simultaneously, the scientists in charge should maintain regular radio contact (2431 kHz).

For each station information about the number of stage 1 eggs per m^2, the temperature in the surface layer and the catch data should be delivered to the coordinator before the beginning of October 1988.

The total egg production estimate and the age/length composition in the spawning area should be made available to the ACFM meeting in November.

It is recommended that the participants meet in November-December 1988 at the Institute of Marine Research in Bergen to assess the results and write a final report.

3. WESTERN MACKEREL EGG SURVEY 1989

3.1 Countries Participating

England, the Federal Republic of Germany, France, Ireland, The Netherlands and Scotland will all participate. The Research Institute for Fish Science and Technology, Basque Country (Spain) will participate subject to the availability of a survey vessel.

3.2 The Western Sampling Area

It was agreed that the spatial and temporal distribution of sampling would be directed at an adequate coverage of the spawning of both mackerel and horse mackerel and that estimates of egg production would be made for both species.

The spawnings of both species were examined from past surveys by analysing their maximum percentage contribution by rectangle to production of stage I eggs during the years 1980, 1983 and 1986, within five time periods (Figs 3.1 to 3.5). All rectangles which had contributed to production within a period in any of those years, together with those rectangles which have been sampled as zeros, are also shown in these figures. Resulting from this analysis it was decided to retain the eastern and western outer limits to the sampling area used in 1986. At the southern boundary the limit was extended to latitude 44°30'N, whilst at the northern edge the area was extended to latitude 56°N. The latter decision was based on the results of surveys conducted by Ireland, in 1986 and 1987, along the shelf edge up to latitude 60°N (Molloy and Barnwall, WD 1988). These surveys showed that, whilst at present the percentage contribution to the western mackerel egg production coming from the area north of latitude 55°N was small, there was the potential for a northwards spread of the spawning. In this context it was accepted that both Ireland and Scotland should sample along the shelf edge north of 56°N on an opportunistic basis in 1989.

3.3 Sampling Strategy

At the planning workshop for the 1986 western mackerel egg surveys it was decided to split the survey area into two zones of potentially high and low mackerel egg abundance (Anon., 1985a). Sampling in each zone was stratified with a higher proportion of the effort being devoted to the potentially high abundance zone. This basic strategy was successfully employed in the 1986 surveys (Anon., 1987a) and is again recommended for the 1989 surveys. However, for the 1989 surveys the potentially high egg abundance zone will not be rigidly defined. Examination of previous survey data shows that, for both mackerel and horse mackerel, this zone may vary for each sampling period. As a consequence a more flexible approach is favoured in which the decision on where to increase the sampling intensity will be left to the scientist in charge of each survey. As a guide to the areas of potential high abundance of mackerel and/or horse mackerel eggs, the rectangles which have previously contributed >2% to the production of either species in any period are shown in Figures 3.1-3.5. These data should be used together with preliminary shipboard enumeration of the samples to evolve a common sense sampling strategy. Once again the aim should be for something between a 1:1 and 2:1 sampling advantage to the rectangles in the high abundance zone. Zero observations should be kept to a minimum by discontinuing sampling along rows once very low numbers of eggs are observed in the sample.

At the planning stage for the 1986 surveys the sampling period was divided into three separate coverages of the spawning area (Anon., 1985a). During subsequent analysis of the results, the surveys were instead grouped into four periods. For the 1989 series some additional shiptime appears to be available which will allow good coverage of the spawning areas of both species within five separate periods. These periods comprise an early (April) and late (July) survey, plus three surveys during May/June. Sampling effort will again be stratified and concentrated into the central period. At least two vessels will participate in each of the May/June surveys with a single vessel only in April and July. At this early stage in planning the exact dates for each vessel's participation, are not available. However, the proposed coverage by participating countries is shown in Table 3.1.

3.4 Sampling Gear and Procedures

No changes in the sampling gear and survey procedures from those employed in the 1986 surveys were deemed necessary. These are described in detail in Anon. (1985a) Section 3.4 and are listed briefly below:

i) The basic sampler will be the modified Gulf III type. If this is not available other sampling systems are acceptable provided that volume filtered can be accurately calculated.

ii) The emphasis in sampling should be directed towards maintaining an even dive profile, with equal volumes of water filtered per unit of depth.

iii) Concurrent collection of relevant physical data during each haul is encouraged. The temperature at 20 m is required for egg production estimates and the temperature profile should again be used to modify the haul in the presence of a thermocline.

iv) The standard fixative should continue to be 4% formaldehyde in either distilled or fresh water, buffered to a pH of 7-8. An alternative fixative giving better definition of egg development stage for a more precise estimation of elapsed time since spawning is:

	Proportion
Ethanol (95%)	95
Formalin (10%)	10 (optional)
Glacial acetic acid	5

v) Only stage 1 eggs (Lockwood, Nichols and Dawson, 1981; Pipe and Walker, 1987) will be used in the production estimates. When calculating their abundance as per meter squared the egg densities as per meter cubed should be integrated over the maximum sampler depth.

3.5 Data Analysis and Coordination/Communication

3.5.1 Data analysis

All sample analysis for both mackerel and horse mackerel eggs should be completed as soon as possible. The data should be worked up to numbers of eggs produced per day using the formula for stage 1 for each species:

Mackerel:	ln time (hours) = -1.61 ln (T°C) + 7.76	(Lockwood, et al., 1981)
Horse mackerel:	ln time (hours) = -1.61 ln (T°C) + 7.71	(Pipe and Walker, 1987)

On completion the data should be sent to J H Nichols, Fisheries Laboratory, Lowestoft, Suffolk NR33 0HT, England. The data should arrive in Lowestoft no later than 6 October 1989 in order that a preliminary estimate of egg production for both species can be given to the ACFM meeting in early November. Copies of all the basic data and the egg production estimates will be sent to each participating country by J H Nichols.

It is recommended that an egg production workshop be held either in Lowestoft or in IJmuiden during the last week of January 1990 for the following purposes:

1. To complete the analysis.

2. To review the methodology of estimating spawning stock size from total fecundity and batch fecundity.

3. To review the estimate of atresia.

4. To prepare estimates of spawning stock size of mackerel and horse mackerel for the appropriate working groups.

3.5.2 Coordination/communication

Coordination of the western egg surveys will be through the workshop chairman (Dr A Eltink). In this context it is particularly important to notify him promptly regarding:

i) the dates on which cruises will start and end.

ii) dates and places of mid cruise breaks.

iii) the name of the scientist in charge of each cruise.

iv) a cruise programme (to all participants).

v) working frequencies and radio watches for ship to ship communication
(NB: 2431 kHz is allocated for research vessel use).

Regular contact should be maintained between vessels surveying within the same time period. Every effort should be made to communicate preliminary data between vessels leaving and entering the spawning area. These contacts are vital in order to maximise the use of research vessel time and ensure an adequate coverage of the spawning area during each period.

3.6 Additional Sampling

3.6.1 Environmental data

All participants should attempt to record temperature/depth profiles concurrent with the plankton tows. The temperature at 20 m depth is required to calculate egg stage duration but if this is not available then the subsurface temperature (3-5 m) should be used. As a minimum requirement at each plankton station, subsurface temperature and salinity must be measured. Participants are encouraged to monitor subsurface temperature, salinity and chlorophyll "a" fluorescence continuously throughout each survey. Such data should be recorded or logged in a format which can be made readily available to other countries. The environmental data will be collated and published on behalf of the workshop as a data inventory as for previous surveys (see Lockwood, 1985 and Milligan, in prep).

3.6.2 Parallel research programmes

Some additional sampling will again be undertaken as a complementary part of the 1989 western mackerel egg survey, to study the environment and recruitment processes in relation to mackerel eggs and larvae. At this stage in planning only the Federal Republic of Germany has indicated an intent to undertake such additional research in 1989. However, it is possible that England (MAFF/IMER) and The Netherlands will also participate. Included in these studies will be research on egg mortality and diel periodicity of spawning, which are aspects of direct interest in relation to egg production estimates.

An interest was expressed by England in the other eggs present in the samples in particular those of commercially important species, eg hake, lemon sole, sole and megrim. It was requested that if these eggs could be removed from the samples and kept in separate vials they should be sent to Lowestoft for subsequent analysis. In addition anchovy and sardine eggs found in the area south of 48°N should be sent to AZTI AB Basque Country, Spain, respectively to the IEO Coastal Centre of Vigo, Spain. An indication of the presence of other eggs in the sample should be made on the basic data sheets sent to Lowestoft.

Dr Julie Fives, University College, Galway, has again expressed an interest in working up some of the samples for fish larvae distribution and abundance. Her Department will sort the samples made available to her and would send copies of the results to the donors.

4. EGG STAGING

4.1 Mackerel/Horse Mackerel Egg Staging

It was recognised that there were no great problems in identifying stage 1 mackerel or horse mackerel eggs. However, attempts to calculate mackerel egg mortality from earlier surveys had highlighted some difficulties with the later stages. It was decided that a further exchange of samples between all participants, to compare staging, would be beneficial and would be arranged from Lowestoft.

4.2 Egg Stage Duration

Data on egg stage duration for both species are available over a relevant range of temperatures (Lockwood et al., 1981; Pipe and Walker, 1987).

An examination of diel periodicity of spawning does require a finer division of the egg development data for stage Ia. The existing experimental data would be re-examined in this context and if suitable would be made available to interested participants. If these data are not suitable consideration would be given to repeating the mackerel and horse mackerel development experiment covering the blastula stage.

5. FECUNDITY

5.1 Estimation of Fecundity

As in previous years, fecundity estimates in 1986 were of potential fecundity rather than realised fecundity. Potential fecundity is the maximum number of oocytes which might be spawned in the current season, with no allowance for resorption of developing oocytes (atresia). The estimation of potential fecundity assumes that the number of eggs destined to be spawned in a season is fixed and that these eggs are identifiable as developing oocytes in the ovary prior to the onset of spawning. The size threshold at which 50% of the oocytes are developing is determined and all oocytes above this size are counted in ovaries from the appropriate maturity stage.

Fecundity estimates used to determine spawning stock size in 1986 were:

Western mackerel: $\text{Fecundity} = 7.791 \times 10^{-7} \times \text{length (mm)}^{4.601}$ n = 113
Greer-Walker et al. (1987)

North Sea mackerel: $\text{Fecundity} = 560\ (\text{weight (g)})^{1.14}$ n = 67
$\text{Fecundity} = 1.35 \times \text{length (cm)}^{3.6}$ n = 67
Iversen and Adoff (1983)

Horse mackerel: $\text{Fecundity} = 0.0154 \times \text{length (cm)}^{4.717}$
Nazarov et al. (1977)

The fecundity-length regression used for western mackerel in 1977, 1980 and 1983 (Lockwood et al., 1981) is compared with the present regression in Figure 5.1. Estimated fecundities at 35 cm are similar, but the present regression indicates an increase in estimated fecundity for larger fish over the previous regression. For a 45 cm fish this increase is approximately 33%. The reason for this difference is not known.

The fecundity-length relationship for North Sea mackerel in 1982 is also comapred with that for western mackerel in Figure 5.1, indicating similar fecundity at length.

