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REPORT OF THE SPRAT BIOLOGY WORKSHOP

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1. INTRODUCTION

1.1 Terms of reference

At its 1983 meeting the Industrial Fisheries Working Group identified the need for a workshop to be held to consider stock separation and other biological problems relating to the assessment of the sprat stocks in the North Sea and adjacent areas. The essential problems were addressed in discussion papers presented at the 1984 and 1985 ICES Statutory Meetings (Bailey 1984,1985), and in 1985 the Pelagic Fish Committee put forward a recommendation that a "sprat biology workshop" should be held late in 1986.

The ICES Sprat Biology Workshop met at the Institute of Marine Research, Bergen, Norway 4-7 November 1986 in accordance with Coun.Res. 1985/2:9 :

a) to use available biological data to establish if there is a basis for stock separation of sprats within the North Sea and adjacent waters,

b) to establish the requirements for an appropriate data base,

c) to consider what evidence exists to explain the recent changes in the distribution and abundance of sprats in different areas of the North Sea.

Dr. R.S. Bailey and Mr. E. Bakken were appointed joint conveners. In preparation for the Workshop the conveners reviewed the data requirements and contacted sprat biologists while ICES Delegates were asked to appoint Workshop participants.

1.2 Participants

J. Alheit	Federal Republic of Germany
E. Bakken (Chairman)	Norway
O. Hagström	Sweden
S.A. Iversen	Norway
P.O. Johnson	UK (England)
K. Popp Madsen	Denmark
D.W. McKay	UK (Scotland)
G. Naevdal	Norway

2. STOCK SEPARATION

In an attempt to identify sources of evidence for stock separation within the North Sea sprat populations the Workshop considered the following:

1. Data on fishing areas in the North Sea giving as much information as possible on the location and timing of the fisheries and their historic development.

2. Data on spawning sites and their spatial and temporal separation.

3. Data on the biological characteristics of sprat from different areas particularly in relation to spatial variations in growth rate.

4. Data from meristic and morphometric studies carried out on sprat, including studies of length at age one (L_1).

5. Data from more direct studies on the population genetics of sprat.

2.1 Areas of sprat concentration

The Workshop considered Feldman's (1986) paper on some special features of North Sea sprat distribution and biology considered in relation to differentiation within the population presented to the 1986 ICES Statutory Meeting. This paper analysed the data produced from a series of Soviet research cruises carried out between 1972 and 1976. From the distribution of eggs and larvae, juvenile sprats (under one year old) and adults, and from knowledge of the prevailing hydrographic conditions, Feldman inferred a system of passive movement of young stages of sprat. This is shown in Fig 2.1, which indicates that after being spawned in the offshore areas off the east coast of the British Isles and along the southern part of the Dogger Bank the eggs and larvae are largely confined to these offshore areas by the presence of two large gyres, one centred in the northern North Sea and another on the Dogger Bank. It also indicates that apart from some migration into Scottish inshore waters the majority of the juvenile sprats undertake a migration to the south and east into the German Bight.

In relation to adult sprats Fig 2.1 indicates winter concentrations in inshore areas along the British coast and in the central North Sea especially to the south of the Dogger Bank. From these winter concentrations the sprats disperse into the offshore spawning area in the summer months and along with the incoming year class of one year olds return to the overwintering areas in the autumn.

Feldman came to the following conclusions:

1. The drift direction for sprat eggs, larvae and fry in the North Sea encourages mixing at the early stages of development, and this represents an integrating factor.

2. Data relating to the size distribution of juvenile sprats indicate the complex character of their migrations. In the northern North Sea, migrations of growing individuals from open sea areas towards western coastal areas are most likely. In the central North Sea, at the wintering sites for adult fish, there is a concentration of young fish coming from southern and eastern areas.

3. The size and sex structure of spawning sprat concentrations are liable to show marked interannual variability, and this has to be taken into account when examining structure.

Because of the shortage of basic data presented in the paper the Workshop found it difficult to evaluate the validity of the conclusions reached by Feldman.

2.2 Spawning areas

Sprats are batch spawners with a protracted spawning period and several spawnings per season (Alheit 1986). A minimum of 9 to 10 spawnings per season has been recorded for Kiel Bay sprats (Heidrich 1925). There is a clear shift from south to north and from west to east in the timing of the spawning period in European waters (Morawa 1954, Bailey and Braes 1976). Depending on the area, the spawning period begins between December and July and ends between April and November (Fig 2.2). This shift in the timing of the spawning period and the protracted spawning season explain why sprat eggs can be found almost all year round in at least some parts of the area between the English Channel and the northern Baltic. The only environmental feature common to all sprat spawning areas and times seems to be a minimum temperature between 5.5^0 and 6^{0}C (Morawa 1954). A time series of egg samples in 1971 from the eastern English Channel and the southwestern North Sea showed that sprat spawning began in early January and continued at least until June during which time the maximum spawning intensity progressed in a northwesterly direction (Fig 2.3). A similar spawning development is illustrated in Fig 2.6.

Aurich (1941) distinguished three main spawning areas of sprat in the southern and eastern parts of the North Sea and in the Channel:

1) the Flemish spawning area: from the Channel entrance to Terschelling Bank and along the English coast, to the Wash estuary

2) the Frisian spawning area: the inner German Bight with Helgoland in the centre

3) the Jutland spawning area: from the Bohuslän coast through the Skagerrak, off the Jutland coast and on the Fisher Bank westward to at least 4^{0}E.

The sprats in the Skagerrak, Kattegat and Norwegian fjords south of 62^{0}N have been considered to constitute a single stock separated from the North Sea stock and the stock in the Baltic. Høglund (1938) and Lindquist (1961,1970) have described the spawning of sprats in the Skagerrak -Kattegat area and identified the main spawning area in the inner Skagerrak and outer Kattegat. There is local spawning in the Norwegian fjords, but recruitment to the fjords in western Norway seems to depend to a considerable extent on drift of larvae from the Skagerrak-Kattegat spawning area. (Bakken 1966, Nævdal 1968, Ellingsen 1979, Torstensen 1984).

The area of spawning in the Skagerrak - Kattegat is indicated in Fig 2.4. The main spawning takes place in the southeastern part of Skagerrak, but spawning also occurs in nothern Kattegat, in fjords and skerries of Bohuslän and along the Norwegian coast. Local, inshore spawning seems insignificant except for northern fjords in West-Norway.

Spawning is reported from january to June with peak intensity in May-June. Spawning later than early July is not observed.

Data on egg distribution shown by Sund (1911),(Fig 2.5, seem to support the scheme of spawning areas of North Sea sprats given by Aurich (1941). The Flemish and Frisian spawning areas are separated by a zone of very low abundance of sprat eggs which extends from the island of Borkum (53°30´N) to the north.

Apart from these three main spawning areas, Aurich (1941) mentions local spawning in firths and bays along the U.K. coast (Firth of Forth, Moray Firth , Firth of Tay, the Wash) and in fjords along the southern and southwestern coast of Norway from Oslo to the Trondheimsfjord.

According to Aurich (1941) sprat eggs in the North Sea are mainly found near the coast. This is also shown by the egg distribution data of Sund (1911) (Fig 2.5). The maps of sprat egg distribution given by both authors show very few sprat eggs in the central North Sea. A transect run by Sund across the North Sea from the Danish to the Scottish coast does not give any indication of sprat spawning off the Scottish coast, and Aurich (1941) does not consider local spawning of sprats in Scottish bays as quantitatively important in comparison with the eastern areas.

There are no data available on the distribution and abundance of sprat eggs in the North Sea in the 1960s. It may be assumed that the general situation was similar to that reported by Sund (1911) and Aurich (1941). However, McKay (1984) gives extensive information on the distribution and abundance of sprat larvae off the east coast of Scotland for the period 1960 - 1983 based on the international herring larval surveys carried out in September-October each year. 1960 -1970 was a period of generally low abundance (Table 2.1) although 1963, 1965 and 1968 showed higher levels of abundance of larvae particulary in the Buchan area with few larvae in the Orkney area.

The situation changed in the 1970s. In June 1972, Johnson and Dawson (1975) found sprat eggs across the entire southern and central North Sea, although the German Bight was not investigated (Fig 2.6). Towards the north, sprat eggs were found at least up to 57°N off the Scottish coast. Similar observations were made in 1972 by Karasiova and Feldman (1980). Egg surveys carried out in 1976 (Fig 2.7) give strong evidence that sprat eggs occurred over the whole southern and central North Sea. Off the east coast of Scotland, plankton surveys carried out in July 1973,1974 and 1975 indicated concentrations of eggs and larvae along the east coast of Scotland, to the east of the Orkney Islands and to the north of the Outer Hebrides west of Scotland (Bailey and Braes 1976, see also Figs 2.8 (and 2.9). During the herring larval surveys sprat larval abundance was generally high from 1971 to 1978 (McKay 1984). In the Buchan area, abundance was in all years higher than the average of the 1960s. It was, however, in the Orkney area that the most pronounced increase took place, this area having a higher abundance of larvae than the Buchan area in at least three of the years.

From 1978 to 1982 the larval abundance in both the Buchan and Orkney areas decreased to a low level. The decline since 1977 has been most pronounced in the Orkney area where no larvae have been caught since 1979 (Table 2.1).

All these observations lead to the conclusion that, up to 1970, the "normal" spawning distribution of the North Sea sprat consisted of three main spawning areas in the southern North Sea as well as the Skagerrak- Kattegat with less important spawning in other areas. It is uncertain if the main spawning areas represent different sprat stocks. The spawning distribution changed dramatically in the 1970s with large parts of the North Sea becoming one single coherent spawning area (Figs 2.6 2.7 and 2.8). In the 1980s the spawning distribution of sprats seemed to return to that reported for the period prior to 1970.

Lindquist (1970) concluded that the main spawning area in the Skagerrak - Kattegat was isolated from that in the North Sea. A more westerly extension of the spawning area was, however, reproted by Sund (1911) and Høglund (1938). This might indicate that shifts in location of the main spawning area may occur.

2.3 Growth (age-length relationship)

Various authors have reported and commented on the high variability in sprat length - at - age. This variability is illustrated in Fig 2.10 which demonstrates typical differences in modal lengths within and between age groups, areas and years.

The Workshop consentrated on revieving observations of length at age one.

2.4 L_1 - studies and otolith measurements

Data on the length of sprats at age one, i.e. on 1 January during their first winter, are obtainable from samples of one year old sprats or by backcalculation from measurements made on otoliths or scales of older fish. Estimates of L_1, however they are obtained, are measures of the amount of growth made during the first year of a sprat's life. In a species such as sprat which has marked geographic differences in spawning time (Fig 2.2) the L_1 will also reflect the time of spawning.

In making direct observations on the length composition of sprats during their first winter great care must be taken to ensure that the sampling gears used catch a representative sample of all the length groups in the population. Johnson and Dawson (1975) showed that the introduction of small meshed codends (approx 11 mm stretched length) in the sprat fishery off northeast England considerably increased the catch of the smaller length groups in the population. On Scottish winter sprat surveys in areas where small sprats predominated both conventional midwater trawls with small (11 mm stretched length) mesh codends and Isaac Kidd midwater trawls produced catches of sprats with the same length frequency distribution. It is therefore considered that for direct observations on the lengths of first winter sprats, only catches made using trawls with codend meshes of 11 mm or less should be used.

Data on the length distribution of first winter sprats (sprats which are in the process of laying down a first winter ring on their otoliths) in the Moray Firth and off the east coast of Scotland in the 1970s and 1980s are presented in Tables 2.2 and 2.3. These indicate that there have been considerable year to year variations in the mean and modal lengths. In the Moray Firth area (Table 2.2) the modal lengths in the 1980s were generally in the range 7-8 cm whereas in the 1970s, apart from the winter of 1972/73, they were rather smaller, indicating the presence of a higher proportion of small first winter sprats. Off the east coast of Scotland (Table 2.3) in the 1970s the populations of one year old sprats appear to have been dominated by small sprats, 4.5-6.0 cm, but during the 1980s there appears to have been a higher proportion of larger sprats present.

Back-calculated length at age one data are available from a number of localities in the North Sea and adjacent areas (Fig 2.11) for the 1983 and 1984 year classes, and from the western English Channel for the period 1969/70-1972/73. These data are shown in Figs 2.12, 2.13 and 2.14. The L_1 data from the 1983 and 1984 year classes indicate that first winter sprats from populations to the west of Britain and those in the northern North Sea and Moray Firth are characterised by having a unimodal distribution with a high mean L_1. However, in the North Sea areas south of 57^0N (Division IVb) the populations have a bimodal distribution of L_1 with a component of sprats with much smaller L_1´s. The relative importance of the component with small L_1´s within the same area differed in the two years (Figs 2.12 and 2.13). The data from the western Channel for the period 1969/70 to 1972/73 (Fig 2.14) also show a unimodal distribution. The mean L_1´s derived from these earlier observations in the Channel are apparently rather lower than those from the larger component of the 1983 year class in the North Sea.

In addition, data were available on the width of the first winter ring on otoliths from sprats taken off the northeast coast of England for year classes 1967-1970 and for the Kattegat-Skagerrak area in 1982 and 1983. The data from the northeast England area shown in Fig 2.15 indicate that the mean width of the first winter ring varies both between year classes and within a year class as the age increases. Each year class appears to consist only of fish with large first winter rings when caught as one year olds. As the fish grow older the samples show an increasingly large component of fish with small first winter rings. This indicates a continuing influx of small first winter ring fish into the fishery. The change in relative importance of the two components within the fishery may also indicate an emigration or higher mortality of fish with large first winter rings. The pattern of influx of the small first winter ring sprats also appears to change from year class to year class . In the 1968 year class the major influx seemed to occur as two year olds whereas in the 1967 and 1970 year classes the influx was most pronounced in the three year olds. In the 1969 year class there was very little evidence of any influx. These data appear to be rather different from the more recent data which indicate that sprat populations in the northeast England area are dominated at least in their second winter by sprats with low L_1´s i.e. small first winter rings.