5.2 Total Fecundity Method

5.2.1 Methodology

Two possible methods of estimating fecundity were discussed - the traditional volumetric method described by Greer-Walker et al. (1987) and two variations on the stereological method described by Greer-Walker (WD 1988), Laird and Priede (1986) and Priede and Laird (WD 1988). The volumetric method relies upon a long period of digestion in Gilsons fluid, subsampling a suspension of the resulting isolated eggs with a Stempel pipette followed by counting and sizing the eggs under a microscope. In addition, histological samples are required to confirm the shipboard classification, to determine the size threshold of oocyte development and to estimate the number of atretic eggs.

The stereological methods enable an estimate of the fecundity to be made from a section through an ovary of known volume. Subsequently, in stained ovary sections, it is possible to count the total number of oocytes and gain the requisite histological information. However, although this method is preferable in many ways to the volumetric method, it is difficult to count the eggs above a fixed size threshold not defined by an objective criterion. For this reason the meeting decided to retain the traditional volumetric method for the 1989 fecundity estimate.

5.2.2 Is mackerel a determinate spawner?

Mackerel to date has been treated as a determinate spawner for the purposes of fecundity estimation. Thus, the total number of eggs counted prior to the onset of spawning is assumed to be equivalent to total fecundity. This assumption of determinate spawning has been questioned and is regarded as untenable for a range of pelagic species including anchovy and Pacific mackerel. An alternative batch fecundity method has been proposed for such species (Lasker, 1985). Mackerel is a multiple batch spawner and methods for estimating biomass used in California (MacCall et al., WD 1988) may be applicable to the western mackerel stock.

The evidence for and against the concepts of determinate or indeterminate spawning in mackerel are summarized below (see also Bailey et al. (WD 1988)). The meeting could not reach a decision as to which was the correct interpretation of the available evidence and further research is detailed in the working document. Although the total fecundity method will be retained in 1989 it was decided to make an estimate of daily egg production and attempt to implement the batch fecundity method in a pilot study.

Arguments that have been Adduced Against Determinate Spawning

"Determinate spawning" refers to the assumption that the standing stock of developing oocytes in the ovary at the beginning of the spawning season represents the total fecundity realised during the subsequent spawning season. There is evidence that true fecundity may be either higher or lower than this predicted value (Priede and Laird, 1986).

1. Varying degrees of atresia are observed, up to 30% of the prespawning standing stock (Mariduena, 1984; Priede and Laird, 1986). Therefore the full "potential fecundity" is frequently not realised.

2. In tank experiments many fish with normal standing stocks of oocytes at the start of the spawning season subsequently did not spawn. Spawning therefore is not physiologically obligatory. Therefore, despite a normal "fecundity" estimated at the start of the spawning season true fecundity can be zero.

3. There is no discontinuity in the size frequency distribution of oocytes between resting and vitellogenic oocytes (Macer, 1976; Priede and Laird, 1986). Egg development appears to be a continuous process and in principle therefore the standing stock at any time can never estimate the rate of egg production or total production (Hunter, Lo and Leong, 1985).

4. Small yolky eggs below 300 microns are present even late in the spawning season indicating that new development of eggs continues throughout the spawning season (Laird and Priede, 1987). This implies the possibility of true fecundity exceeding the standing stock at the start of the spawning season.

5. The population of previtellogenic oocytes is large, typically 10-15 times the standing stock of yolky eggs (Laird and Priede, 1987; Greer-Walker et al., 1987). This provides a vast reservoir of potential oocytes which can develop at any time.

6. The size threshold between vitellogenic and previtellogenic oocytes decreases after the onset of spawning (Priede and Laird, 1986). This implies that the previtellogenic oocyte are not resting cells but do develop into viable eggs during the course of the spawning season. This has been partially allowed for in the 1986 fecundity estimate by setting a size threshold lower than vitellogenic threshold (Greer-Walker et al., 1987).

7. There are indications that mackerel may be able to spawn every two days (Laird and Priede, 1987). Depending on the batch size this rate of spawning over the 100 days spawning season could realise a total fecundity far exceeding the prespawning standing stock of oocytes.

8. At the start of the spawning season the size frequency distribution of oocytes shows that only about 10% of the vitellogenic eggs are in the largest size category. The vitellogenic egg population is dominated numerically by small oocytes (Bara, 1960; Macer, 1976; Laird and Priede, 1987). Successful spawning requires a vast input of yolk to develop all these eggs to maturity. Spawning fish are observed to be actively feeding and they probably require continuing food intake to realise their full spawning potential. This has been shown experimentally in anchovies (Hunter and Leong, 1981; Hunter and Macewicz, 1985).

9. McCall et al. (WD 1988) regard spawning in Scomber japonicus as indeterminate and show that fecundity probably exceeds the prespawning standing stock of oocytes. To argue that Scomber scombrus is a determinate spawner requires that it differs fundamentally from this closely related species and all other Scrombridae so far investigated.

Laird and Priede (1987) argue that spawning output of Scomber scombrus depends on food availability and favourable conditions during the course of the spawning season. Total fecundity can be high or low depending on prevailing conditions and the end of spawning is marked by "mass atresia" of any remaining vitellogenic oocytes. This

model, if accepted, is incompatible with the "determinate spawning" hypothesis. Therefore, even if the determinate fecundity hypothesis is rejected, mean total fecundity realized by the population may remain close to previous estimates. Adjustments can be made to the estimate for some of the variations indicated above.

Argument in Favour of Determinate Spawning

1. Although oocyte maturation must continue after the first batch of eggs has been released, the existence of all stages of oocytes in the ovary does not of itself indicate that de novo production of developing oocytes occurs during spawning. Similar observations have been made on whiting in the aquarium where estimates of fecundity have been checked by counting the number of eggs produced over the spawning season (Hislop and Hall, 1974). Whiting shares with mackerel the characteristic of having all stages of oocytes present in the ovary during the spawning season.

2. The interpretation of data on changes in the number of vitellogenic oocytes during the spawning season depends on how fish are classified by maturity stage and in particular on where the boundary between partially and fully spent fish is drawn. Using the criterion of Hunter and Macewicz (1985) to define this boundary (spent fish being defined as those in which over 50% of vitellogenic eggs are atretic), the data indicate a downward trend in the number of vitellogenic oocytes through the spawning season. The absence of a downward trend is only apparent if ovaries with less than 50% atresia are classifed as spent. A second, independent, set of data also indicates a clearcut downward trend in the number of vitellogenic oocytes in ovaries as the season progresses. The documentation for these conclusions is given in Walsh (WD 1988d).

3. Although the size frequency distribution of oocytes prior to spawning suggests a continuous oocyte production a few ovaries possibly closer to spawning do show a discontinuous distribution with the discontinuity around 130 µm.

4. Atresia is not related to the question of whether potential fecundity is determinate or indeterminate and may simply be the means of reducing the output of eggs according to resources available.

5. The fact that the vitellogenic size threshold decreases as the season progresses (Priede and Laird, 1986) and is significantly higher just prior to spawning than the maximum size of resting oocytes in spent fish indicates that it may not in fact be a reliable measure of the size at which oocytes begin to develop from the resting stage. Bara (1960) suggests shrinkage of previtellogenic oocytes after spawning.

6. The critical question is whether oocytes smaller than the largest resting oocytes in spent fish (ie those smaller than 130 µm) cross this lower threshold, after spawning has begun. There is no evidence for this.

7. To argue that closely related species have common spawning mechanisms does not always bear scrutiny. For instance Scomber japonicus (McCall et al., WD 1988: Table 2) appears to have two spawning peaks in May and August. This is not the case for Scomber scombrus, which has a single spawning peak.

8. Further light is cast on the question of determinacy by using a stereological analysis to count the numbers of resting or previtellogenic oocytes over the spawning season. There is significant evidence that the number increases at some time between the beginning of spawning in March-April and after the end of spawning in September by about the equivalent of the potential fecundity (roughly 500,000-600,000). There is also evidence from the size distribution of resting oocytes, moreover, that their proliferation does not occur until after spawning has ended. Combined with the fact that there is no evidence of any depletion of resting oocytes during the spawning period, this suggests that there is no de novo proliferation of developing oocytes once spawning has begun (Greer-Walker et al., WD 1988).

The workshop agreed that mackerel could reduce fecundity through atresia. Disagreement centered on whether development of new eggs could occur to realize higher fecundity than indicated by the prespawning standing stock of oocytes. Analysis of batch fecundity and batch intervals in Scomber scombrus will help to resolve this difficulty.

5.2.3 Size threshold selection

An estimate of the total number of vitellogenic oocytes present prior to spawning is required for the total egg production method. The threshold at which eggs become vitellogenic was determined by Macer (1976) as 130 µm. Both MAFF (Greer-Walker et al., 1987) and the Aberdeen University have used cytological features from histological sections to identify the threshold and report values of 147 µm and 160 µm respectively. Because of the variations in thresholds, it was decided in 1986 to adopt the maximum size for previtellogenic oocytes after spawning as the threshold for counting. This will be re-evaluated in 1989.

5.2.4 Estimation of atresia

Preliminary estimates of atresia were made in 1986 using stereological techniques. It was noted that there were relatively high levels in spent fish but no correction was made for this in the final fecundity estimate. The meeting decided to make a full estimate of atresia in 1988 and 1989, both by maturity stage and in random samples of the population.

5.3 The Batch Fecundity Method and its Application

An egg production method for estimation of spawning biomass has been fully evaluated and described for the northern Pacific anchovy (Engraulis mordax L.) (Lasker, 1985). The method is being applied to a number of other stocks of pelagic fishes and it has been suggested that it could be applied to the mackerel stock assessment (Priede and Laird, 1986; Alheit et al., 1987).

The batch fecundity method avoids difficulties with estimation of total annual fecundity by basing the stock size calculation on samples taken during a short time span during the middle of the spawning season. Daily egg production is divided by mean daily female fecundity to give an "instantaneous" measure of biomass. Ideally, a measure of daily egg production is obtained in a single plankton survey. A random sample of fish is taken from the population and estimates are made of the proportion of fish spawning on that day together with batch fecundity in those that are spawning.

The main advantages of the batch fecundity method are:

a) Less shiptime is required since all the samples are taken during a short part of the spawning season.

b) Determinate fecundity is not assumed. Therefore, atresia and de novo vitellogenesis during the spawning season which give rise to potential errors in the total fecundity method do not affect the precision of the biomass estimate.

c) Potentially a quicker method since there is no need to wait till the end of the spawning season before the biomass estimate can be completed.

Disadvantages of the method are:

a) It is presumed that the entire spawning stock is represented in the spawning area when the sample is taken. There is evidence in the western mackerel stock that larger fish spawn earlier in the season than smaller fish (Dawson, 1986; Eltink, 1987).

b) Mackerel spawning is not as clearly synchronised to the diurnal cycle as in the anchovy. This can pose problems for sampling of the spawning population.

The main obstacle to application of the method to mackerel is sampling difficulties posed by the wide spread and patchiness of mackerel spawning both in time and space.

Bailey et al. (WD 1988) concluded that in view of these uncertainties abandonment of the total fecundity method would be premature, but necessary samples could be collected in order to carry out the biomass calculation using the batch fecundity method.

The measurments required to carry out the batch method calculation are:

P = daily egg production rate
W = average female weight
R = female fraction
F = batch fecundity
S = fraction of population spawning per day (or batch interval in days)

All these variables except F and S are already estimated for the total fecundity method. F requires a sample of fish in spawning condition. S requires a random sample of fish from the population.

F Batch fecundity:

The recommended method for estimation of batch fecundity is the "hydrated oocyte method" in which the hydrated oocytes are counted in a sample of ovarian tissue. Samples are required from at least 50 females together with the ovary free body weight (Hunter, Lo and Leong, 1985).

Trial estimates of batch fecundity in Scomber scombrus have been independently carried out by Priede and Laird (1986) (21 females) and Alheit et al. (1987) (22 females). The batch fecundity increases with fish length according to the relationship:

Priede and Laird (1986)

$$\text{Ln } F = 1.6590 \text{ Ln } L - 0.05433$$

Alheit et al. (1987) (refitted to data read from figure)

$$\text{Ln } F = 7.3319 \text{ Ln } L - 16.9538$$

where L is the length in mm and f is the batch fecundity. Both sets of data overlap but the Alheit data is restricted to a narrower range of fish lengths predicting a steeper increase in fecundity with fish length. Combining the two sets of data gives the relationship:

$$\text{Ln } F = 3.0617 \text{ Ln } L - 8.51019$$

Both sets of data agree that the mean batch fecundity for a typical 350 mm long fish would be of the order of 10,000. This is very much lower than equivalent data for Scomber japonicus giving a mean batch fecundity of 68,356 (13 females) (McCall et al., WD 1988). Priede and Laird (1986) did find three fish with F in excess of 30,000 and one with a batch fecundity of over 80,000.

The possibility remains that delayed release of eggs following ovulation in Scomber scombrus leads to low estimates of fecundity if the hydrated oocyte method is used (Alheit et al., 1987). The batch fecundity must be verified using an independent method and counting of eggs in the most advanced development phase prior to hydration is suggested by Hunter, Lo and Leong (1985). This could be accomplished using stereological methods (Laird and Priede, 1986).

S Fraction of spawning fish:

It is possible to recognise histological fish in various prespawning and post spawning states. If a given state has a duration of 24 h then the proportion of fish in that state indicates the proportion spawning within a 24 h time span. Thus, if the proportion of fish is 20% then the mean batch interval is five days. McCall et al. (WD 1988) recognised two such states which gave independent estimates of daily spawning fraction, 8.2% and 9.3% indicating a mean spawning interval of 12 days for Scomber japonicus. Some active spawning fish were spawning at an average interval of 1.3 days.

Priede and Laird (1987) detected multiple spawning states in Scomber scombrus samples indicating that these fish may also spawn at an interval of two days or less. Suitable samples for estimation of the mean spawning interval of mackerel have never been collected. Mariduena (1984) does give the percentage of fish in spawning condition (Stage 5) throughout the 1984 spawning season. This varies between 9% and 70%. This indicates that usually 50% or more of the population comprises non-spawning fish, indicating a mean batch interval greater than four days. It seems likely that the batch interval is normally in the range of 5-10 days.

There seems to be no reason why suitable random samples from the population should not be collected to estimate batch interval. Further tank experiments are necessary to estimate the duration of different oocyte development states in Scomber scombrus.

Within the context of the present egg survey plan a separate biomass estimate can be made associated with each egg survey.

It is concluded that batch fecundity calculations of biomass can be made in parallel with the total fecundity method. This will produce several quasi-independent estimates of spawning biomass to help assess the potential of the new technique.

5.4 Spawning Stock Size Estimates from Western Egg Surveys and VPA

The spawning stock estimates from the western egg surveys were compared to those derived from a number of VPAs, with input F values in 1986 ranging from half to double those used by the 1987 assessment working group (Hopkins and Bailey, WD 1988). All other parameters in the VPAs were those used by the 1987 working group except for input F values for the oldest ages, which were taken to be the unweighted averages of F for ages 4-9.

It was found that for 1977 the VPAs converged to agree reasonably closely with each other and with the 1977 egg survey estimates of SSB. More recent egg survey estimates agreed most closely with the VPA using F values in 1986 equal to those used by the 1987 working group. There is therefore no evidence to suggest that the egg survey estimates are seriously biased.

The results are summarized in the text table below. Results in columns headed F are from the VPA using input Fs in 1986 equal to those used by the 1987 mackerel assessment working group. Columns headed 0.5 x F and 2 x F are the results from VPAs using half and double these values respectively. Also shown are the egg survey estimates which would be obtained if the fecundity estimates were in error by a factor of two.

	Egg survey estimates (million tonnes)			Estimates from VPA (million tonnes)		
	Actual	(x 0.5)	(x 2)	F	0.5 x F	2 x F
1977	3.0	(1.5)	(6.0)	3.3	3.8	3.0
1980	2.9	(1.5)	(5.8)	2.3	2.9	2.0
1983	2.4	(1.2)	(4.8)	2.4	3.6	1.8
1986	1.5	(0.8)	(3.0)	1.8	3.6	0.9

5.5 Evaluation of Different Methodologies for Estimating Spawning Stock Biomass of Mackerel

In converting estimates of total egg production to spawning stock size, estimates of absolute fecundity (the number of eggs actually liberated) are of critical importance. While it has been recognised for some time that mackerel are batch spawners with a protracted spawning season, it has been assumed that the number of eggs destined to be liberated by a female during a single spawning season can be determined from counts of developing oocytes at some point prior to the onset of spawning (determinate spawning). From histological work on the development of mackerel ovaries, two potential sources of systematic error have been identified, namely atresia and de novo recruitment of new oocytes from the resting stage during the period of spawning (indeterminate spawning).

As described above, whether mackerel are determinate or indeterminate spawners is not finally resolved and there are two opposing views. Using the argument that they are indeterminate spawners, Alheit et al. (1987) have concluded that reliable spawning stock estimates cannot be obtained using current methods and that the "batch fecundity method" developed by Lasker (1985) and colleagues, for other batch spawners should be used. It is important to note, however, that application of the "batch fecundity method" involves a different set of requirements, including the need for an estimate of the percentage of the population spawning within a 24 hour period at the time of the relevant survey. In the first place the spawning area of western mackerel is immense and sampling of mackerel difficult. In addition it would be impossible with existing techniques to estimate the proportion of the total spawning stock that was in the spawning area at any particular time. For these reasons it is premature to abandon the current method of estimating mackerel spawning stock size in favour of a new method with another set of exacting requirements. There is, however, no reason why data amenable to analysis by the "batch fecundity method" should not be collected on future mackerel egg surveys.

While the current method of estimating spawning stock size from egg surveys and fecundity estimates may be subject to some error, comparison with VPA indicates that these errors are not large. The workshop therefore recommends that the current method used for the last four surveys should continue to be used, and that research be continued to evaluate the magnitude of any likely errors. In particular, the question of whether mackerel are determinate or indeterminate spawners needs to be resolved and the level of atresia to be quantified.

5.6 Horse Mackerel

In line with recommendations from the horse mackerel working group (Anon., 1987c) and the mackerel egg production workshop (Anon., 1987a) fecundity estimates will be made during 1988 by the Netherlands and possibly France. It was decided that the total fecundity should be estimated by volumetry in the same manner as the mackerel fecundity assessment (Greer-Walker et al., 1987) and the levels of atresia estimated. Arrangements have been made for the Netherlands to use the histological facilities at Lowestoft.

5.7 Fecundity and Maturity Requirements for the Western Mackerel Egg Survey 1989

1. A stratified fecundity sample of 10 fish/cm at maturity stage 4.1 will be collected from the central spawning area. One ovary lobe from each fish to be preserved in formalin for histological analysis and the other in Gilsons fluid or 50% ethanol for volumetric analysis. This sample will be evenly divided between MAFF and DAFS laboratories for working up.

2. To estimate the level of atresia and the interval between egg batches in the population a random sample of 100 fish will be collected from the central spawning area and preserved in formalin. This estimate will be made on three occasions, before, during and after peak egg production.

3. Length, age, sex and maturity will be recorded to produce a monthly maturity index.

4. As part of the pilot project to estimate daily egg production (batch fecundity method) batch size will be estimated. A sample of 50 ovaries containing hydrated eggs will be preserved in formalin for laboratory analysis on each of three occasions, before, during and after peak egg production.

5.8 Results of 1987 Captive Mackerel Experiments

In order to obtain further information on spawning a shoal of approximately 150 mackerel was maintained and some brought successfully through to spawning in the Marine Laboratory behaviour unit Aberdeen.

Spawning commenced in mid-April and continued until mid-June showing approximately the same seasonal pattern as the western stock from which they were obtained. Monitoring of egg production indicated some egg production on a daily basis until the beginning of June after which it became more spasmodic. A large proportion however, had been culled at this stage for histological analysis. An analysis of egg production on a 24 hour basis indicated that in the majority of cases spawning took place at night, however, this was not invariably the case and on two occasions spawning took place during the day and not during the preceding or following nights. This information is relevant to the timing of sampling at sea for application of the batch fecundity method.

Histological examination of ovaries prior to spawning indicated normal development prior to the migratory nucleus stage in most fish. The condition factor was higher than in wild fish at the same time of year. Although some fish successfully spawned some egg batches, histological examination of ovaries indicated high levels of atresia and that only a minority of fish had succeeded in releasing eggs.

6. MATURITY

6.1 Maturity Stage Classification

Most ICES countries use an eight stage maturity key described in Macer (1976). For the purpose of recent fecundity investigations a modified version of this key was used (Greer-Walker et al., 1987). Neither of these keys, however, has proved entirely satisfactory and it was agreed that a simpler standard key for adoption by all ICES countries would be useful.

A working paper outlining the purposes, requirements and problems associated with the currently used keys was presented (Walsh, WD 1988c) together with proposals for a new six stage maturity key.

Shortcomings of the Macer key were identified as follows:

1. The descriptions of external appearance are very imprecise and allow for too much between-sampler variation.

2. No purpose is served by having two mature stages.

3. Spent and recovering spent fish are difficult to tell apart.

4. Early post-spawning fish are almost impossible to distinguish from late pre-spawning ones.

The requirements of a good maturity key are:

1. That it should be simple and easy to apply, using well defined and objective criteria for distinguishing between stages.

2. The stage should enable the investigator to define the point reached in the spawning cycle.

3. The macroscopic stages should be as consistent as possible with underlying histological events.

In the case of a serial spawning fish, like mackerel, it is unfortunately impossible to meet all these criteria and it was agreed that a new scale should concentrate on meeting the first objective and that the second and third objectives could only be met by histological investigation.

The proposed new key was considered an improvement on the old, but requires further refinement to fully meet the first objective. It is recommended that the improved new key be circulated to all field workers for comment and revision to be coordinated by M. Walsh. If the new key receives general acceptance it is proposed that it be ratified by ICES and a small photographic manual be prepared for use by all ICES countries.

6.2 Spawning Ogives by Age

Until now spawning ogives by age were estimated from the number of immature and mature fish from both the juvenile and the spawning area (Lockwood et al., 1981; Anon., 1985a). These were estimated without weighting the samples from both areas according to the relative abundance of the immature fish of a particular age group in the juvenile area and the mature fish of that age group in the spawning area. This weighting could not be applied and its absence could therefore cause a severe bias.

A working document (Eltink, WD 1988) was presented at this meeting, which showed a method of estimating the percentage spawning fish by age group based on L1-measurements, which is independent of this weighting. Preliminary results of this method, which was carried out only on otoliths of the 1981 year class of mackerel (626 otoliths), indicated that about 35% of this year class 1981 at age 2 was actually spawning (c.f. 60% according to the maturity ogive presently in use (Anon., 1987b)). Further work is necessary to check the validity of this method. This method might also be applied for horse mackerel, since the same problems in estimating the spawning ogive occur for this species.