The reasons for the bimodality of the L_1 distributions in the Central North Sea area were considered to be either

> that overwintering of sprats as larvae produces a group of sprats which have not laid down a recognisable winter ring during their first winter and so appear to be one year younger than they actually are (Iles and Johnson 1962). This would result in the apparent presence of a group of sprats in the population with large L_1´s.

or

> that there are sprats in the Central North Sea which are the product of

spawnings much earlier in the year. Such early spawning is recorded in the southern North Sea, the western nglish Channel and to the west of Scotland.

If the second explanation is correct the Central North Sea area is a nursery ground for sprats from various spawning populations. The decline in the large L_1 component in the population could therefore be due to older sprats returning to their parent spawning grounds.

The Workshop, however, considered that even though there are regional differences in L_1´s in the North Sea, indicating that sprats in different areas could have originated from different spawning stocks, the lack of any consistent long term differences in L_1´s made it impossible to use this character to define areas within the North Sea in which sprats have been predominantly from one spawning area or another.

The data from the Skagerrak/Kattegat area (Fig 2.16) also indicate a bimodality in the distribution of L_1´s in this area.

Evidence of the occurrence of two cohorts of sprat with different growth in the Skagerrak - Kattegat is further strengthend by the presence of metamorphosing sprat larvae and small sprat with a modal lengths of 4-5 cm in IKMT samples in February (IYFS). Length frequency distributions in samples 1975-1986 indicate a decrease in the proportion of the small length cohort in the 1980s. This cohort is not sampled representatively by bottom trawl and the IYFS indices of sprat abundance are dominated by the cohort with a model length of 8-10 cm.

Larvae from the main spawning in May-June are likely to metamorphose during the summer period and normally 0-group sprats appear in coastal water by the end of June. IKMT sampling in September shows that a second cohort of larvae have then reached coastal water. This cohort is not likely to have orginated in Skagerrak - Kattegat, and the observations could indicate an immigration of larvae from the North Sea area where later spawning are reported.

Possibly, the observed biomodality is best explained by the first hypothesis mentioned above, i.e. an influx of late spawned larvae from the North Sea.

2.5 Meristic studies

Although no new data on meristic studies were presented at the Workshop, the Workshop reviewed all the extant information on meristic studies on sprats carried out in the North Sea and adjacent waters including the Skagerrak and Kattegat.

The main characters investigated have been vertebral number and number of ventral keeled scales (both K1 and K2). Some authors have also investigated the number of fin rays and the number of gill rakers. Values for each of the above characters found over the whole geographic range are summarised by Anon. (1969) and given here as Table 2.4. All the recent available information on meristic characters is given in Table 2.5. Feldman (1981) carried out counts on vertebrae and keeled scales but unfortunately gives no actual values.

From Table 2.5 it can be seen that by far the most common meristic observation made on sprats is the number of vertebrae. Throughout the area studied the mean vertebral count varied from 47.12 to 48.66. Apart from one sample taken in Mariager Fjord (Kattegat) the VS counts made in the southeastern and southern North Sea appear to be the lowest and those in the Skagerrak and Kattegat the highest. Dannevig A (1947) and Dannevig G (1951) found that in 0-group sprats on the Norwegian coast the number of vertebrae was related to the length of the fish. These authors doubted that Vs could be used to differentiate between populations because of the difficulty in obtaining valid population means. Moreover, differences in vertebral number in fishes are environmetally induced by changes in water temperature during the spawning season rather than inherited. This observation is not unexpected in a species with as long a spawning season as sprat. The Dannevigs´ comments on the problem of obtaining valid population means may hold true for 0-group sprat because of the difficulty of obtaining very small sprats. However, it should be possible to obtain random samples of sprat from older age groups. Gilis (1951) studying sprats caught off the Belgian coast found large variations in the mean vertebral number between different year classes. During the period 1930/1 to 1946/7 the mean vertebral number varied between 47.31 and 47.69. No lengths or ages were given for the sprats sampled in each year so this variability cannot be evaluated in relation to the observations made by the Dannevigs. Although no exact data are given, Feldman (1981) also indicates that there was some age related variability in vertebral number in the North Sea.

Lindquist (1968) studied variations in gill rakers (RFC), length of head and number of vertebrae in material from the Skagerrak and adjacent areas. He concluded that none of the characters could sucessfully be used to distinguish different races or populations in Swedish waters.

Of the characters other than VS used in meristic studies only K2 has been used with any regularity. However, the data presented in Table 2.4 show no pattern in the variation of K2.

Morphometric studies

Several authors, notably Koval and Feldman (1978) and Feldman (1981) have attempted to use the relative sizes of various parts of the sprat anatomy as a means of separating sprat stocks in the North Sea. The characters used were vertical eye diameter, length of the median ray of the caudal fin, length of the pelvic fin, greatest body depth, snout length, length of the lower jaw, length of the dorsal fin, preventral length, and preanal length. The vertical eye diameter, snout length and length of the lower jaw were given as a percentage of the length of the head and the other characters as a percentage of the total length.

The studies compared sprat from four areas, Farne Deeps, Dogger Bank, Southern North Sea and the Danish Coast. The studies indicated that there were no consistent differences between fish from the first three areas but that the sprats from these areas were rather different from those found off the Danish Coast.

General conclusions

The data currently available from meristic and morphometric studies of sprats in the North Sea and adjacent waters do not provide a means of dividing sprats in these areas into separate stocks. Some of the available data nevertheless indicate that differences occcur between different areas. Before the usefulness of these techniques in identifying sprat stocks can be fully evaluated, however, they need to be applied in a much more structured study which will collect data from as wide an area as possible in a reasonably short period of time, say no more than five years.

Studies on variability of the mean width of the growth zones of Baltic sprat otoliths were initiated at the beginning of the 1970s (Lindquist 1971). Some years later the idea was advanced that the mean width of the first and second growth zones of otoliths and their statistical characteristics might serve as "natural tags" for studying populations (Aps, Falk and Oeberst 1981). Thus these characteristics were applied in distinguishing sprats of the Gulf of Finland from those of other Baltic Sea regions. Furthermore these characteristics enable one to distinguish single sprat generations in the Gulf of Finland (Aps and Lotman 1984). These morphometric analyses provide a means of evaluating the degree of morphological similarity. However, they do not directly reflect genetic relationships, and it is still not possible to indicate how morphological differences relate to the degree of reproductive isolation of sprats in the areas studied.

2.6 Population genetics

The population structure of sprats has presented seemingly unsolved problems for fishery biologists for several decades. As described above, meristic and morphometric methods have been widely used, although the interpretation of the results has frequently been difficult because of the complexity revealed. Typically, Dannevig (1951) concluded that different shoals of sprat, even from adjacent localities, may be of different origin. Doubt about the validity of such results has led to the search for characteristics that are independent of environmental variation, and thus solely controlled by heredity. The outline below gives a short account of the use of such characteristics in the sprat and their advantages compared to conventional characteristics, and discusses the prospect for their further use.

Biochemical polymorphism

Biochemical polymorphism is a type of discontinous variation and the individuals may be separated into distinct groups (usually few) on the basis or such variation. The variation is caused by variation in structural or control genes within species, and is revealed as variation in the primary gene products i.e. enzymes and other proteins. Owing to the close connection between the gene and gene product (protein) the variation is independent of environmental variation (except for natural selection, see later). Variation in protein structure is revealed by electrophoresis or isoelectrofocusing. Both these techniques are based on protein variation (variation in rank and type of aminoacids in peptide chains) which may give the total protein a different isoelectric point, pI, i.e. the pH at which the protein is without net electric charge. The aminoacids,and thus the total protein are of amphoteric nature, i.e. the charge may be positive or negative depending on pH. In a gel with a pH gradient (isoelectrofocusing), the proteins will migrate in an electric field to the location at which they are not charged. After staining they give distinct band patterns. In a gel with a fixed pH (electrophoresis), the proteins in an electic field will migrate according to their net charge and will show up as band patterns when the process is discontinued and the proteins stained.

In the 1960s and early 1970s mostly blood proteins were subjected to such processes. Subsequently, different enzymes in muscle, blood, liver and other tissue have been used. Enzymes may be stained by selective histochemical stains ("staining of activity"), and are thus more easily interpreted than total blood or tissue proteins. Haemoglobins are easily identified owing to their natural colour.

Intrapopulation variation in sprat

Wilkins and Iles (1966) first reported polymorphism in sprat haemoglobins. They found three haemoglobin patterns corresponding closely to some length-associated haemoglobin patterns in herring. However, no association between length and haemoglobin patterns were found in sprat. The authors concluded that the patterns might represent the phenotypic expression of a complex genetic segregating mechanism in this species.

Later Nævdal (1968, 1970) described additional haemoglobin patterns in sprat. These patterns were also independent of age or length of individual, but their genetic background could not easily be revealed. They were also subject to changes due to denaturation, thus producing "artificial" patterns.

Nævdal (1968) described variation in patterns of serum transferrins, which were found to be more complex than those in other species. The genetic background for the variation could partly be explained by use of Hardy - Weinberg´s formula and population data. Further, Nævdal (1969) described very complicated variation in non-specific esterases in sprat serum, but the associated population data gave no indication of the underlying genetic system or systems. Koval and Feldman (1978) described similar variation in esterases and suggested that genes at three polymorphic loci control this variation.

Howlett and Jamieson (1971) described a system of muscle esterase variants in sprats from two areas in the North Sea. Five alleles and totally 14 out of 15 expected genotypes were found.

Veldre and Veldre (1982) found polymorphism in serum albumins and transferrins as well as in haemoglobins in sprats from the Baltic. The authors claimed that these variations were made up of distinct bands and of simple band combinations.

Koval (1976) and Koval and Feldman (1978) described variation in the enzyme malate dehydrogenase (MDH). In a recent publication (Koval 1986) new data on the distribution of MDH phenotypes in the North Sea and Danish waters are given.

Jørstad and Nævdal (1981) described new polymorphic systems in sprat, in addition to malate dehydrogenase described by Koval (1976): lactate dehydrogenase (LDH), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI) and isocitrate dehydrogenase (IDH). These were clearly polymorphic, although many variant genes were rare. L - glycerophosphate dehydrogenase (GPD) showed great individual variation, but the genetic basis of the variation could not be revealed.

Interpopulation variation

Nævdal (1968) used frequencies of the most common haemoglobin type (called Hb I-1) and frequencies of the supposed gene Tf A as sample parameters. Significant variation in sample parameters and distributions of haemoglobin and transferrin types were found among the samples. No marked geographical trend could be discovered, and in some cases great differences were found among samples from adjacent areas on the Norwegian coast. Later (Nævdal 1970), samples from the North Sea and Kattegat areas were included as well as additional samples from the Norwegian coast. The former conclusion was confirmed and the samples from offshore areas coincided with the majority of the samples from the coast. The conclusion was drawn that the sprat populations in Norwegian waters consist of one major component recruited from the Skagerrak-Kattegat and/or the North Sea and minor components recruited from local spawnings in the fjords.

Howlett and Jamieson (1971) found clear differences indicating that their two sprat samples were drawn from different population units. Koval and Feldman (1978) could distinguish between sprats from different areas in the North Sea and the Danish coast in frequencies of two supposed esterase genes and of one gene in the MDH-system.

Jørstad and Nævdal (1981) found only little variation among their (rather few) samples from the North Sea, Kattegat and the Norwegian coast in two systems of LDH variations, MDT and PGI.

Veldre and Veldre (1982) found that sprats in the middle Baltic differed both from sprats in the southeastern part of the sea and from the Gulf of Finland. These differences were based upon distributions of transferrin, albumin and haemoglobin phenotypes.

Studies of sprat population structure in the Baltic

The Baltic sprat, Sprattus sprattus balticus (Schneider 1908), has been considered a subspecies of the European sprat, Sprattus sprattus (L.); a subspecies adapted to living conditions in the low salinity Baltic Sea. Mixing of Baltic sprat with the populations of the adjacent North Sea is hindered by the remarkable physical and chemical gradients in the Sounds. Sprats of that area may be considered as a transitional group (link) between sprats of the Baltic and the North Sea (Aps 1978). The population structure of the Baltic sprat has so far remained a problem, but a majority of authors indicate that Baltic sprats consist of local groups.

Differences between the authors concern the number of groups, and principles of differentiation. The concept of biological species (as understood by E. Mayr) serves as a basis for studies on sprat populations. Presence of that or another degree of reproductive isolation (reproduction criterion) plays a decisive role in determining the level in a population hierarchy. Morphological criteria play a secondary role (Aps 1978).

The Baltic sprat probably consists of some subpopulations which unnoticeably merge into adjacent subpopulations. Their origin and existence are related to the attachment of the fish to areas of higher productivity (Aps 1977, Aps, Falk and Oeberst 1981 and Ojaveer 1981 etc.). On the basis of existing data ICES has differentiated three units for regulating the sprat fisheries in the Baltic.

North Sea and Baltic sprats differ considerably from one another in basic charateristics. As a rule, the maximum age in North Sea catches does not exceed 6 years (Bailey 1980). In commercial catches from the northern Baltic the maximum age of sprat reaches 17-20 years (Aps 1986). The difference can evidently be accounted for by a higher mortality rate in North Sea sprat.