7. RECRUITMENT SURVEYS

7.1 North Sea

Recruitment indices for I- and II-group mackerel have been calculated from the North Sea International Young Fish Surveys (IYFS) for the period 1970-1986 inclusive (Walsh, WD 1988a). A more detailed analysis of mackerel data from the surveys up to and including 1979 is given in Walsh 1974, 1977 and 1979.

When the year class abundance indices are compared with estimates of the numbers of one year olds from VPA the relationship is very poor and the mackerel working group (Anon., 1985b) concluded that "the IYFS data are of little value as an indicator of year class strength, except for extremely strong year classes and they could not be used to assess recruitment". It is, however, possible that this conclusion was premature, since the 1969 and 1974 year classes were indicated by both VPA and the IYFS to be more abundant than the average of adjacent years. Also both VPA and IYFS data indicated a scarcity of all year classes since that of 1974. The workshop concluded that juvenile mackerel abundance indices should continue to be calculated from the IYFS data. For purposes of calculation the workshop endorsed the standard sampling area proposed in Walsh (WD 1988a) as shown in Figure 7.1.

7.2 Western Area

7.2.1 Available recruitment survey data

Several series of research vessel data covering varying time intervals are available from England, Scotland, Ireland and The Netherlands. The English survey data covers the Celtic Sea and Biscay. The Scottish surveys cover the west and north of Scotland, the Irish survey covers the inshore area to the west and north of Ireland and the Dutch the Celtic Sea and English Channel. The survey details and the time series they cover are summarised in Table 7.2.1. Although there has been extensive coverage of the juvenile area in recent years, the number of rectangles sampled during the survey period has varied considerably. Therefore it is difficult to calculate and compare abundance estimates from one year to the next with any reliability.

The fishing gear used on individual surveys has also been inconsistent in the past. The details of the fishing gear used by each country for the western mackerel recruit surveys is presented in a working document (Walsh, WD 1988b).

With these reservations in mind, the numbers of juvenile mackerel have been estimated from these surveys and used in a recruit indices programme using weighted averages (RCRTINX2, Shepherd pers. comm.). The method used to make these predictions allows different survey series to be used in the calculation. The technique has been discribed in the Methods Working Group Report (Anon., 1984; Anon., 1987d). The mackerel data used to run this program and the results are presented in a working document (Dawson, WD 1988).

Although the western area recruit surveys are primarily for mackerel, the more recent survey, 1985-1987, may also give an indication of horse mackerel abundance because their coverage has been more extensive.

7.2.2 Recommendations for future surveys

Although it is possible to combine the results from different series of surveys the changing migratory behaviour of mackerel makes it difficult to analyse the data in this way. In recent years the distribution of juvenile mackerel has changed considerably (Anon., 1987b; Anon., 1987e), and this makes it difficult to use a time series of data from any one series of surveys in isolation. The Working Group feels that the results from these surveys could be greatly improved if the surveys were combined as a single survey with standardized fishing gear, fishing method, survey area and time.

Gear

The working group agreed that consistent sampling of juvenile mackerel could best be achieved by a standard bottom trawl and that the GOV trawl would be the most practical to use. It also has the advantage that two countries already use this gear for the winter surveys so only two countries would have to change gear.

Survey area

Historical distribution data obtained during the period 1980-1987 give a good indication of where juvenile mackerel are most likely to be found. Figures 7.2 and 7.3 show the maximum abundance per rectangle taken per hour by bottom trawl for first winter (0/1 group) mackerel and second winter (1/2 group) mackerel respectively. Future surveys should therefore cover the areas where the highest concentrations are most likely to be found as a first priority. Also as much of the area as possible should be covered where lower concentrations have been found, so that possible shifts in distribution of juvenile fish may be detected.

A proposed standard sampling area based upon the juvenile distribution charts is given in Figure 7.4. It has been divided into two strata, one in which high abundances of juvenile mackerel are expected and the other in which low abundances are expected. High priority should be given to the area of high abundance and the workshop recommended that two stations be sampled in these rectangles, and one station in rectangles with low abundance.

Timing of surveys

The workshop feels that the appropriate time to carry out recruit surveys is November-March. The advantages of an early survey (November-December) are:

i) they have been carried out at this time during the past three years,

ii) the abundance indices will be available for assessment purposes early in the year,

iii laboratory research vessel time tends to be less committed to other work at this time.

Fishing stations

These should be at fixed positions within allocated statistical rectangles. This would reduce the risk of gear damage and increase comparability between different years and vessels. The stations should be spread over the sampling area, such that they are not concentrated in adjacent corners of neighbouring squares or along rectangle boundaries.

The proposal for standardisation of young mackerel surveys of the western stock is discussed in more detail in a working document (Walsh, WD 1988b).

7.2.3 Recommendations

The workshop recommends: 1) that all historical data available on the distribution and abundance of juvenile western mackerel be written up jointly by representatives of countries participating in these surveys, 2) a manual of standard survey procedure be prepared for future surveys similar to that used for the North Sea International young fish surveys, 3) if standardization of fishing gears is not possible, the different gears used should be calibrated by overlapping the area coverage of different countries.

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TABLE 2.1

1988 North Sea Mackerel Egg Survey. Available shiptime.

Research vessel	Period
Tridens & Isis & chartered vessel	4-15 April, 25 April - 6 May, 16-27 May, 20 June - 1 July, 18-29 July
Michael Sars	15 June - 15 July
Dana	31 May - 17 July

TABLE 3.1

Proposed deployment of research vessel time for the 1989 western survey by participating countries; Federal Republic of Germany (FRG), Scotland (SCO), France (FRA), The Netherlands (NET), England (ENG), Ireland (IRE) and Spain (SPA).

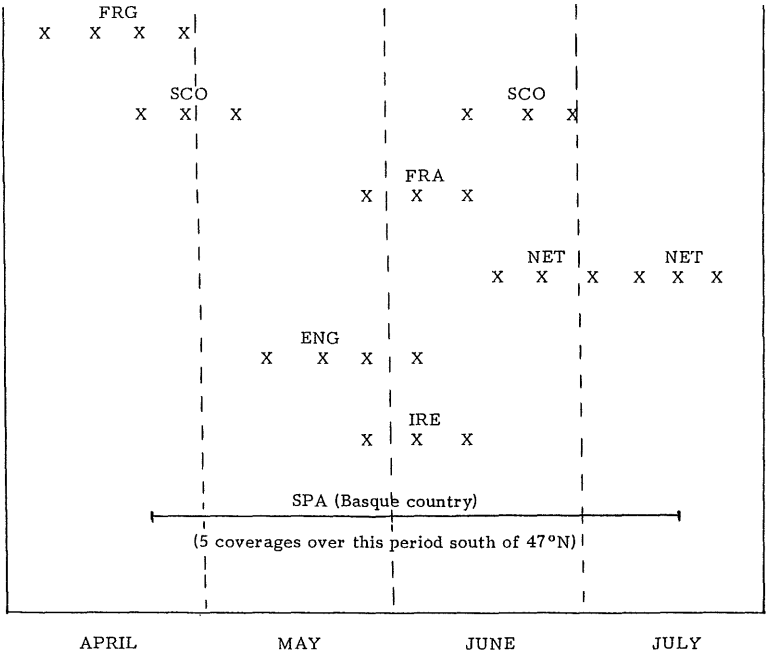


TABLE 7.1

Western mackerel juvenile areas surveyed.

Survey	Area	Month	Years	
English	VII & VIII	March	1982-1987	NB 1982 (Apr)
English	VII	December	1981-1987	
English	VIII	December	1983-1985	
Scottish	VIa	March/April	1980-1987	NB 1985 (Jan)
Scottish	VIa	December	1985-1987	
Irish	VIa/VIIb	October/November	1981-1987	
Dutch	VII	November/December	1985-1987	

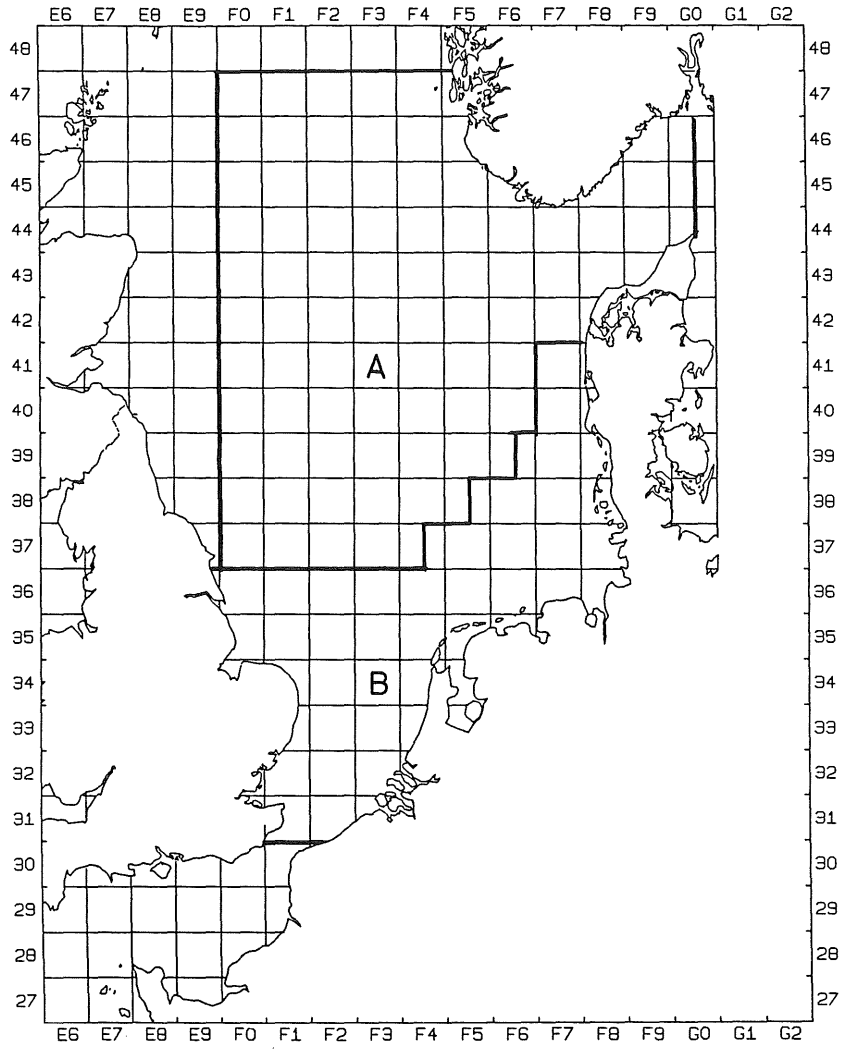


Figure 2.1 The area to be surveyed in 1988 by Denmark and Norway (A) and by the Netherlands (B).

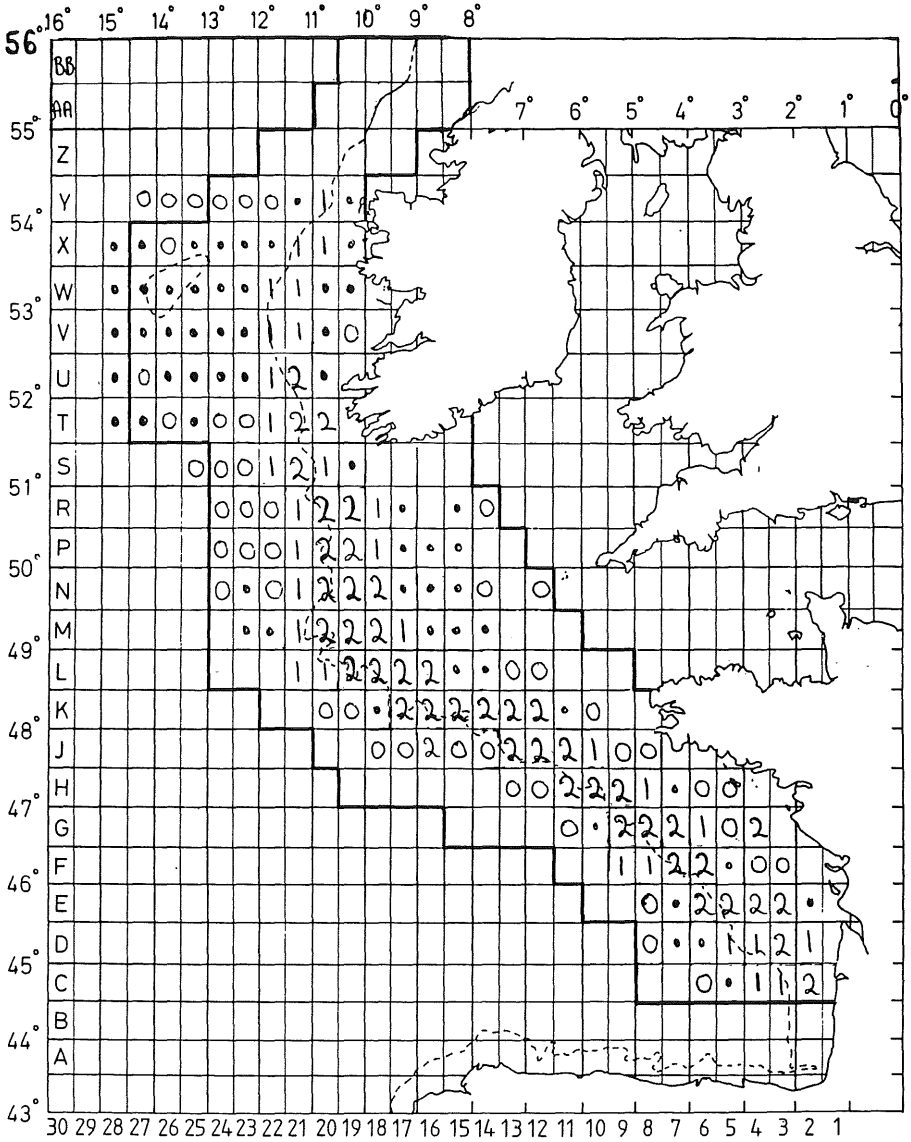


Figure 3.1 The limits of the survey area for 1989 showing the maximum contribution of any rectangle to the stage 1 egg production of either mackerel or horse mackerel from previous surveys during the period 9 March - 27 April.

0 = no contribution; . = < 0.5%;
1 = 0.5% - 1.9%; 2 = > 1.9%.

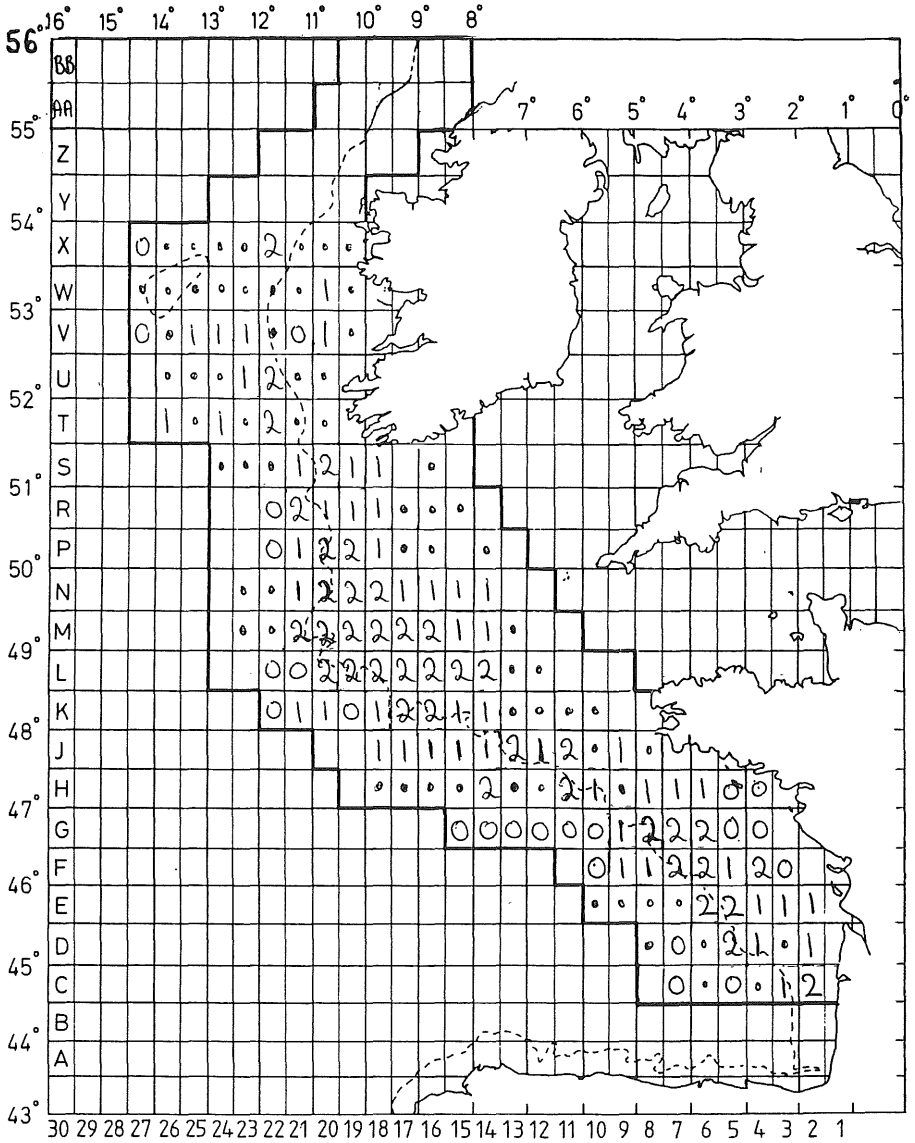


Figure 3.2 The limits of the survey area for 1989 showing the maximum contribution of any rectangle to the stage 1 egg production of either mackerel or horse mackerel from previous surveys during the period 29 April - 18 May.

0 = no contribution; . = <0.5%
1 = 0.5% - 1.9%; 2 = >1.9%.

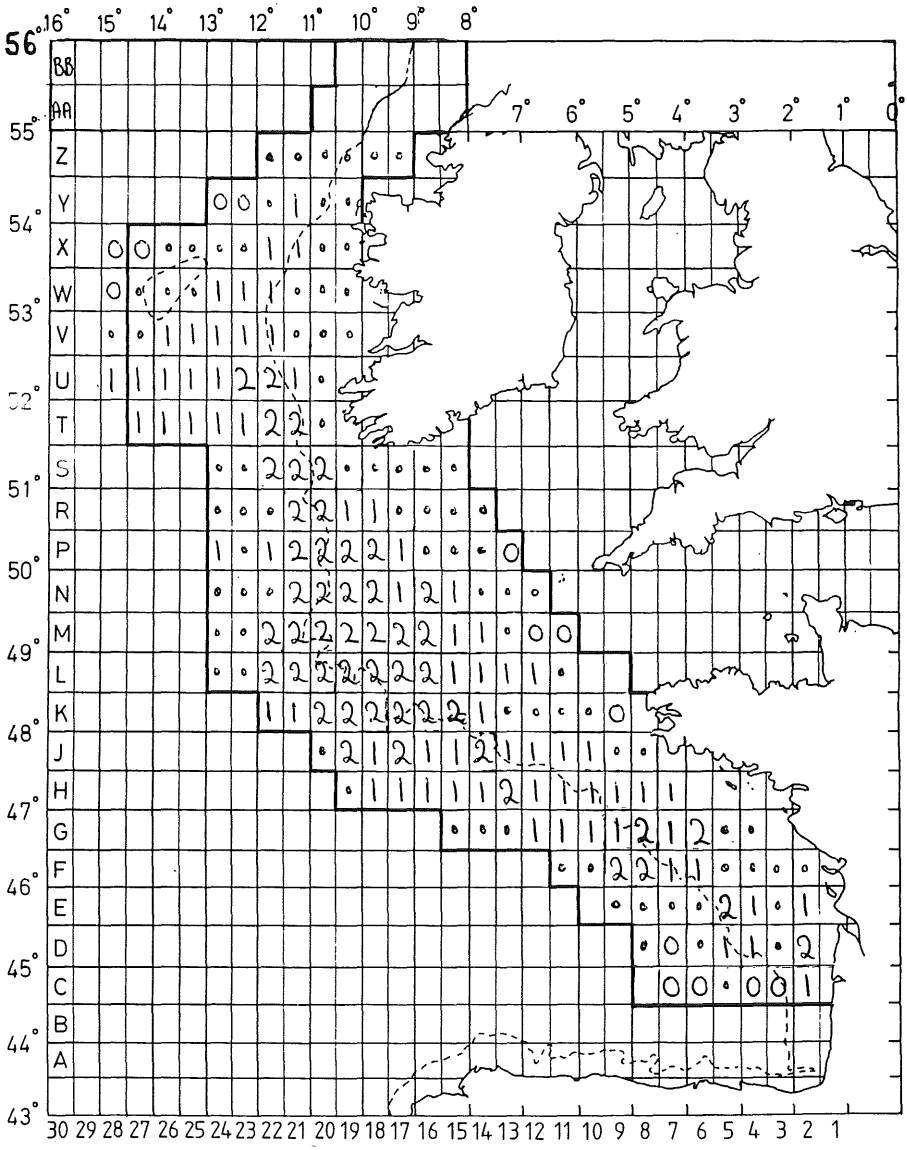


Figure 3.3 The limits of the survey area for 1989 showing the maximum contribution of any rectangle to the stage 1 egg production of either mackerel or horse mackerel from previous surveys during the period 11 May - 17 June.

0 = no contribution; . = < 0.5%;
1 = 0.5 - 1.9%; 2 = >1.9%.