Validity of polymorphic traits for population unit identification

The distribution of genotypes in a polymorphic system is assumed to be in accordance with the Hardy-Weinberg formula which is based on simple probability calculations. Assumptions required for the validity of this formula are, among others, that the samples are sufficiently large to be representative of their population, and that the gene frequencies and/or distribution are not affected by selection or other population disturbance ("the samples are drawn from populations in equilibrium"). Under such assumptions, statistical methods may be applied to compare samples. The samples are drawn from different population units when significant differences are found and the distributions are in accordance with the Hardy-Weinberg formula.

However, selection against a gene will not necessarily cause significant disturbance of the Hardy-Weinberg equilibrium, and agreement between the observed and expected distribution will not necessarily imply that the genes are neutral. The concept "neutral" is not always well defined, but for utilization in studies of population structure, we must assume that the genes in question are not affected by selection to such a degree that statistical tests of samples of "normal" numbers (100-200 individuals) are affected.

Furthermore, selection may work on genotype distributions more than on gene frequencies. Stabilizing selection working in favour of hetero-zygotes may affect gene frequencies very little even though the distribution of genotypes may be considerably altered. Samples drawn from a mixture of different population units with different gene frequencies will show a deficit of heterozygotes when treated as one unit (Wahlung´s effect).

Disruptive selection working against heterozygotes will have the same effect, as will inbreeding caused by low effective number of brood-fish or assortative mating. Observed deviation from the expected Hardy-Weinberg distribution may therefore be difficult to interpret.

Nævdal (1969, 1970) found no indication of a connection between gene frequencies or phenotype distribution and age or size of individual fish (sex was not tested). However, Koval (1986) found a peculiar deficit of MDH hererozygotes in some of his samples, and the frequencies of some of the genotypes and alleles seemed to be associated with sex. The heterozygote deficit could be associated with physiological condition of the fish. Because he also found a sex-dependent growth rate, the differences between sexes could intead be associated with (genetic?) differences in growth rate rather than directly with the sex of the individual fish. An alternative explanation is that a mixture of population units was sampled.

Different migration activity for the two sexes could explain part of the results. However, the overall conclusion is that the alleles of the MDH system are not neutral, and cannot at present reliably be used to study population structure of the sprat.

Concluding remarks

Polymorphism in enzymes of tissue extract and blood proteins seems to be extensive in the sprat. Reports on geographic variations are numerous while similarities over greater distances are also reported. Indication of selection of some genes or genotypes makes interpretation of the results rather difficult as far as population structure is concerned. To investigate the neutrality of actual genes or genotypes should therefore be an important first step in such studies. This may be conducted by studying gene frequency stability, indications of selection, sex differences and year class differences, preferably in isolated or captive populations.

2.7 Conclusions

During periods of low abundance sprats are found in concentrations only in some identified coastal areas (Sec 2.1). These concentrations are unlikely to constitute separate stock units, since discrete spawning locations cannot be identified and the larvae seem to be distributed over a wide area.

The characters examined demonstrated large variability. No basis for stock separation was found, but the differences appeared to be related to very small groupings and to be of a transient nature. Typically, the variation within an area was as high as or higher than variation among areas.

The Workshop analyses, therefore, give no basis to establish stock units of a more permanent character needed for fisheries management purposes. The present system of two larger management areas, the North Sea (ICES Sub-area IV) and the Skagerrak-Kattegat (ICES Division IIIa), has little biological justification. No alternatives can, however, be suggested.

3. CHANGES IN ABUNDANCE AND DISTRIBUTION

3.1 The Northwestern North Sea

Recent ICES assessments of the North Sea sprat stock have shown that a major decline took place over the period 1978 to the present (Anon. 1987a). Broad analyses of this sort, however, can obscure important events that take place on a more local scale. The North Sea sprat fisheries, moreover, are not continous in time and space but are more or less concentrated in particular areas and seasons. The purpose of this section is to document the decline in the northwestern part of the North Sea; a decline which is one of the most dramatic in a fish population that have taken place in the northeast Atlantic in recent years.

Time series of data on the various life-history stages of sprats are available from:

Catch and effort data in the Scottish coastal fisheries, 1964 - 1986.
Biological sampling of landings in Scottish ports, 1964-1982.
Winter acoustic surveys 1978-1986.
Summer acoustic surveys 1978-1986.
Sprat egg surveys.
Herring larvae surveys 1960-1986.
Midwater trawl surveys for 0-group sprats in late autumn 1980-1983.

The anatomy of the decline

Data from the Scottish winter fisheries show that a sharp decrease occurred in landings in Division IVa over the period 1979-1982 (Table 3.1). This decrease was evident in both the Moray Firth and the smaller Shetland fishery, but was not reflected in the catch per fishing trip. In spite of this, anecdotal information indicates that there was a decrease in the availability of sprats to the fishery over this period. Events from 1980 onwards, however, are to some extent obscured by the implementation of a regulation in the winter of 1980-1981 preventing landings of sprat catches that contained more than 10% herring, and a closure in 1982 of the sprat fishery west of $3^0 30'$W in the Moray Firth to protect immature herring.

The most rapid decrease in landings in the Moray Firth appears to have taken place between 1979 and 1981 (Table 3.1). In the 1979-80 season the sprats caught were predominantly of the 1978 year class indicating poor recruitment of the 1979 year class, and in neither the 1980-81 nor 1981-82 winters were sprats of the recruiting year class (1980 and 1981 respectively) recorded in the few samples obtained (Table 3.2). On this evidence there thus appears to have been a recruitment failure starting with the 1979 year class.

Some independent evidence is available from acoustic surveys carried out in January each year from 1978 onwards. These indicate that the sprat population in the Moray Firth (excluding the inner Firths which were not covered) was reasonably high in 1978 and that a significant decrease occurred by January 1980, the 1979 survey being incomplete in this are (Edwards and Bailey 1978, Edwards 1979; Edwards and Wilson 1980). The population has remained at a low level in the Moray Firth up to the present time (McKay, Armstrong and Hutcheon 1986). While acoustic surveys are not available for the years prior to 1978, the results from the fishery indicate that sprats were present in much higher quantities in the Moray Firth in the mid 1970s.

While the Scottish winter fisheries have traditionally been carried out in inshore waters, their precise distribution has varied, and in some years adult sprats were also caught by Norwegian and Faroese purse-seiners further offshore (Table 3.3). It is thus possible that the decrease in availability inshore in the Moray Firth in winter resulted from a decrease in inshore movement rather than a decrease in population size. Neither catches in the offshore fishery nor the acoustic surveys, however, provide any evidence that there were sprats in offshore waters after 1980 and the only sizeable offshore catches in this area were made between 1974 and 1977.

Egg surveys carried out in 1973-1975 indicated that there was a population of sprats spawning in the northwestern North Sea of the order of 40 000 - 50 000 tonnes (Bailey and Braes 1976, Bailey and Pipe 1977). From 1974 to 1977 a series of summer acoustic surveys of the northwestern North Sea were mounted to estimate the size of the spawning stock of sprats and these were superseded in 1979 by acoustic surveys targeted at herring. In 1975 a provisional acoustic estimate of the spawning biomass of sprat in this area was 150 000 tonnes (Bailey 1978). Because of changes in coverage, ships and methodology it is not possible to obtain a comparable series of sprat biomass estimates for the period after 1977. Catches of fish made to establish the identity of echotraces, however, provide an indication of the relative abundance of sprats over the period covered (Table 3.4). Although the codend mesh size used on these surveys was increased in 1979, the new 20 mm mesh size was able to catch sprats, as shown by catches of this species made in 1985 and 1986. Thus, there appears to have been a major decrease in the spawning population sometime between 1977 and 1979 , although sampling in 1979 was very poor in the appropriate area. By 1979 and 1980 , furthermore, there was no evidence of echotraces that in previous years had been identified as attributable to sprats. Thus, these surveys also indicate a major and sudden decrease in the abundance of spawners between 1977 and 1980.

Further evidence is available on the abundance of each year class at an early stage in its life history from the international herring larvae surveys (McKay, 1984). Larval production as measured by the abundance of larvae in September was high in the 1970s (Table 2.1). In the Orkney area it decreased significantly in 1978 and in the Buchan area in 1979. This could be due either to poor survival of larvae from a large spawning or to a decrease in the spawning stock itself. In either case the evidence from these surveys supports the evidence from the fishery that a sudden decrease in recruitment occurred with the 1978 and 1979 year classes.

It was also in the mid 1970s that sprats were widely dispersed over the North Sea in late autumn (Feldman 1976). On later Scottish autumn surveys carried out from 1980 to 1983, the recruiting year class was more or less confined to coastal waters (Bailey and Edwards 1981). Thus, the decrease in recruitment was associated with a marked change in distribution.

Discussion

From all the above evidence it is clear that a significant decrease in the spawning stock and in recruitment of sprats occurred in the northwestern North Sea in the period 1978-1980. Gaps in the available data unfortunately rule out a precise description of the events and it is therefore difficult to elucidate whether recruitment failed because the spawning stock and egg production decreased or because early survival was poor.

Catches and catch rates in the Moray Firth fishery tend to indicate that the adult population was reasonably large in the winters of 1977-78 and 1978-79 but the critical point is whether the residual stock at the end of these winters was depleted by fishing. The acoustic surveys suggest that in January 1978 the population was still at a reasonable level in the Moray Firth but the survey did not cover the inshore firths where historically the sprats have regularly concentrated.

No survey was carried out in the summer of 1978 and the survey in January 1979 was incomplete. Larval production was good in 1978 in the Buchan area (potentially larvae from spawnings in the Fair Isle area) but poor in the Orkney area. This suggests that a reasonable spawning stock produced a reasonable number of larvae. The population size in January 1979 is not known, but the catches in that winter do not themselves indicate a population collapse. There was, however, no evidence of the usual spawning population in the Fair isle area in 1979 so that the possibility of a stock-induced recruitment failure in that year cannot be ruled out.

3.2 Central and Southern North Sea

The North Sea sprat was exploited on a small scale in rather localised inshore fisheries for many years. Total annual catches reported in the "Bulletins Statistique" show that over the period 1903-1960 catches exceeded 30 000 tonnes in only two years (1929 and 1959). In the 1960s a marked increase in the average level of catch occurred; the annual catch first exceeding 100 000 tonnes in 1966, largely due to the Moray Firth fishery in Division IVa. Subsequently marked increases took place in the 1970s with catches rapidly escalating to peaks of 620 000 - 640 000 tonnes in mid decade. Subsequently they entered a downward trend, with a rapid decrease from 1980 on, until in 1985 they declined to about 50 000 tonnes with the catches in most recent years around 1960 levels.

There thus appear to have been some remarkable changes beginning in the early 1970s which led to the greatly increased landings, while the process became reversed from about 1980 on.

Changes in catch

Catches over the period 1970-1985 are shown for the whole North Sea and for various ICES sub-divisions in Fig 3.1. It will be noted that catches from different areas of the North Sea follow broadly similar trends although the timing of peak years and the beginning of the decline varied by a year or so between areas. The overall decline first registered in the northwestern North Sea (Area 1 in Fig 3.1) from 1978 on, in the west central North Sea (Area 2) from about 1979-80 and the east central North Sea (Area 3) after about 1980-81. The notable exception to these trends has been the southern North Sea (Area 4) which registered generally very low catches over most of the period of peak abundance in other areas of the North Sea, but showed a marked improvement from 1980-82 when catches elsewhere were on the decline, although they have more recently declined in this area also.

Distribution of fishing in the 1960s

The general situation relating to the distribution of fishing in the 1960s is provided in Fig 3.2. At this time catches were mainly derived from rather localised winter fisheries along the U.K. coast, coastal areas of the German Bight and Danish coast, and in the west coast fjords of Norway, although the latter fisheries probably exploit populations relatively isolated from those in the North Sea. Sprats were also taken as a by-catch in the Danish juvenile herring fishery in the area of the Bløden ground southeast of the Dogger Bank (area A in Fig 3.2).

Seasonal landings from some of the U.K. coastal fisheries are presented in Fig 3.3 covering the period from 1960/61 to date, and it is evident that these showed considerable fluctuations in the 1960s. However, fluctuations in these localised coastal fisheries may not necessarily reflect true changes in the abundance of sprat over large associated areas since availability and economic constraints have often influenced levels of catch in these fisheries.

In the 1960s new fisheries developed within the U.K. coastal belt north of the Wash, where in earlier years sprat had not been exploited on a significant scale. These involved the Moray Firth in 1961, where traditionally a juvenile herring fishery had taken place, Aberdeen Bay in 1963, Shetlands in 1965 and off North Shields in 1962.

There were thus some indications of changes already developing in the western North Sea sprat population in the 1960s.

Distribution and abundance in the 1970s and 1980s

In the early 1970s the Danish industrial catches from the open sea showed a change in species composition from predominantly juvenile herring to sprat. Sprat catches increased and the fishery expanded over a wider areas of the central and northern North Sea. This change is well illustrated by Fig 3.4 which shows distributions of Danish sprat catches by ICES rectangles over the years 1974-1984. Fig 3.4 also cover the period of overall decline from 1980 to 1984. The expansion of fishing to deeper water areas of the western and northwestern North Sea in the years 1975-1977 is clearly shown by changes in catch distribution. The catch data also demonstrate the subsequent contraction of the area fished from 1978-1979 until 1981 and later years when catches were mainly taken southeast of a line between Flamborough Head and the entrance to the Skagerrak, i.e. in shallow water areas of the central and southern North Sea. This is shown in Table 3.5 which gives the proportion of Danish catch in the central North Sea (Division IVb) taken in the deeper water rectangles in the northwestern and western North Sea.