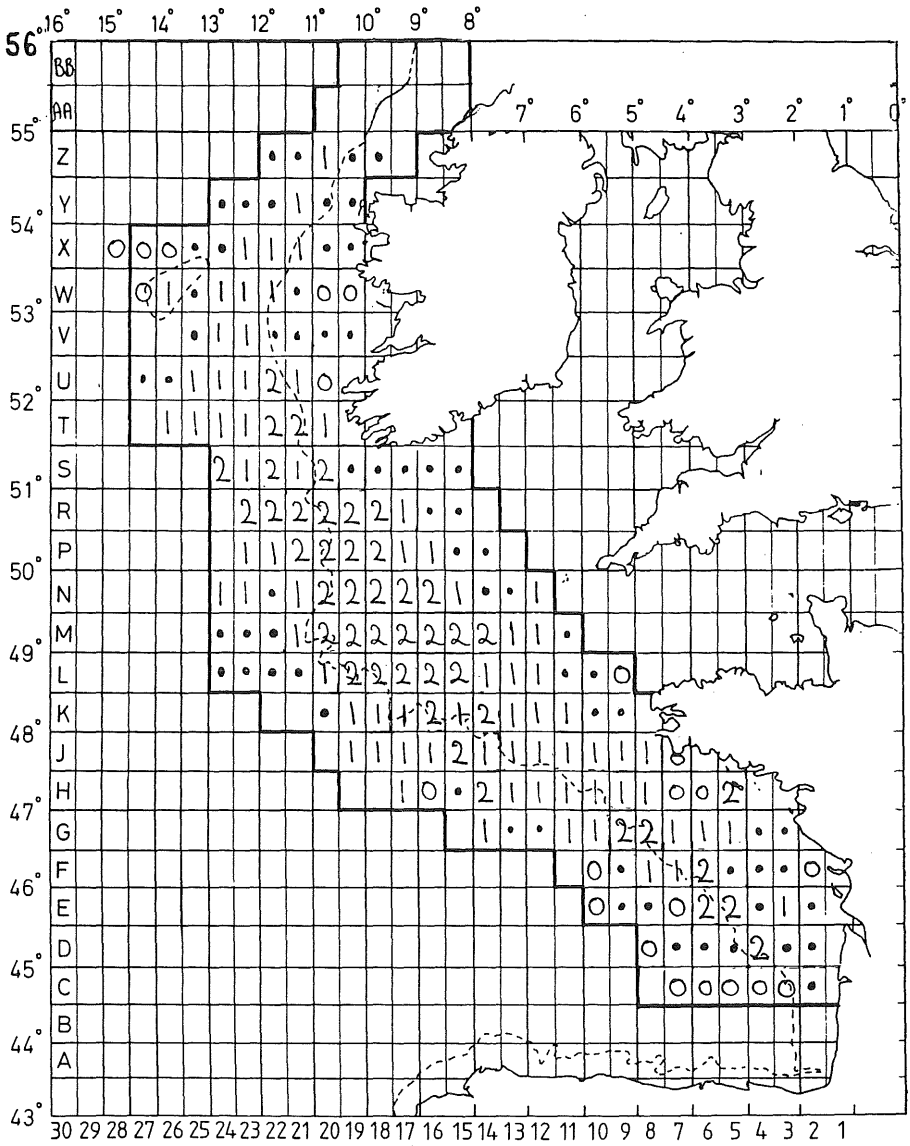


Figure 3.4 The limits of the survey area for 1989 showing the maximum contribution of any rectangle to the stage 1 egg production of either mackerel or horse mackerel from previous surveys during the period 11 June - 5 July.

0 = no contribution; . = <0.5%;
1 = 0.5 - 1.9%; 2 = >1.9%.

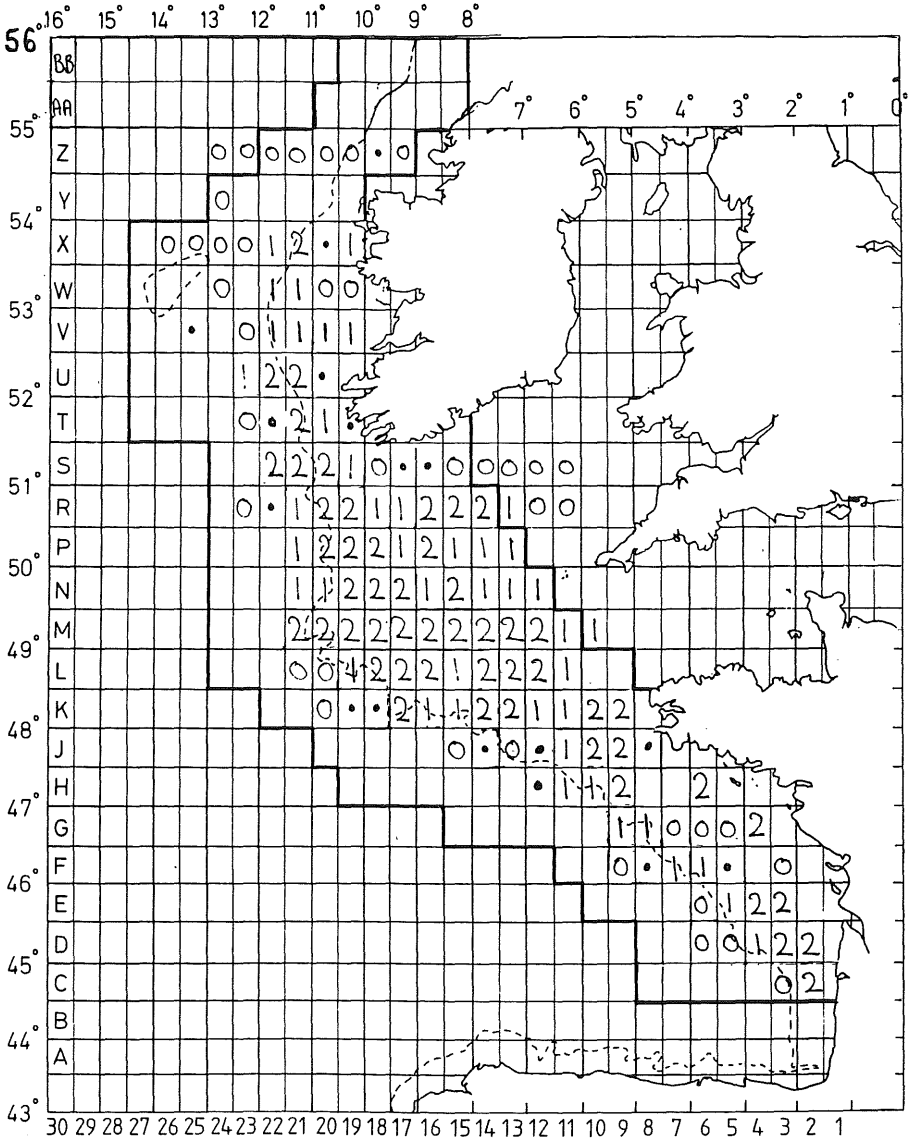


Figure 3.5 The limits of the survey area for 1989 showing the maximum contribution of any rectangle to the stage 1 egg production of either mackerel or horse mackerel from previous surveys during the period 21 June - 30 July.

0 = no contribution; . = <0.5%;
1 = 0.5 - 1.9%; 2 = >1.9%.

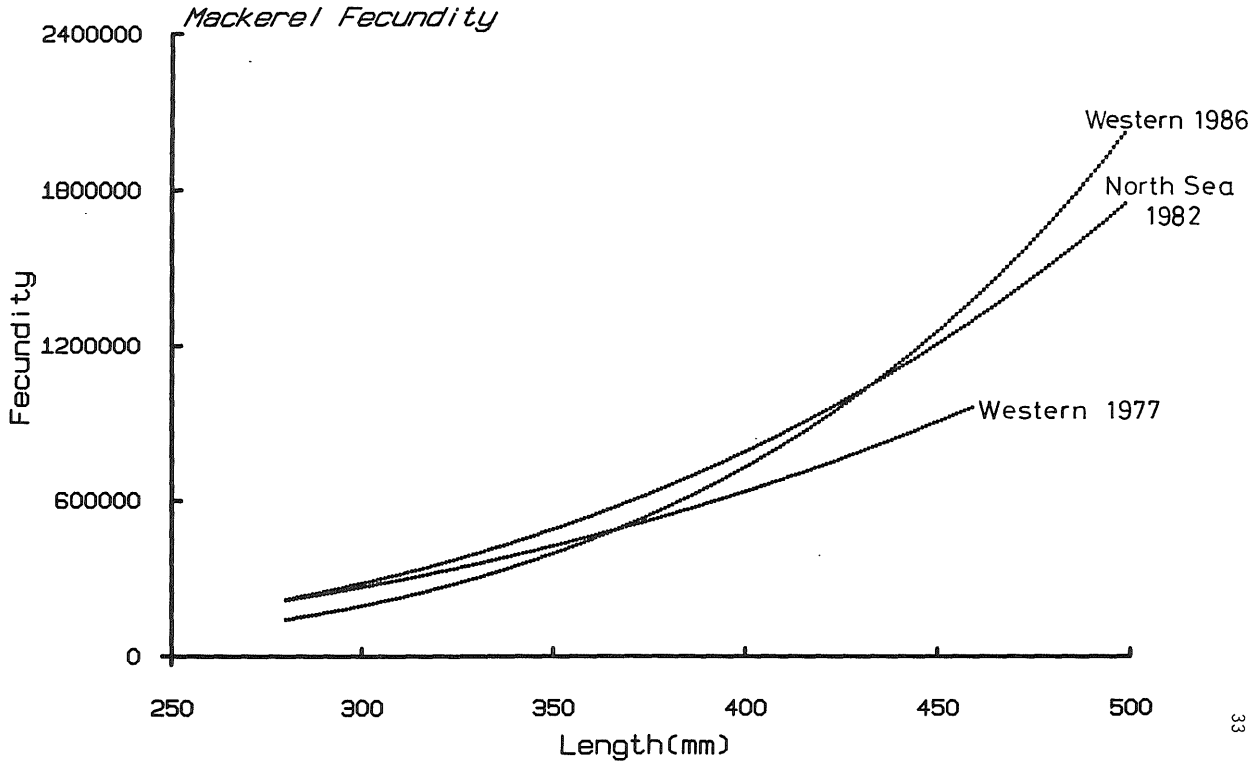


Figure 5.1 A comparison of the Western Mackerel fecundity estimates in 1977 and 1986, and the North Sea Mackerel fecundity estimate in 1982.

Figure 7.1 Proposed standard area for calculation of mackerel abundance indices from the North Sea International Young Fish Surveys.

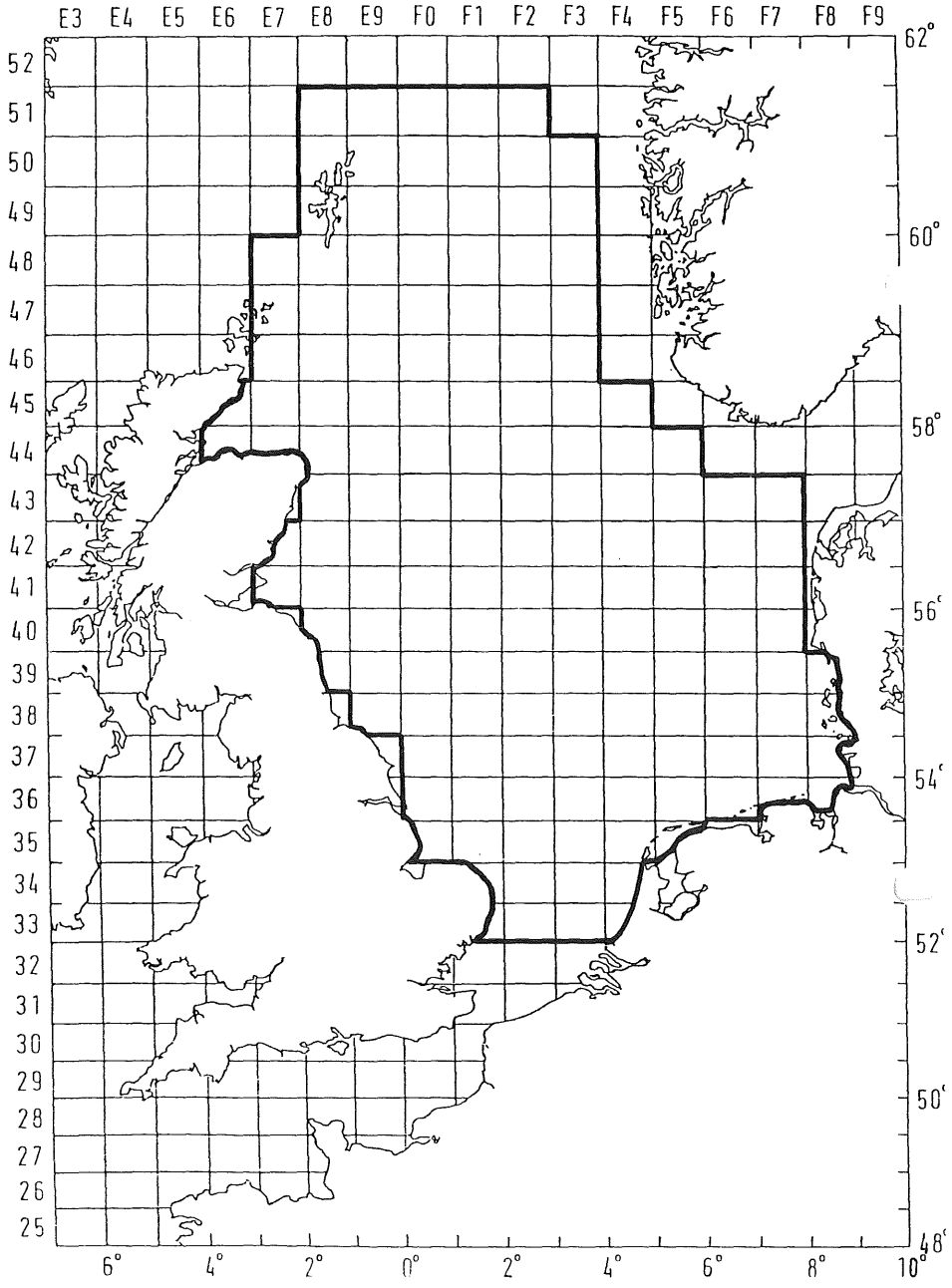


Figure 7.2 Distribution of first winter (0/1 group) mackerel in winter research vessel botton trawl surveys 1980-1987 (English, Irish, Scottish data).

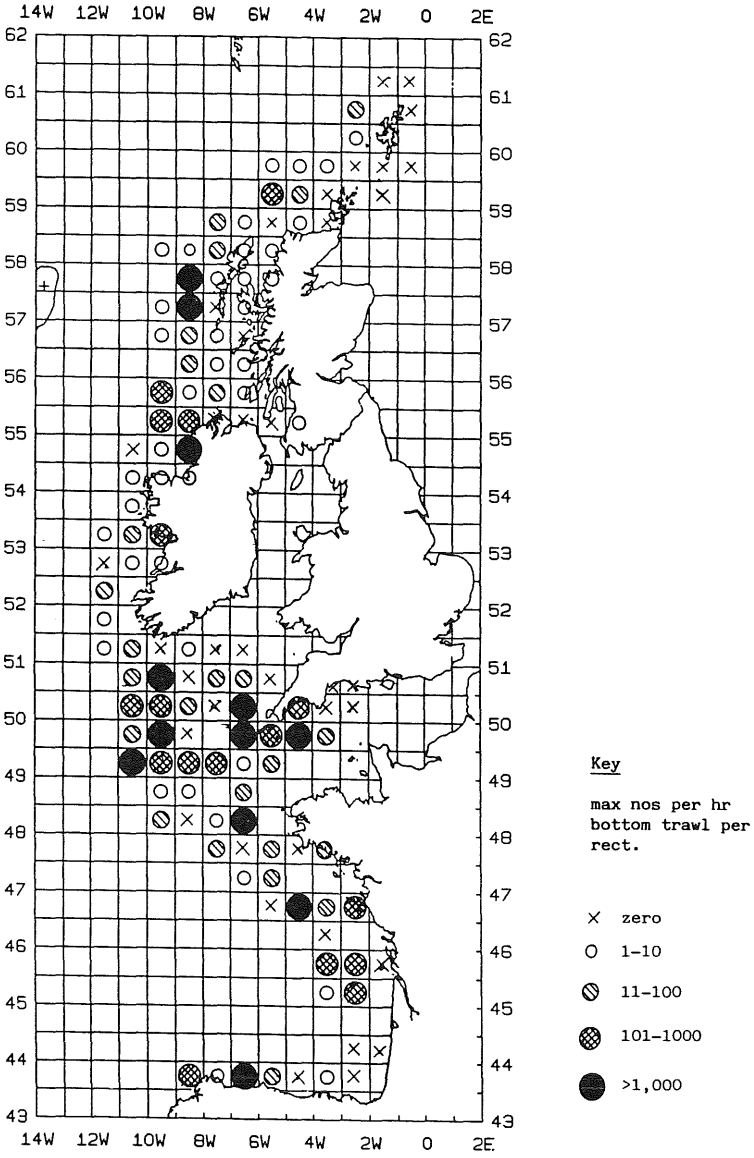


Figure 7.3 Distribution of second winter (1/2 group) mackerel in winter research vessel bottom trawl surveys 1980-1987 (English, Irish, Scottish data).

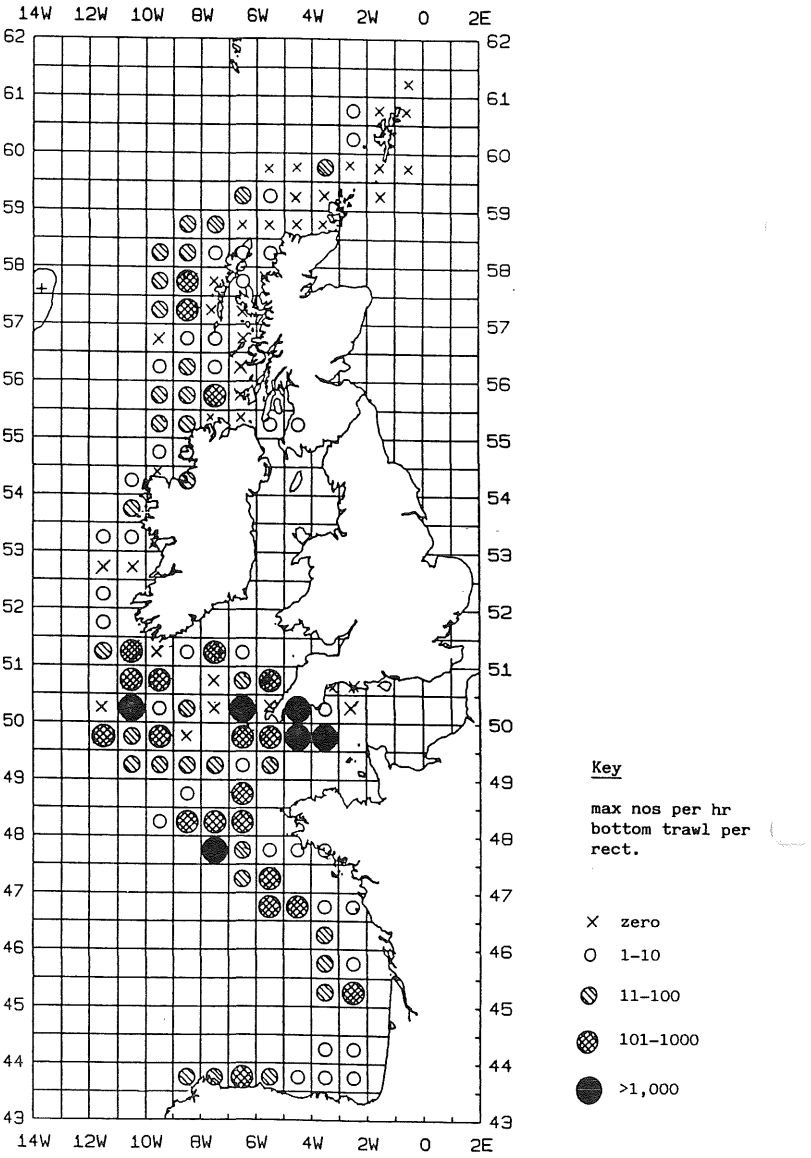
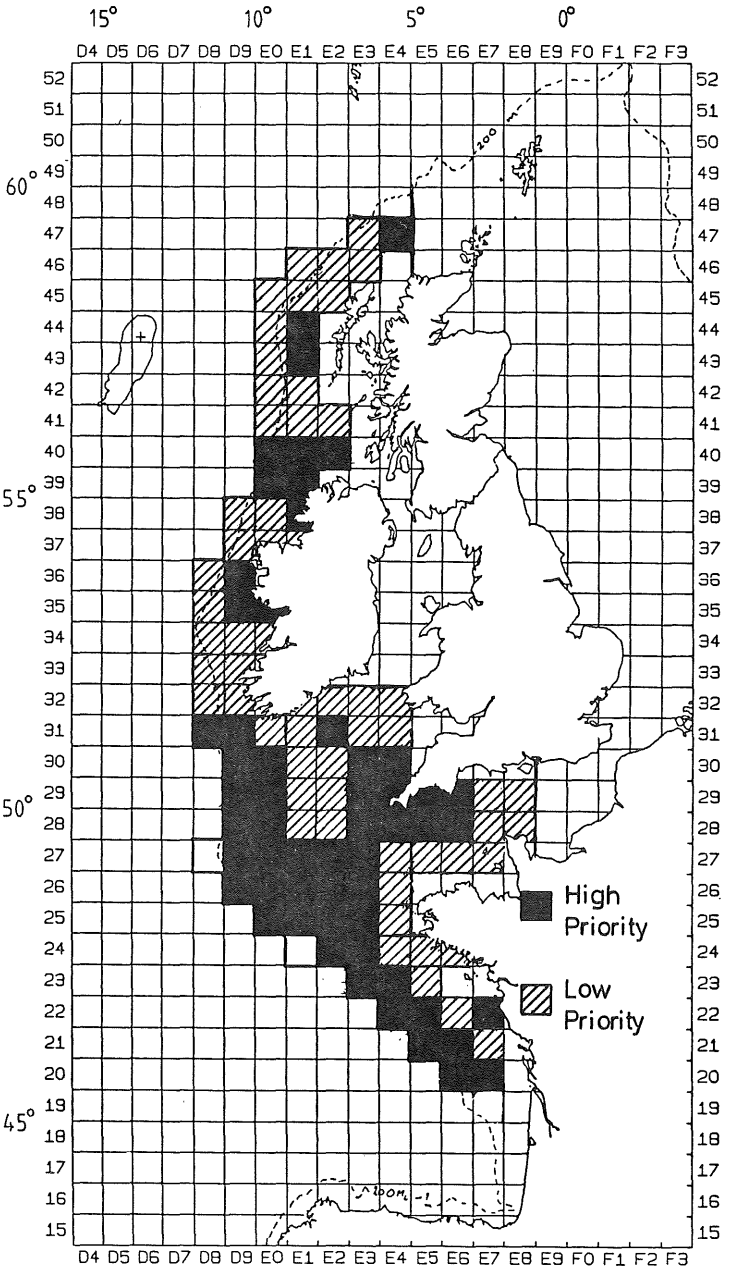


Figure 7.4


15°
10°
5°
0°
D4 D5 D6 D7 D8 D9 E0 E1 E2 E3 E4 E5 E6 E7 E8 E9 F0 F1 F2 F3
52 51 50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15
60°
55°
50°
45°
High Priority
Low Priority

APPENDIX

Memorandum for: Participants of Mackerel egg and Recruitment Workshop.