Prior to the 1960s only fragmented evidence is available from supplementary sources such as research vessel surveys to provide an overview of sprat distribution. Some data on sprat distribution over a wide area of the North Sea are available from Danish bottom trawl surveys undertaken in 1956 and 1957 to investigate the distribution and abundance of whiting. A number of surveys were carried out in each year and a composite chart showing the distribution of sprat has been compiled from them (Fig 3.5). It will be noted that sprats were at that time mainly confined to shallow water areas of the central and southern North Sea, off the east coast of Scotland and the Skagerrak.

A striking similarity with this distribution pattern is shown by the results of a survey carried out in October-November 1984 using a high headline (G.O.V.) bottom trawl (Fig 3.6) where again the main distribution areas are confined to the southeastern part of the central North Sea, and off the eastern and northeastern coastal areas of Scotland, (the latter region not covered in 1956 - 57). The significant feature is the absence of fish in the northeastern coast sector of England between Scotland and Flamborough Head.

The most recent period from the late 1970s to the 1980s is better covered by large scale acoustic and fishing surveys covering a large part of the North Sea involving a number of countries. The International Young Fish Surveys undertaken in February of each year have covered most of the North Sea and sprat data from these have been summarised and analysed by Johnson (1974, 1978, 1982,1984) covering the years 1972-1983. It is generally concluded that data provided by the IYFS proved of some value in giving a measure of year class strength as shown by regression with VPA, and also showed changes in distri- bution and abundance. This is illustrated in Fig 3.7. The changes correspond to that recorded by the Danish industrial fishery (Fig 3.4).

Table 3.6 summarises the data series to-date on estimates of year class strength provided by both 1- and 2-group fish from the 1971-1985 IYFS and, for comparison estimates from a Multiple Species VPA for the same series of year classes (Anon. 1987b). A reasonable measure of agreement is evident. Also shown are estimates for the more recent year classes (1979-1985) provided by Isaacs-Kidd mid-water trawl (IKMT) hauls in Division IVb. However, this net samples only the smaller component of 1-group sprat, with typical mean lengths in the range 4.5-6.0 cm, compared with the bottom trawl samples which are also biassed, only in this case towards the larger 1-group sprat with mean lengths of 7.5-8.5 cm. The IKMT samples of smaller 1-group nevertheless also register a clear downward trend from 1979 on. The 1985 year class appears as the most weakly represented to date.

A series of ICES co-ordinated acoustic surveys for sprat were undertaken regularly in each winter in the North Sea from 1979 - 80 to 1982 - 83. These involved research vessels from Norway, Scotland and England. Additional more restricted surveys have been carried out by these countries in other years or times of year.

Results from these acoustic surveys in the North Sea have been evaluated and reported on by the participants. These include Aglen and Iversen 1980, Bailey and Edwards 1981, Edwards and Bailey 1978, Edwards, Wilson and Bailey 1979, Edwards and Wilson 1980, Iversen, Aglen and Bakken 1981, Iversen and Ljøen 1984, McKay and Edwards 1985, Johnson 1979, 1980, 1981, Johnson et al. 1982, Johnson, Edwards and McKay 1983.

The results provide evidence for a progressive decline in the population of the central North Sea, and a concurrent shift in the centre of abundance towards the southern and southeastern North Sea.

A critical shift became evident in the surveys conducted in the winter of 1979-80, when a comparison of the distribution in November -December 1979 with that in January 1980 indicated a movement of population towards the southeast such that most of the population became concentrated southeast of a line between Flamborough Head and the north coast of Jutland (Fig 3.8). This evidence was also supported by a coincidental shift in the main areas of fishing by the Norwegian purse-seine fleet (Fig 3.9) and the disappearance of sprats from the North Shields area early in the New Year when the fishing came to a premature close. The distribution pattern of sprats shown by the February IYFS in 1980 (Fig 3.10) also provided evidence that the main concentration of sprats was within the southeastern half of the central North Sea.

3.3 Skagerrak - Kattegat

Available indicators of stock development in this area are: landings, acoustic estimates and indices of 1-group and all age groups sprat from IYFS.

The fishery independent indicators are of recent date starting in 1970, whereas landings statistics are documented further back in time. Lindquist (1964, 1966) reported on the catches in the human consumption fishery on the Swedish west coast from the 1860s onwards. Even though this fishery has been, and still is, regulated by quotas for economic reasons it is likely that the landings statistics can be used to indicate periods of high and low abundance of sprat in the Skagerrak-Kattegat area (Division IIIa), at least for the five most recent decades.

The human consumption landings in the period 1936 to 1956 varied between 8 000 and 10 000 tonnes with maximum landings of about 15 000 tonnes. In comparison with preceding and subsequent years, it appears that this period could be characterized as a period of high stock abundance. In 1957 the Swedish landings decreased to about 3 000 tonnes after which they did not exceed 5 000 tonnes up to 1970. International landings figures are available from 1966 onwards (Table 3.7). The total international and the Swedish human consumption landings in general show the same trend. This seems to supports the view that the level of the human consumption landings indicate high and low abundance periods.

Catches of sprats from 1966-1985 in the Skagerrak and Kattegat (Division IIIa) are shown in Table 3.7. In 1973 a period of high landings began with mean landings of about 80 000 tonnes and peak values of about 100 000 tonnes.

The period of high abundance appeared to end in 1981 when the stock indicators show that the stock decreased rather rapidly. The indicators of stock development are shown in Fig 3.11. Although each indicator is likely to be subject to different errors, in general they show the same trend. The stock is at present at a very low level. The decrease in the stock started with the weak 1980 year class. The subsequent 1981 and 1982 year classes were also weak and the landings decreased to a level not recorded since the 1960s. The 1983 year class appeared to be strong but the landings and acoustic estimate in 1984 did not indicate a proportional increase in the stock. The subsequent year classes of 1984 and especially 1985 are indicated to be very weak and a continued decrease of the stock is to be expected, again supported by the landings figures and acoustic estimate.

In contrast to the acoustic estimates and landings, the indices of all age groups and the proportion of 2-group and older indicate that the "adult" stock has increased since its low 1983 level and that it remained stable in 1984-1986. A stable or increased abundance of older sprats is also indicated in the human consumption fishery for sprats along the Swedish west coast. Sprat landings by purse seine and pair trawl indicate an increased abundance of large sprats (>12 cm) in the autumn-winter fishery. This fishery is regulated by weekly boat quotas which to some extent influence the landings. The demand for large sprats has been high during this period and the quotas have been increased to fill the demand. The landings therefore indicate at least a stable adult stock. Reports from the fishery corroborate this and in the season that started in September 1986 adult sprats were reported to be abundant along the Swedish coast from the Sound to the Norwegian border. The main problem for the fishery in the most recent season has not been to locate adult sprats but to locate "pure" sprat shoals owing to the abundance of herring in the area.

The abundant herring year classes that have appeared in the Skagerrak - Kattegat in recent years must have affected both the landings statistics of sprats and the errors in the acoustic estimate of sprats. It is likely that the industrial fishery, which has been responsible for the majority of the sprat catches, has changed over to the more abundant herring. The reliability of the landing statistics of sprats in the industrial fishery is also dependent on the sampling intensity which has been far from satisfactory during the most recent years. Because of insufficient sampling and changes in exploitation pattern it seems possible that landing statistics (Table 3.7) could to some extent exaggerate the decrease of the stock.

Although the method varied during the series of acoustic surveys they reflect the general trend in stock development as described above. At the present low level of stock size, however, the acoustic method appears not to provide a precise indication of stock development. It is reasonable to assume that errors in the sprat estimate have increased with decreasing sprat abundance and with a simultaneous increase in herring abundance in the areas surveyed. Although the coverage is comparable in the acoustic series the archipelago and areas with water depth less than 20 m are not covered by the surveys. Part of the stock could be distributed within these areas and not covered by the acoustic survey.

It seems reasonable to conclude that sprat abundance increased during the late 1970s and later decreased as a result of a series of weak year classes in the 1980s. The stock is now at a low level compared with the 1970s. In contrast to the development of the total stock, the abundance of 2-group and older sprats appears to be stable or increasing. This could possibly be related to changes in the exploitation pattern of the sprat stock.

3.4 Norwegian fjords

The Norwegian fishery for sprats in the fjords is carried out by small purse seiners in summer and autumn. Catches are used for canning purposes, and market requirements influence the fish size (age groups) and quantity landed. Year to year variations in annual landings and changes in catches by area, however, reflect to a large extent changes in sprat abundance.

Fig 3.12 shows sprat catches 1962 - 1984 by areas in the Norwegian fjords. On the Skagerrak coast (Division IIIa) catches have remained fairly stable. On the west coast south of 62^0N (Division IVa) catches declined prior to the early 1970s but have shown no trend in more recent years. In fjords north of 62^0N (Division IIa) catches were at a high level in the 1970s due to a northward extension of the fishery. During this period high catches were taken in fjords as far north as $65^0 30'$N, while prior to and after the 1970s catches in the northern area were mainly from the Trondheimsfjord, about $63^0 30'$N.

As mentioned above, landings in this fishery are influenced by market demands. However, two features related to the abundance of sprat seem clear. In the west coast fjords abundance decreased from the mid 1970s onwards, while the abundance in the northernmost fishing area was high only during the 1970s. In this area juvenile spring spawning herring were present prior to 1976-1977, disappearing later owing to the stock collapse and extremely low recruitment. There seems to be a relationship between the disappearence of juvenile herring and increased abundance of sprats in the northern area. This is, in general, similar to that observed in the North Sea (see Sec 3.5.3).

The changes in abundance and distribution as reflected in the fjord fisheries indicate variations different from those described for the Skagerrak - Kattegat and the North Sea. This leads to the conclusion that although sprat abundance in the southern fjords may be influenced by developments of stocks in the North Sea, Skagerrak and Kattegat, the northern fjords seem to constitute a separate unit. The mechanisms of sprat recruitment in this area, however, are poorly understood.

3.5 Possible explanations for changes

It was noted by the Workshop that an increase and subsequent decrease in sprat catches occurred over apparently the same time period over a large area reaching from the North Sea via the Skagerrak -Kattegat into the Baltic. Such a simultaneous event affecting all sprat stocks within this large area (with different fisheries) might indicate that the stock development was influenced by a common effect.

The annual catches in each area shown in Fig 3.13 indicate similar trends in the Baltic, the North Sea and the Skagerrak-Kattegat. The catch development in the Baltic, however, is about 2 years ahead of the development in the other areas. Despite the time difference, the comparison indicates that variations in recruitment to these stocks are not likely to be explained by the fishery alone but rather by other, at present, unknown climatic factors.

3.5.1 Fishery effects

Bailey (1980) described and discussed exploration and management of sprat in the North Sea. By yield isopleth diagrams he demonstrated rather critical values of fishing mortality above which eguilibrium yield falls rapidly. The stability of the stock, however, depends to a large extent on the variability about the stock recruitment relationshop at low levels stock. At high levels of natural mortality the variability appears to be very high, in which case two successive years of poor recruitment resulting from natural causes would result in a very low level of stock.

Bailey (1980) also pointed out that when sprats become scarce, effort is directed to other fisheries and since sprats are not in most areas a high-priced commodity the fishing mortality rate is unlikely to increase disproportionately to effort as stock declines, a situation different from that of the herring. The sprat fisheries, therefore, may seem to be self regulating. The main question is whether this would occur at stock levels above or below those inducing recruitment failure.

As the sprat stock in the North Sea was observed to decline, Burd and Johnson (1983) discussed the stock development and fishery influence. They showed that all available evidence indicated declining recruitment. With yield being so dependent upon recruitment (which has varied by over an order of magnitude), the concept of attempting to manage the sprat stock on a long-term yield basis was considered impracticable. Management policy had been based on two different yield per recruitment analyses and on average recruitment leading to the conclusion that the sprat stock could be exploited at a fishing mortality (F) of ca 0.5. At average recruitment level, this would imply catches of the order of 300 000-400 000 tonnes per year. Catches in the late 1970s (Fig 3.13) were above 300 000 tonnes in all years, and around 1980 the mean value of F on the 1- and 2-group was about 0.9 which is almost double the recommended level.

Burd and Johnson (1983) concluded that overexploitation was a major contributor to the decline of the sprat stock and that it might well have suffered recruitment overfishing.

On this basis the possibility can not be excluded that the fishery in the 1980s, during the period of stock decline, had an effect by increasing the rate at which the sprat stock declined. The observation that both the increase and the subsequent decrease in sprat abundance apparently occured almost simultaneously over a very wide area led the Workshop to belive that the fisheries were unlikely to be the major cause of the stock decline. Evidently, environmental changes in the North Sea took place during the period of reduced sprat abundance, and although the Workshop was unable to identify the relationship, it was felt that the observed stock fluctuations were likely linked to longer term environmental changes (see Sec 3.5.2).

3.5.2 Environmental influences

Corten (1986) discusses the possibility that in years with low inflow of Atlantic water around the northern coast of Scotland the sprat larvae will not be carried far away from the important spawning areas in the western and northwestern part of the North Sea. As a result these larvae might recruit directly to the adult stock in the spawning area at the age of two years. In years with high influx the sprat larvae might be carried too far away to make their way back to their place of origin. Veley (1951) investigated brood strength fluctuations in sprat stocks in relation to wind observations. He found that good brood years were associated with low west wind resultants for May - July and poor brood years with high resultants. Johnson (pers.comm.) investigated later years in the same way as Veley did for the period 1927 - 1933, but was unable to find the same association between year class strength and west wind resultants.

Molander (1939,1943,1952) shows how sprat catches and recruitment strength depend on hydrographic and meteorological conditions. Along the Swedish west coast easterly and northerly winds caused diminishing catches while southerly and westerly winds were favourable. Years with relatively weak predominant winds had the richest year classes of sprat.

During the best period of the fishery from 1975 to 1979 in the North Sea, the bulk of the catches were taken north of 55^{0}N, while in the subsequent period the main fishing area was south of 55^{0}N. This is well illustrated by the shift in the offshore fisheries. Such a fishery was that carried out by Norway.

The Norwegian sprat fishery in the North Sea in the 1970s took place in the fourth and first quarters of the year. The fishery was dependent on the location of sprat shoals suitable for catches by purse seine, and is likely to reflect the geographical distribution of sprats at that time of the year. Catches were usually landed in Norway, and the fleet avoided fishing further away from the landing places than necessary.

Investigations of sprat distribution in November 1979 and January 1980, 1981 and 1982 have shown that the main abundance of sprat was observed in waters with salinity ranging from 34.3 to 34.8 o/oo with a maximum near 34.5 o/oo (Iversen and Ljøen 1984).

According to Aglen and Iversen (1980) the distribution of sprats in November 1979 had shifted rather far south by January 1980. This was observed on surveys and reflected by the fishing area of the Norwegian fleet in November and January. The shift might be explained by an influx of Atlantic water (salinity greater than 35 o/oo) from the north, as the 35 o/oo isohaline moved southeast during the same period (Aglen and Iversen 1980).

This southeasterly distribution was observed in the following winters (Iversen, Aglen and Bakken 1981, Johnson, Iversen and Edwards 1982, Johnson, Edwards and McKay 1983). According to Corten (1986) the southeasterly distribution might be the normal one, while the observed distribution in the 1970s was abnormal owing to a reduced inflow of Atlantic water around the north coast of Scotland.

Dickson et al (1986) demonstrated a long-term increase in northerly wind component associated with a decline in zooplankton biomass in the central and southern North Sea from 1950 to 1980 and discussed possible implications for pelagic fish stocks. There are no analyses of the relationship between long term changes in environmental parameters and variation in sprat abundance.

R. Ljøen (pers.comm.) noted, however, that the observed average salinity in summer along a section at 57^0N in the North Sea showed a tendency of increase during the period 1968 - 1984 (Fig 3.14). This could indicate higher inflow of Atlantic water, a situation considered unfavourable to the sprat stock by Corten (1968). A possible relationship between changes in the hydrographic regime and sprat abundance (indicated by catch in Fig 3.14) needs to be thoroughly analysed before any conclusion can be drawn.

3.5.3 Sprat - herring relationship

In a paper on the causes of the recruitment failure of herring in the North Sea, Corten (1986) discussed possible interaction between the two species herring and sprat. In the 1970s the distribution of sprat larvae overlapped to a considerable extent with that of herring larvae and competition for food might occur. Corten found, however, little support for a food competion theory pointing out that the sprat stock in the northern area had declined substantially two years before herring recruitment recovered.

As outlined above (Sec 3.5.2) Corten (1986) concluded that the decline of the sprat stock in the late 1970s was directly related neither to the changes in the herring stocks nor to fishing, but most likely to an environmental change.

3.5.4 Sprat predators

The ICES Multispecies Assessment Working Group has provided estimates on consumption of sprat by the main predators in the North Sea. The estimates are based on an extensive fish stomach sampling programme in 1981 and assessments of various prey and predator stocks.

The estimates (Anon. 1987b) show that mackerel, whiting and cod are important predators on sprat. The relative importance of the predators as well as the proportion and absolute quantity of the sprat stock eaten have varied in accordance with fluctuations in the various stocks. Data are given in Table 3.8.

The sprat stock declined sharply during the analysed period, and the total quantity of sprat consumed fell from about 720 000 to 112 000 tonnes. The proportion of the stock eaten by the predators changed much less, but the relative importance of the predator species was altered. Mackerel for example, was an important predator in 1974 when the North Sea mackerel stock was still above 1 mill tonnes. This species alone accounted for 44% of the estimated total consumption. In 1985 the mackerel stock was reduced to a level of about 100 000 tonnes and accounted for only 2% of what predators consumed.

The Working Group on Industrial Fisheries (Anon.1987a) commented on the estimates referred to above and evaluated the natural mortality (M) of sprat resulting from all predators, including seebirds and seals. The calculated M values were:

Age	M
0	0.76*
1	1.20
2	1.87
3	0.81
4+	0.93

* Only third and fourth quarters

These M values are generally in conformity with earlier estimates of M of 0.8 on fully recruited age groups. The Working Group, however, could not find a biological explanation for the marked difference in values of M for the 1- and 2-groups if they were equally exposed to predators. It was suggested that the difference could reflect a different distribution of 1- and 2-group sprats in relation to the observed distribution of the main predator (whiting) as 2-group whiting and 2-group sprats overlap to a greater extent than 2-group whiting and 1-group sprats.

4. SPRAT DATA BASE

The Workshop discussed the need for and feasibility of establishing a data base for sprat. A data base exists already for assessment purposes. This contains data on sprat catch in number by age and quarter of the year and by subarea of the North Sea from about 1975 onwards. A new data base was intended to cover all types of data on sprat biology, e.g. growth parameters, morphometrics, population genetics, fecundity, egg abundance and distribution etc.

The Workshop found that specific requirements should be clearly identified before establishing a data base. At present this cannot be done, although data on growth, particulary L_1-measurement, would seem useful. It is, however, necessary to agree on various standards of measurement and on the format of the data before compiling a data base. This could best be done if a research project was initiated by a person or laboratory which then specified all requirements. Colleague scientists or institutions would most likely contribute data, from files or from future collections. Having an identified and interested initiator would ensure the necessary follow-up and access to the data base.

5. FUTURE RESEARCH

5.1 Recruitment related studies

In early 1986, a project was initiated in the German Bight to investigate the causes of recruitment variability in sprat in a similar way to that proposed for the SARP studies of California, South America and the Iberian peninsula (Anon. 1986, Annex III). The project will be conducted as a cooperative effort between the Alfred Wegener Institute for Polar and Marine Research (AWI, Bremerhaven), Biologische Anstalt Helgoland and Institut für Hydrobiologie und Fischereiwissenschaft (Hamburg). Other German institutes are likely to join the project.

IMER (Plymouth) and the Fisheries Laboratory, Lowestoft have proposed a joint programme for the period 1987-1989 to study pelagic production processes in the Irish Sea with relevance to fisheries. Particular emphasis will be given to feeding and survival of larval sprat and several of the techniques of the SARP programme will be applied.

There are contacts between scientists of the different projects on sprat and the possibility of cooperative work is under discussion.

5.2 Other studies

Several biological phenomena of sprat which were addressed during the Workshop require further investigations:

In a recent paper, Whitehead et al. (1985) show on the basis of protein analysis that sprats inhabiting New Zealand waters and believed to belong to one species have to be grouped into two different species, the more slender S. antipodum and the more common and deeper-bodied S. muelleri. The separation is further justified by distinct differences in shape and dentition of the basihyal plate, vertebral numbers, scale sculpture and fresh colour. A study to investigate if there are further meristic and morphometric differences and different traits in reproductive biology in North Sea sprats will now be initiated in the Alfred Wegener Institute (Bremerhaven).

It was demonstrated during the Workshop that the early egg production in North Sea sprat in 1971 and 1976 was not reflected in the larval production (Fig 5.1, P.O. Johnson pers.comm.). It would be important to investigate if this high egg or larval mortality in the early spawning season is a common phenomenon in North Sea sprat and what are its implications for sprat recruitment.

The birthdate of some fish species can be back calculated by means of daily growth rings on otoliths of larvae and juveniles. Evidence for daily growth rings on sprat otoliths was presented by Dayaratne (1984). The problem of the bimodal distribution of length of sprat at age one (Section 2.4) might be solved by using daily growth rings on otoliths. Also, daily growth rings represent a powerful tool for investigating the types of phenomena causing recruitment variability by comparing the distribution of larval production and the distribution of birthdates of resulting recruits. Studies on daily growth rings are in progress for the Irish Sea sprat at the Marine Sciences Laboratory, Menai Bridge and are planned for sprat of the German Bight.

0-group herring of 6 cm and larger feed heavily on post-larvae of sprat (Last 1982, 1985). Similar studies and investigations on egg cannibalism are under way in the Alfred Wegener Institute, Bremerhaven. It is important to clarify the role that predation by young herring and other fish plays on sprat eggs, larvae and juveniles for sprat recruitment.

Adult sprats are heavily predated upon by cod, whiting and mackerel (Anon. 1987b). From 1974 to 1984, the annual sprat production was almost equal to annual yield. The question if changes in predation pressure on sprat had an infuence in the recent decline of North Sea sprat needs to be investigated.

In 1988, there will be an egg survey for North Sea mackerel. As the information on the extent of the spawning areas of North Sea sprat is very incomplete since the decline of the sprat stock, it is recommended to examine the possibility of including a sprat egg survey in the mackerel egg survey.

It is recommended, also, to examine if an egg survey for mackerel and sprat could be combined with an estimate of spawning biomass of North Sea sprat using the "Egg Production Method ", "EMP", (Alheit 1985, Lasker 1985). The "EMP" is an instantaneous method and it is not necessary to integrate egg production over the whole spawning season. Required ship time is thus reduced to a few weeks. The "EMP" is at present being modified for sprat (Alheit, pers.comm.).

Further studies of populations genetics could produce results of relevance to the questions of sprat stock delineation. The Workshop advocate that future studies include comparisons and combinations with studies of meristic and morphometric characters, and there seems to be a need for an integrated approach (Section 2.5). Analyses of biochemical polymorphism of eggs and nearly hatched larvae could be included in such studies. Although data are available from a number of areas at different times they cannot be analysed to give information of use for stock separation.

Although no data were presented on variations of the shape of otoliths from area to area, various members of the Workshop pointed out that there were obvious differences in the shape of sprat otoliths. It was felt that with the advent of the new techniques for measuring otolith shape studies of the variation in shape of sprat otoliths might be fruitful.

The Workshop recommend that possible studies of meristics, L_1, otolith shape etc. should cover the entire North Sea and adjacent waters including the Skagerrak-Kattegat, the English Channel and areas west of Britain. In studies of this type full opportunity should be made of existing surveys such as the IYFS to provide maximum coverage.

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Table 2.1 Indices of abundance of sprat larvae off the east coast of Scotland, 1960-1983.

Year	Estimated abundance of sprat larvae x 10						
	1 - 15 September			16 - 30 September			Annual
	Orkney	Buchan	Total	Orkney	Buchan	Total	Total
1960	NS	NS		0	0	0	0
1961	0	2	2	NS	1	1	2
1962	0	18	18	0	38	38	28
1963	NS	362	362	0	20	20	191
1964	23	50	73	0	42	42	69
1965	31	358	389	NS	111	111	263
1966	5	25	30	0	8	8	22
1967	6	8	14	2	3	5	9
1968	15	264	279	NS	NS		279
1969	2	10	12	5	NS	5	13
1970	NS	5	5	1	4	5	5
1971	207	41	248	153	18	171	209
1972	1025	116	1141	77	64	141	641
1973	76	275	351	47	3	50	337
1974	206	140	346	70	92	162	258
1975	186	240	494	112	NS	112	389
1976	8	292	300	97	39	136	218
1977	145	NS	145	53	133	186	232
1978	15	NS	15	3	263	266	272
1979	39	82	121	7	28	35	78
1980	0	66	66	0	23	23	42
1981	0	5	5	0	0	0	3
1982	0	8	8	0	1	1	4
1983	0	38	38	0	53	53	46

NS = No sampling during that period.
From McKay (1984).

Table 2.2 Percent length frequency distribution of first winter sprat in the Moray Firth.

Length (cm)	Winter 72/3	75/6	76/7	78/9	79/8	80/1	81/2	82/3	83/4	84/5	85/6
3.0	.4		.2		.3						
.5	2.1	.2	.3	.4	1.1	.4			.3	.3	
4.0	2.3	1.2	.6	2.2	16.0	.4		.2	.7	.3	.1
.5	3.1	5.4	1.1	7.7	28.7		.4		.5	.4	2.5
5.0	5.2	17.3	2.4	9.1	12.1	.6		.2	.2	1.7	
.5	6.0	17.6	4.6	15.2	3.9	1.8	.3	.4	1.1	2.3	7.5
6.0	3.8	22.2	13.2	16.6	5.1	5.2	1.1	.6	5.6	5.6	18.7
.5	3.1	11.6	14.6	15.4	15.0	15.6	4.2	4.6	13.1	16.7	17.2
7.0	5.4	9.6	17.2	13.6	11.8	21.2	18.1	25.1	23.3	19.2	19.6
.5	9.8	5.8	15.7	13.3	5.9	24.3	30.6	37.6	24.7	18.2	15.3
8	17.2	5.5	15.6	6.3	.6	21.4	33.0	22.7	22.6	12.4	8.8
.5	14.3	3.4	10.6	1.4		8.0	13.2	8.1	7.7	11.2	1.4
9	18.6	2.1	4.7	.4		1.9	1.2	2.4	1.2	8.2	
.5	7.4	0.4				1.4				2.8	
10	1.4									.7	
.5											
Mean length	7.80	6.39	7.61	6.50	5.61	7.60	7.90	7.80	7.57	8.16	6.79

Table 2.3 Percent length frequency distribution of first winter sprat off the coast of Scotland.