From: J. Roe Hunter, Southwest Fisheries Center, La Jolla Ca. 92038 U.S.A.

Subject: Miscellaneous Thoughts on Estimation of Fecundity.

THE ASSUMPTION OF DETERMINATE FECUNDITY

Fishes with determinate fecundity are those in which the standing stock of advanced oocytes at the beginning of the spawning season are considered to represent the total potential fecundity for the season. All oocytes to be spawned in a season are drawn from this stock. In contrast, fishes with indeterminate fecundity continuously mature oocytes from the small mature oocyte classes throughout the season and the standing stock of oocytes at the beginning of the season gives no definitive indication of the fecundity for the season. Hence indeterminate fecundity can only be estimated by measuring the numbers of eggs released per spawning (batch fecundity) and the frequency of spawning. Batch fecundity and spawning frequency may be measured over the entire season or over a shorter interval of time within the spawning season. The differences between determinate and indeterminate fecundity are described and discussed in greater detail in Hunter et al., 1985.

A serious underestimate of total fecundity may result if a species having indeterminate fecundity is analyzed as though it has determinate fecundity because small oocytes usually not included in estimates of total fecundity may mature and be spawned during the season. On the other hand, estimates of spawning frequency and batch fecundity are usually an appropriate method for estimating fecundity in fishes with either determinate or indeterminate fecundity. This is because most fishes, including those with determinate fecundity probably spawn more than once during a season. Thus the most conservative policy is to assume fecundity is indeterminate and measure spawning frequency and batch fecundity. These data not only provide an estimate of fecundity but provide the data needed to evaluate the assumption of determinate fecundity. This is the policy I recommend if the oocyte size-frequency distribution is continuous as is the case for Scomber and Trachurus. If the analysis of batch fecundity and spawning frequency indicates that fecundity is determinate then the less costly method of estimating total standing stock of oocytes could be used.

IS FECUNDITY DETERMINATE IN SCOMBER AND TRACHURUS?

My guess is that both Scomber scombrus and Trachurus trachurus have indeterminate fecundity but this assumption needs validation. The following evidence supports this assumption:

1. All scombroids studied so far, including Scomber japonicus (MacCall et al., 1988), Katsuwonus pelamis (Hunter et al., 1986) and Euthynnus lineatus (Schaefer, 1986; cited in Hunter et al., 1986) have indeterminate fecundity. All are reported to spawn at high rates (every 1-5 days).

2. In both Scomber and Trachurus the oocyte frequency distribution appears to be continuous; no gaps exist between small unyolked oocytes and large yolked oocytes. The oocyte frequency distributions for Trachurus given by Macer (1974; Fig. 5) are typical of fishes with indeterminate fecundity.

3. The data of Macer (1974) indicates that the frequency of female Trachurus trachurus with hydrated oocytes may be high, indicating many spawnings. In Figure 4 of his paper he gives the frequency of females with hydrated oocytes (his stage 5). In four samples taken in June-July about 45, 27, 14 and 10% of the females in these samples had hydrated ovaries. If the hydrated stage lasts less than a day, which seems likely, these numbers mean that 10 to 45% of the population were spawning per day or an average of 24% of the population per day over the two months. Thus on the average Trachurus spawned about every four days over a 60 day period and consequently, the average female spawned about 15 batches of eggs. Batch fecundity in Trachurus symmetricus is about 115 eggs per gram of fish (MacGregor, 1975). Hence total fecundity in Trachurus spp may be about 1725 eggs/g and a 180 g fish (about 25 cm FL) may spawn 310×10^3 eggs per season according to this calculation. This is about half the standing stock estimated for 25 cm T. trachurus by Macer (1974). Clearly, many uncertainties exist in this "back of the envelope" calculation, but it seems to indicate that total fecundity may be underestimated in T. trachurus.

METHODS FOR VALIDATION OF FECUNDITY DETERMINATIONS

A number of methods and approaches for validation of determinate fecundity are discussed below.

Oocyte frequency distribution

Determinate fecundity may occur only in fishes in which mature ovaries have a discontinuous oocyte size-frequency distribution, or at least determinate fecundity is far more common in such fishes than in those with a continuous oocyte size-frequency distribution. Continuous oocyte frequency distributions such as those seen in Trachurus trachurus and Scomber scombrus are evidence for indeterminate spawning because: 1) such a distribution is necessary if oocytes are continually matured during the spawning season; and 2) anchovy and other fishes in which indeterminate fecundity has been documented have such a distribution.

Spawning frequency x batch fecundity

If a fish has determinate fecundity the product of the mean spawning frequency and mean batch fecundity for the spawning season should be equivalent to the mean standing stock of oocytes assumed to represent the total production of eggs for a season. If this product exceeds the numbers included in the standing stock, indeterminate fecundity is indicated. If the survey is shorter than the entire spawning season then spawning frequency x batch fecundity should be equivalent to the observed reduction in the standing stock of oocytes if fecundity is determinate. If indeterminate, this product should exceed the observed reaction.

Clearly: if one assumes that fecundity is determinate and uses a very small oocyte size criteria for separating the advanced standing stock from the rest of the immature "resting" oocytes then the observed fecundity for the season (batch x spawning

frequency) might equal the standing stock of oocytes on the basis of chance alone. In addition indeterminate fecundity is a variable, and is environmentally adapted to a particular season. Thus confirmation of determinate fecundity in a fish with a continuous oocyte distribution might require measurements over several seasons and close examination of differences in fecundity and spawning frequency between females of different lengths or ages.

Decline in the standing stock of oocytes

A decline in the standing stock of advanced oocytes during a portion of the spawning season may provide some evidence for determinate fecundity in fishes with a discontinuous oocyte distribution. Clearly, comparisons of the beginning and end of the spawning season are not a valid test since such a comparison would show a decline in fishes of either indeterminate or determinate fecundity. If the ovary has a continuous oocyte distribution, within season comparisons of oocyte standing stocks method may be ambiguous. The oocyte distributions used as evidence for utilization of a standing stock of oocytes in Trachurus by Macer (1974, Fig. 5) closely resemble those of fishes with indeterminate fecundity. His data can be used as easily to support an assumption of indeterminate as to support determinate spawning.

The quest for the true vitellogenic size threshold for oocytes

The true vitellogenic size threshold for oocytes is of interest biologically but is not very useful for validating the assumption of determinate fecundity. Knowing when vitellogenesis begins does not answer the key questions, whether or not maturation of smaller oocytes ceases or continues during the spawning season. Certainly a discontinuous oocyte size-frequency distribution is evidence for cessation (or a pause) of maturation of the smaller oocytes, whereas a continuous distribution indicates that maturation may continue. If the vitellogenic size threshold is considered a central issue it implies to me that fecundity has already been assumed to be determinate. That the oocytes that comprise the total fecundity for the season are so indistinct that detailed histological analysis is required to identify them indicates to me that it is unlikely that such predetermined stock of oocytes exists.

Atresia

The incidence and extent of atresia (resorption of oocytes) is presently a more qualitative than quantitative tool. Nevertheless, such qualitative information has some inferential value. I expect extensive atresia of yolked oocytes to be more common in fishes with indeterminate fecundity than in those with determinate fecundity. This is because fishes with indeterminate fecundity must maintain a continuous size distribution of oocytes as long as they continue to mature spawning batches. After the last batch is spawned the oocytes in mid-size ranges are no longer needed for production and are resorbed. Thus at the end of the season fishes with high levels of atresia can be found relatively frequently. The occurrence is not as frequent as one might expect because the period that atretic yolked oocytes can be easily detected is short, resorption being rapid. Our experience indicates that the incidence of high levels of atresia is relatively rare in fishes with determinate fecundity and a discontinuous oocyte size frequency distribution. Thus the realized and the potential total fecundity may be relatively similar in such fishes and it may be only in unusually unfavorable years that they resorb large numbers of advanced oocytes.

The pattern of atresia in the two scombroids we have studied (Scomber japonicus and Katsuwonus pelamis), differed from patterns observed in anchovy although we believe both species have indeterminate fecundity. In these two scombroids high levels of atresia (alpha atresia of yolked oocytes: see Hunter and Macewicz, 1985 and Hunter et al., 1986) were encountered midseason in some collections. This information along with data on the incidence of post-ovulatory follicles indicated that these scombroids may not spawn at a steady rate throughout the season, but rather spawned at a high rate over a relatively short period (perhaps 20 days) than resorbed the remaining oocytes. The incidence of post-ovulatory follicles indicated the rate of spawning within the period was high, on the order of every 1-2 days. Thus owing to the nature of their shorter but more intense spawning behaviour less synchrony existed in spawning among fishes in the population, hence high levels of atresia were detected more frequently in mid season than in anchovy where more synchrony exists because of a slower spawning rate. An alternate explanation of the scombroid data is that such fishes may undergo more than one cycle of spawning and resorption within a season.

Re-examination of old data

It seems reasonable to assume that fishes which spawn many times a year are more likely to have indeterminate fecundity than those that spawn only a few times. Thus a crude estimation of spawning rate may be useful for deciding what type of fecundity analysis to use. Such information may exist if gonads have been routinely staged. The stage for hydrated ovaries (clear translucent oocytes, running ripe, etc) is included in every gonad grading system. This stage is ephemeral, usually having duration of less than 24 hours and the stage ends when the hydrated batch is ovulated and spawning occurs. This means that the fraction of females with hydrated oocytes, is equivalent to the fraction of the population that is spawning per day; if no serious sampling biases exist. As the hydrated condition may be detectable for only a few hours and often at only night, it is not uncommon for fish taken from a fishery to contain few or no females with hydrated oocytes. For example, in the anchovy, samples taken after the night's spawning is completed (2400) and before hydration of oocytes for the next night's spawning begins (0600) will contain no or very few females with hydrated ovaries. However, if they are taken, a rough calculation can be made as I have done above using Macer's data for Trachurus. This calculation indicated that spawning rates were high. If hydrated ovaries were preserved, then the batch fecundity can be estimated and an even better test of the determinate fecundity assumption can be made using (batch x spawning frequency) where spawning frequency is the function of females spawning per day.

GILSON'S FLUID

The above discussion brings to mind one last point. I believe it would be beneficial if the use of Gilson's fluid were completely eliminated until it is known beyond a shadow of a doubt that fecundity is determinate. Gilson's fluid destroys hydrated oocytes, prevents histological analysis, and thereby eliminates the best evidence for validating the assumption of determinate fecundity. By using this technique the investigator makes a tacit assumption that the species has determinate fecundity, that is all eggs to be spawned in a season can be consistently identified. This often has been a false assumption.

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