Length (cm)	Winter 68/9	69/7	75/6	77/8	78/9	79/8	80/1	81/2	82/3	83/4	84/5	85/6
3						4.1	1.6	.3		5.5		
.5			1.2	2.0		22.4	6.4	.6		11.1	.6	1.2
4	2.1	22.2	5.6	4.9	4.1	30.9	17.2	3.5	3.2	17.5	5.9	6.4
.5	19.7	25.7	21.0	9.8	24.6	27.2	24.1	15.2	15.1	13.4	17.2	14.2
5	31.2	18.3	29.2	12.0	32.8	7.4	20.6	18.9	22.2	8.9	12.2	13.0
.5	33.1	8.7	22.2	16.2	20.5	3.1	12.6	14.2	16.0	7.2	6.2	6.9
6	10.3	7.8	10.4	18.6	10.2	.5	11.8	8.6	9.6	8.1	3.1	11.8
.5	4.7	3.9	4.1	15.3	4.8	.8	3.0	12.8	5.5	8.8	8.8	17.5
7	.6	5.2.	1.8	10.4	1.7	1.9	2.5	14.0	8.9	11.6	17.4	17.0
.5		5.2	2.3	7.2	.8	1.2	2.4	8.2	8.2	4.5	17.4	10.2
8		3.6	1.6	4.6	.4	1.6	1.0	3.4	5.4	2.1	9.8	2.8
.5			.9	1.0		.8	.5	.9	2.8	1.4	9.8	1.7
9			.6	.4		.4	.1	.4	2.8	1.3	1.9	
.5			.2						2.8	.2	.6	
10											.6	
.5												
Mean length	5.48	5.41	5.51	6.16	5.44	4.56	5.31	6.12	5.99	5.27	6.47	5.95

Table 2.4 Observations on meristic characters over the whole geographic range of the sprat distribution.

Area	VS	K2	RFC	PF
Baltic Belt Sea	46-49	10-13	18-20	16-18
Kattegat Skagerak	46-50	11-12	18-20	16-18
North Sea British Isles	46-49	11-13	18-20	16-18
Atlantic Coasts	46-50			
Mediterranean	46-49	10-12		
Adriatic	45-49	10-12		
Black Sea	45-50	9-13		

From Anon.(1969).

VS = Vertebrae
K2 = Keeled scales
RFC = Gill rakers
PF = Pectoral fin rays

Table 2.5 Values for meristic characters of sprat observed in the North Sea and adjacent waters. From Anon. (1969).

Area	Authority	VS	K1	K2	AF	DF
W. Norway	Dannevig G.(1951)	47.54-48.70				
S.E. Norway	Dannevig A.(1947)	47.59-48.11				
"	Dannevig G.(1951)	47.42-48.66				
Skagerrak	Jensen (1961)	47.95-48.10				
Skagerrak/ N	Jensen (1960)	48.06-48.20		11.68-11.87		
Kattegat	Paulsen (1951)	47.96		11.74		
Kattegat	Dannevig G.(1951)	47.82-47.94				
"	Morowa (1982)	47.80(46-50)				
"	Paulsen (1951)	47.90		11.70		
" (Mariager fj.)	Paulsen (1951)	47.12				
" (Ise fj.)	Paulsen (1951)	47.78		11.50		
"	Jensen (1961)	47.88-48.12		11.78-11.97		
W. Denmark (Lim fj.)	Jensen (1961)	47.33-47.43				
" "	Jensen (1960)	47.40		11.42		
" "	Paulsen (1951)	47.50		11.50		
" (Ringköbing fj.)	Jensen (1961)	47.38-47.68		11.55-11.64		
" (Thyborøn)	Jensen (1961)	47.87-47.77		11.78-11.93		
German Bight	(Morawa 1982)	47.54(46-49)				
S.E.N. Sea	(Jensen 1960)	47.64-47.92		11.48-11.78		
S.N. Sea (Belgian Coast)	Gilis (1951)	47.50(45-49)	21.38 (19-23)	11.82(10-14)		
" "	Leloup (1954)	47.39(46-49)				
" (off Dunkirk)	Forest (1951)	47.64(46-49)				
English Channel	Forest(1951)	47.67(46-49)				
W. Scotland (S. Minch)	de Silva (1973)	47.80(45-49)		11.50(10-13)	19.2 (17-21)	17.0 (16-19)
Isle of Man	Bowers (1950)	47.67(46-49)				
"	Smith (1949)	47.53				
Severn Estuary	Potter/Claridge(1985)	48.60(47-50)		11.50(10-13)	18.8 (17-20)	16.4 (15-18)

References given in Anon. (1969).

Table 3.1 Scottish landings of sprats from ICES Division IVa.

Winter season	MORAY FIRTH Landings * (tonnes)	MORAY FIRTH No of fishing trips	MORAY FIRTH Catch per trip (pair trawl)	SHETLAND Landings (tonnes)
1960-61	0	-	-	0
61-62	276 (276)	-	-	0
62-63	213 (119)	-	-	0
63-64	8747 (4319)	493	9.0	0
64-65	9767 (1990)	799	9.7	0
65-66	70682	8676	8.1	1355
66-67	19699	3137	6.3	875
67-68	18425	2570	7.2	1
68-69	3464	519	6.7	42
69-70	13245	1892	7.0	33
70-71	5201	1069	4.9	19
71-72	28312	4311	6.6	0
72-73	40516	2942	13.8	14
73-74	29914	3202	9.3	76
74-75	32747	3591	9.1	238
75-76	9428	905	10.4	169
76-77	15916	1056	15.1	2264
77-78	18510	939	19.7	482
78-79	14649	796	18.4	579
79-80	9089	632	14.4	18
80-81	591	30	19.7	0
81-82	456	17	26.8	0
82-83	0	-	-	0
83-84	3	1	3.0	0
84-85	0	-	-	20
85-86	0	-	-	0

* Ring-net landings included in total are shown in parenthesis.
All other landings were by two boat pelagic trawl.
Source Annales Biologique and unpublished data.

Table 3.2 Age composition of sprat in the Scottish fishery in the Moray Firth. (Millions).

Winter season	Age group 0/1	1/2	2/3	3/4
1964-65	3223	48	0	+
65-66	1554	6769	368	31
66-67	309	375	599	84
67-68	292	1088	60	19
68-69	10	88	32	4
69-70	390	1233	18	13
70-71	924	255	28	1
71-72	2188	2000	75	18
72-73	3435	2326	454	6
73-74	3083	863	110	18
74-75	1191	1033	323	52
75-76	1748	406	35	8
76-77	1700	931	63	11
77-78	337	1207	280	20
78-79	693	946	119	40
79-80	275	931	79	9
80-81	0	20	5	+
81-82	0	33	6	+

Table 3.3 Offshore catches of sprat in Division IVa W.(Thousand tonnes).

Year	Denmark	Faroe	Norway	Scotland (purse seine)
1972	-	-	2.2	-
1973	-	-	-	-
1974	5.3	0.2	-	-
1975	0.5	12.9	1.5	-
1976	0.6	2.5	29.9	1.9
1977	0.1	0.4	16.0	-
1978	-	-	1.3	-

Table 3.4. Mean numbers of sprat caught in midwater trawl hauls in the area 58-60°N, 1-4°W.

Date of survey		Mean no	No of trawl hauls
1975	June	4200	10
1976	July	5800	9
1977	June	1300	7
1978	no survey	-	-
1979	July/Aug.	2	2
1980	June/July	0	24
1981	August	0	11
1982	July	0	16
1983	July	0	13
1984	July	12	18
1985	July	810	11
1986	July	332	16

Table 3.5 Catches of sprat (thousand tonnes) by the Danish industrial fishery within the central North Sea (Division IVb).

Year	Catch in deeper water rect. of IVb	Total catch	% in deeper water NW and N of Dogger
1974	30.1	158.7	18.9
1975	66.7	321.1	20.8
1976	75.8	302.6	25.1
1977	31.3	177.3	17.7
1978	53.7	184.5	29.1
1979	15.1	236.8	6.4
1980	9.4	223.4	4.2
1981	1.5	180.7	0.8
1982	1.1	118.2	0.9
1983	4.9	71.6	6.9
1984	2.6	67.7	3.9

Table 3.6 Abundance indices of 1- and 2-group sprat in the North Sea derived from International Young Fish Surveys (IYFS) and Multispecies VPA (MSVPA) results.

Year class	IYFS Div IVb 1-group	I.K.M.T. Div IVb 1-group	IYFS 2-group	MSVPA 1-group N x 10^{-9}	MSVPA 2-group N x 10^{-9}
1971	90				
1972	123		1963		35
1973	481		no data	201	79
1974	no data		854	108	34
1975	1186		1912	170	53
1976	136		730	86	30
1977	1474		(192)*	94	22
1978	(248)*		2709	153	41
1979	1402	109	1102	76	18
1980	886	36	356	48	12
1981	183	16	316	24	5
1982	512	4	306	11	2
1983	347	6	228	27	
1984	659**	2	146		
1985	68**	2			
1986	809**				

* Catches were generally very depressed due to extreme weather conditions during the 1979 survey.

** Preliminary
From Anon. 1987a and Anon. 1987b.

Table 3.7 Landings of sprat in the Skagerrak-Kattegat (Division IIIa) and in fjords of western Norway. (Thousand tonnes).

Year	Div. IIIa	Norw. fjords	Total
1966	9.9	10.7	20.6
1967	12.9	10.2	23.1
1968	9.8	6.4	16.2
1969	6.8	11.8	18.6
1970	15.0	6.4	21.4
1971	17.1	4.4	21.5
1972	25.8	6.9	32.7
1973	60.6	8.8	69.4
1974	71.3	3.3	74.6
1975	100.6	2.9	103.5
1976	58.8	0.6	59.4
1977	67.4	5.4	72.8
1978	77.9	5.2	83.1
1979	95.6	5.0	100.6
1980	83.9	2.9	86.8
1981	76.3	3.1	79.4
1982	45.2	6.0	51.2
1983	26.5	3.0	29.5
1984	36.5	3.6	40.1
1985	21.9	7.1	29.0
1986	18.0	1.8	19.8

From Anon. (1987a).

Table 3.8 Consumption (tonnes) of sprat by individual predators.

Predator	1974	1981	1985
Cod	48 301	30 390	6 582
Whiting	323 267	124 374	98 685
Saithe	27 484	7 129	4 170
Mackerel	314 909	6 794	2 467
Haddock	5 832	1 764	527
Total	719 344	170 450	112 430
Average sprat stock biomass	1 615 810	305 056	368 216
% consumed	44.5	55.9	30.5

From the Multispicies Assessment Working Group (Anon. 1987b, Table 7.1.1).

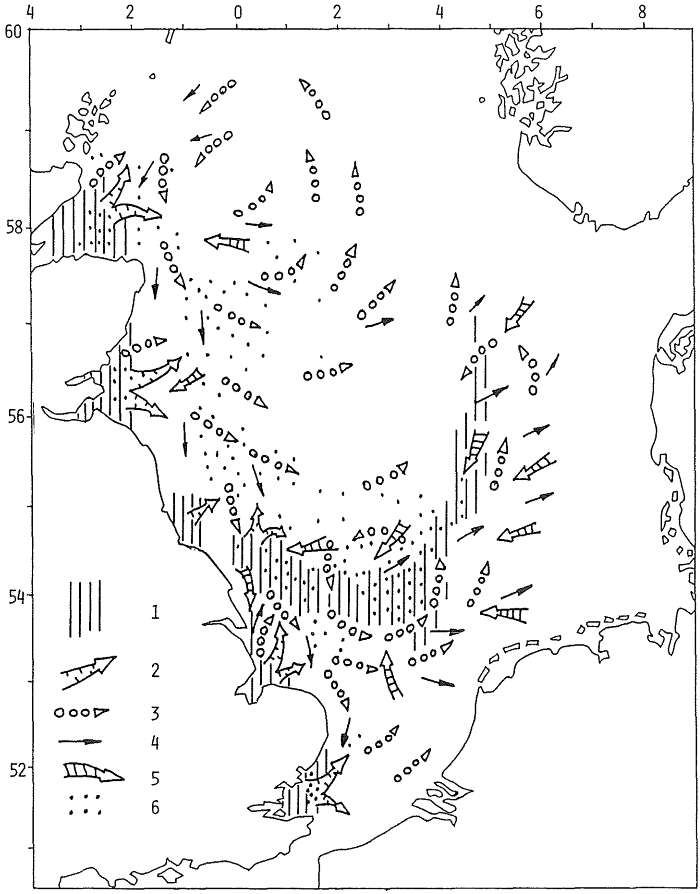


Fig. 2.1 Migration pattern of sprat in the North Sea. From Feldman (1986).

I - wintering sites;
2 - spawning and feeding migrations;
3 - passive drift direction for eggs and larvae;
4 - migrations of fingerlings (individuals under one year old);
5 - migrations of growing young fish towards the wintering sites of mature fish;
6 - main spawning areas.

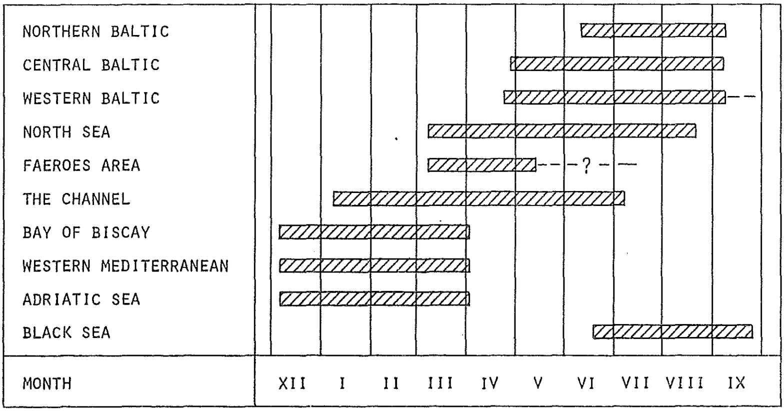


Fig. 2.2 Spawning period of sprat in different areas.
(Morawa 1954)

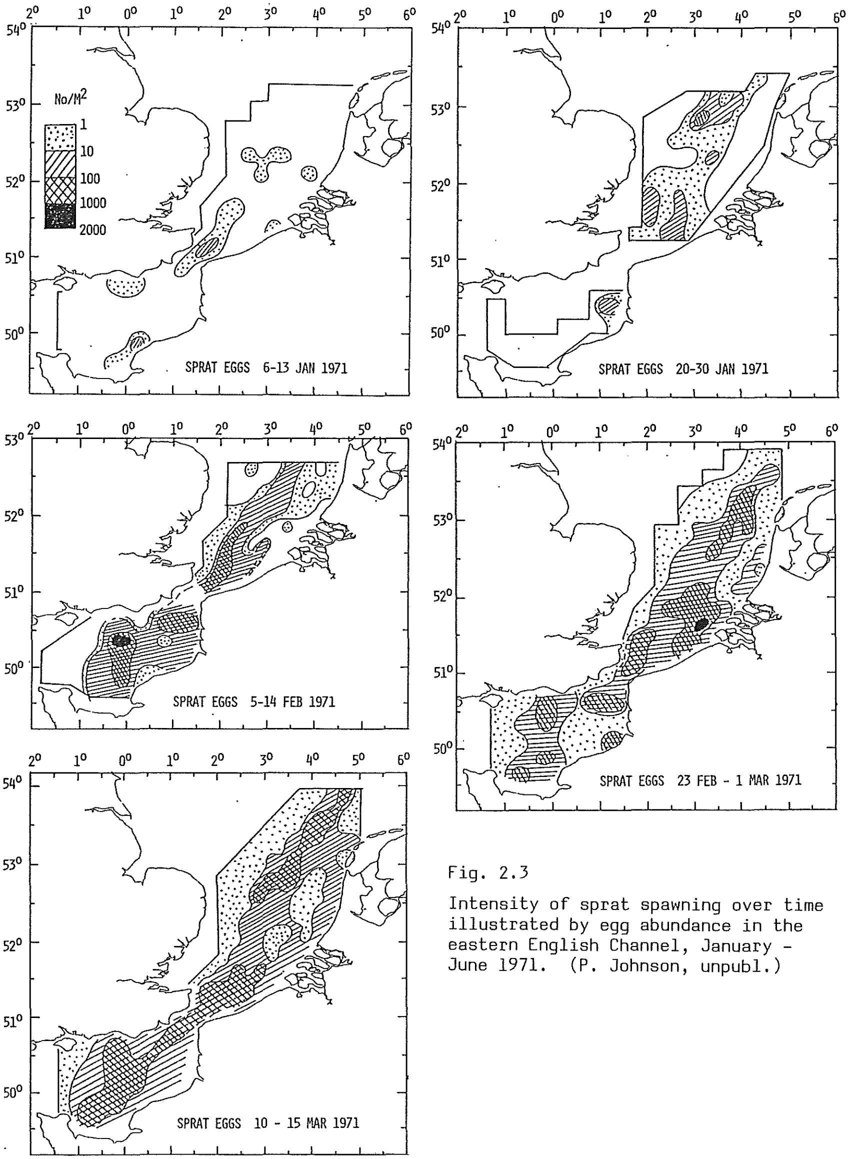
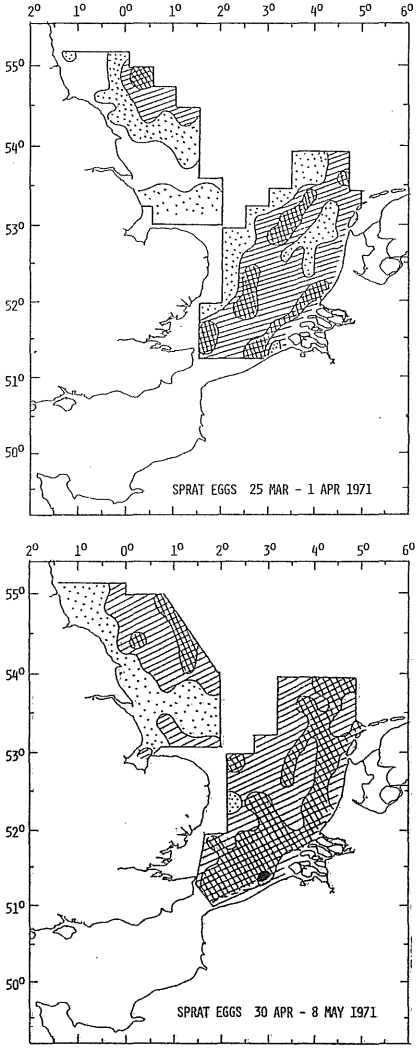


Fig. 2.3

Intensity of sprat spawning over time illustrated by egg abundance in the eastern English Channel, January - June 1971. (P. Johnson, unpubl.)



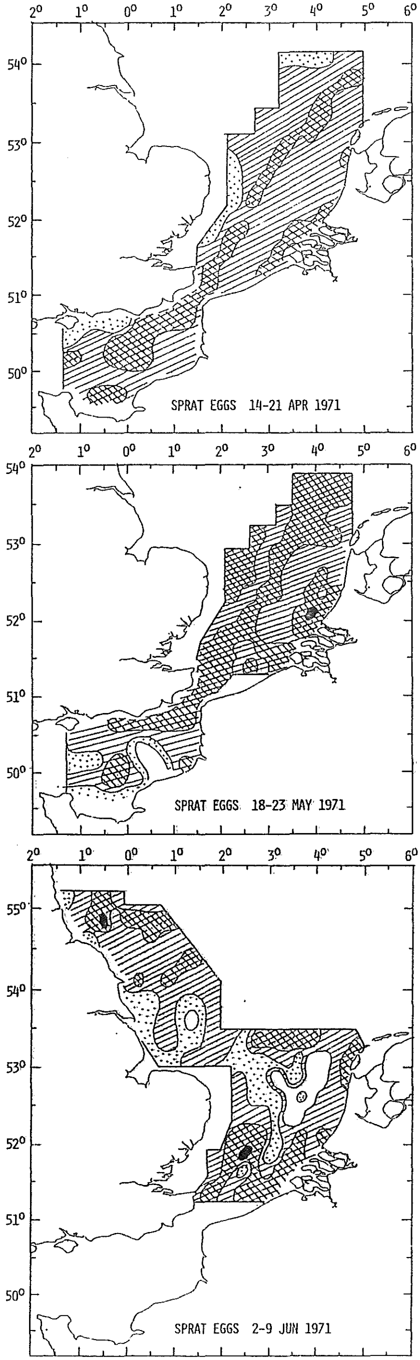


Fig. 2.3 (continued)

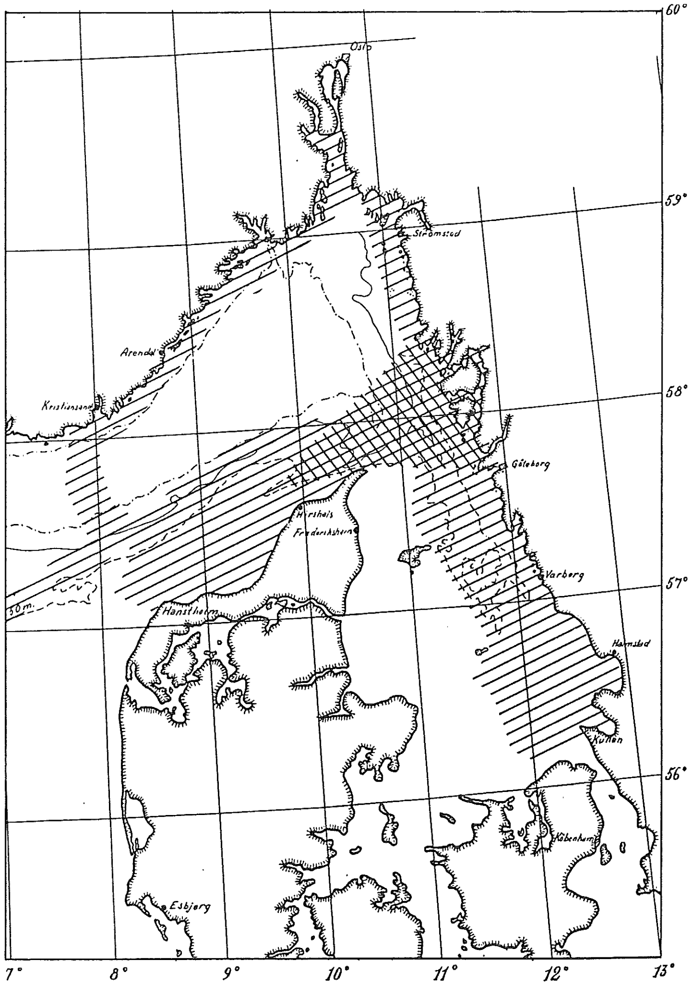


Fig. 2.4 Sprat spawning areas in the Skagerrak-Kattegat. Cross hatching indicate the area of main spawning. (Based on reports by Höglund, Lindquist, Dannevig etc.)

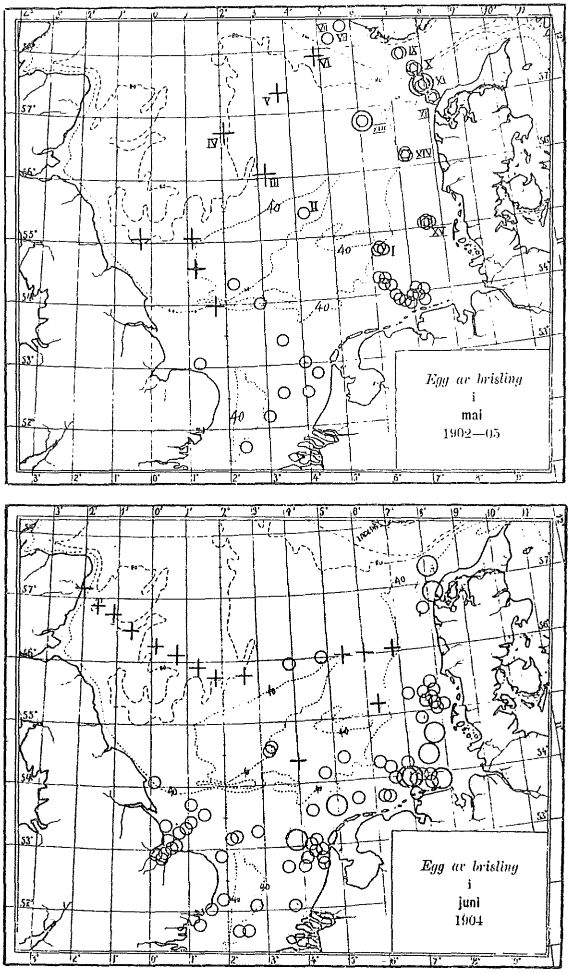


Fig. 2.5 Distribution of sprat eggs in May 1902 - 1905 and June 1904.
Large circles: >100 egg/m^2
Small circles: <100 egg/m^2
Crosses : No eggs
(Sund, 1911)

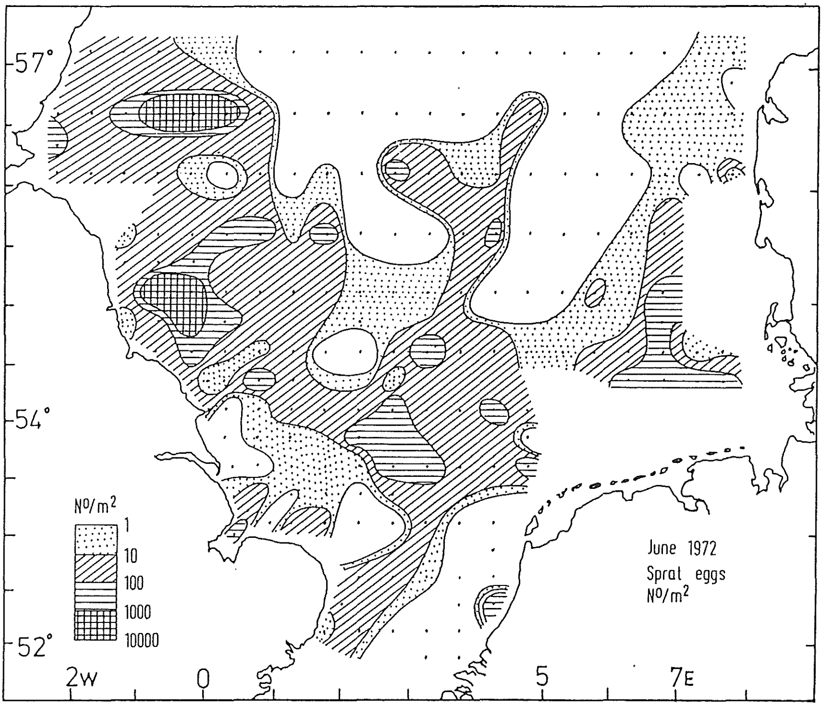


Fig. 2.6 Distribution of sprat eggs in June 1972. (Johnson and Dawson, 1975)

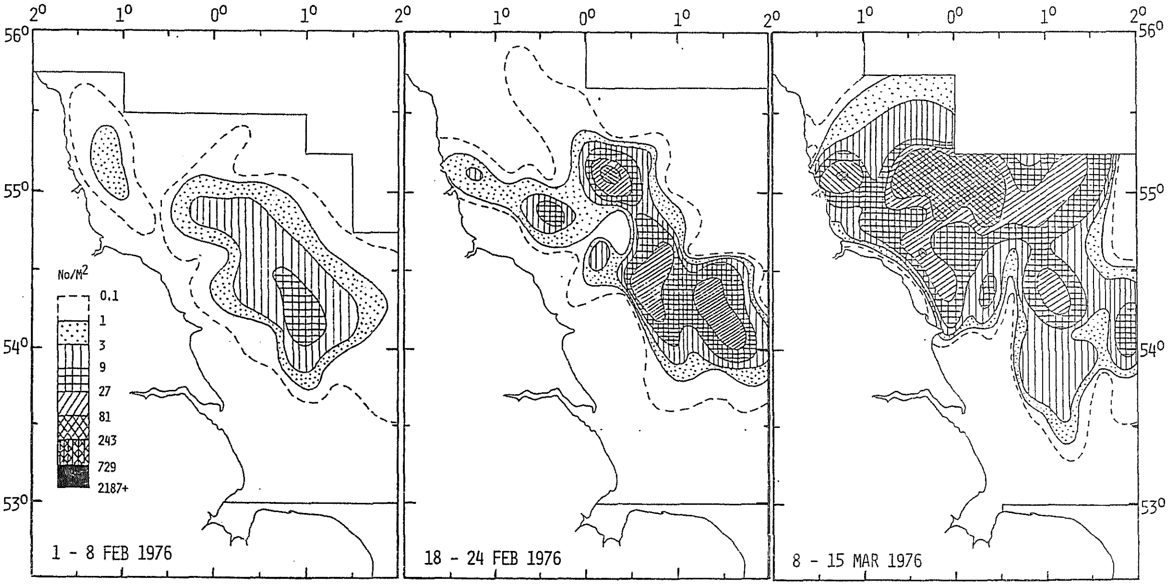


Fig. 2.7 Distribution fo sprat eggs February - August 1976.

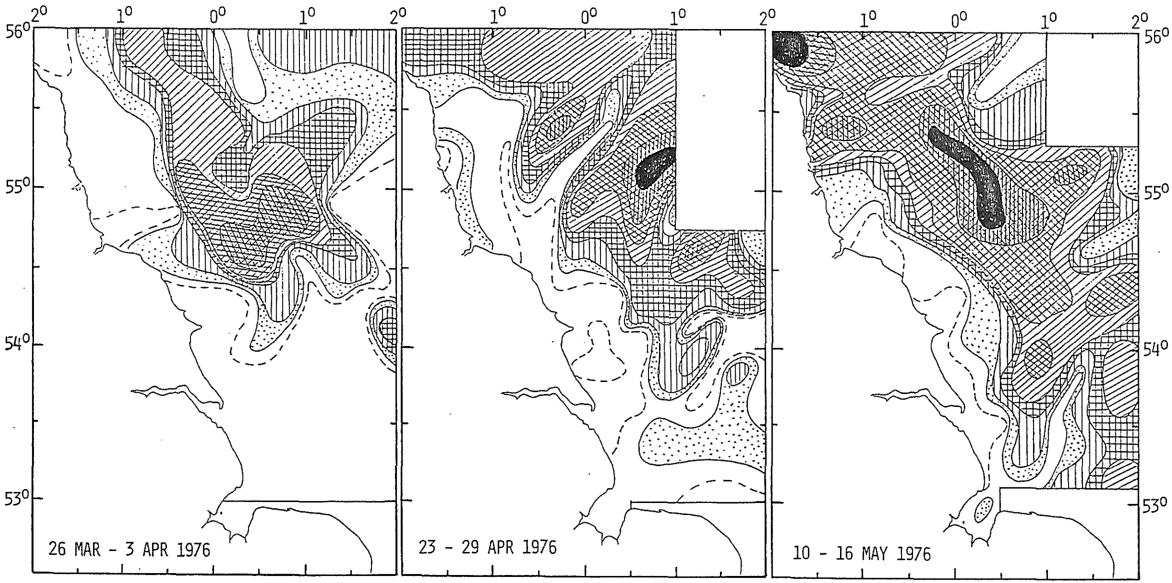


Fig. 2.7 (continued)

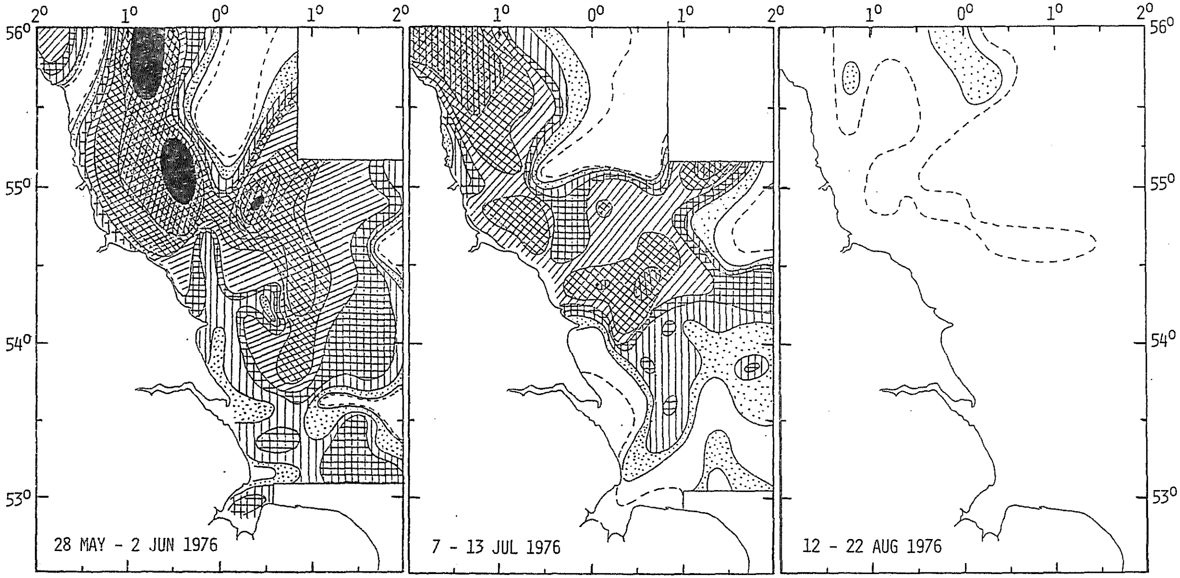


Fig. 2.7 (continued)

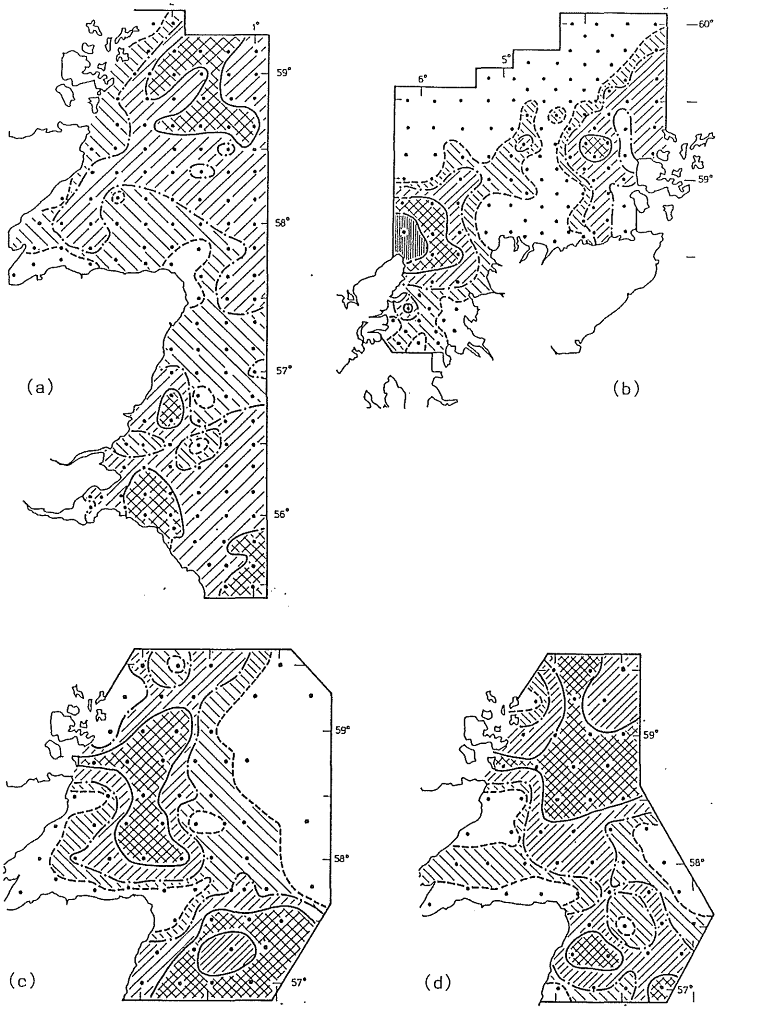


Fig. 2.8 Distribution of sprat eggs off the north and east coasts of Scotland. a) 1-19 July 1974; b) 13-27 July 1974; c) 3-15 July 1975; d) 15-25 July 1975. Grades of hatching show orders of magnitude of abundance: Vertical hatching >1000 eggs below 1 m^2; cross hatching 100-1000 eggs below 1 m^2. (Bailey and Braes, 1976)

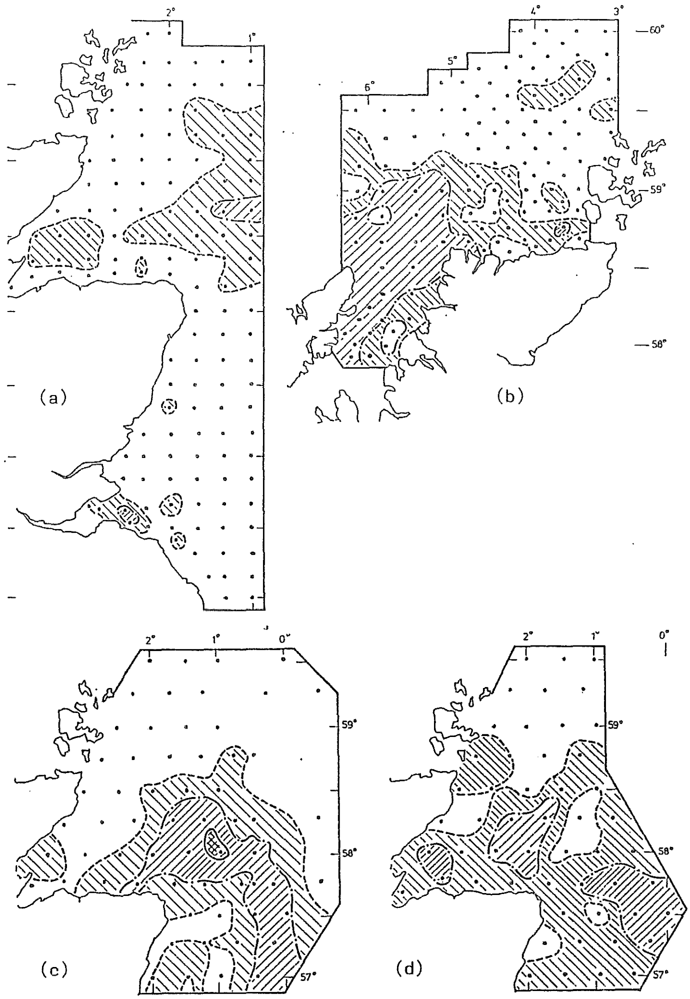


Fig. 2.9 Distribution of sprat larvae (3-10 mm in length.
a) 1-19 July 1974; b) 13-27 July 1974;
c) 3-15 July 1975; d) 15-25 July 1975.
Key as in Fig. 2.8
(Bailey and Braes, 1976)

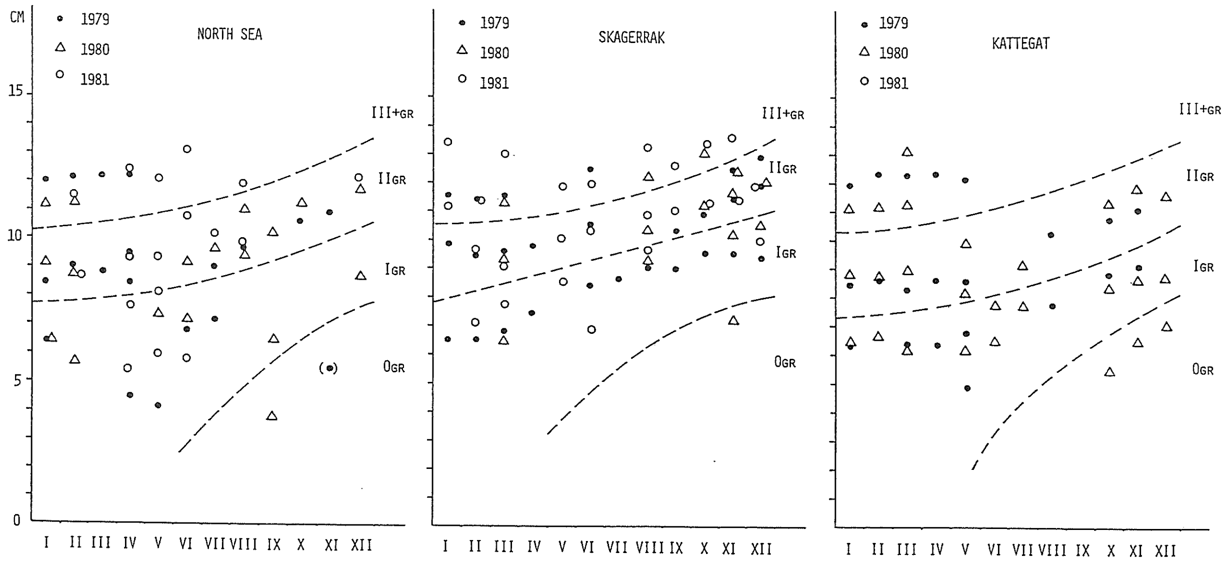


Fig. 2.10 Modal lengths in monthly length distributions 1979 - 1981. Danish commercial landings. (K. Popp Madsen, pers.com.)

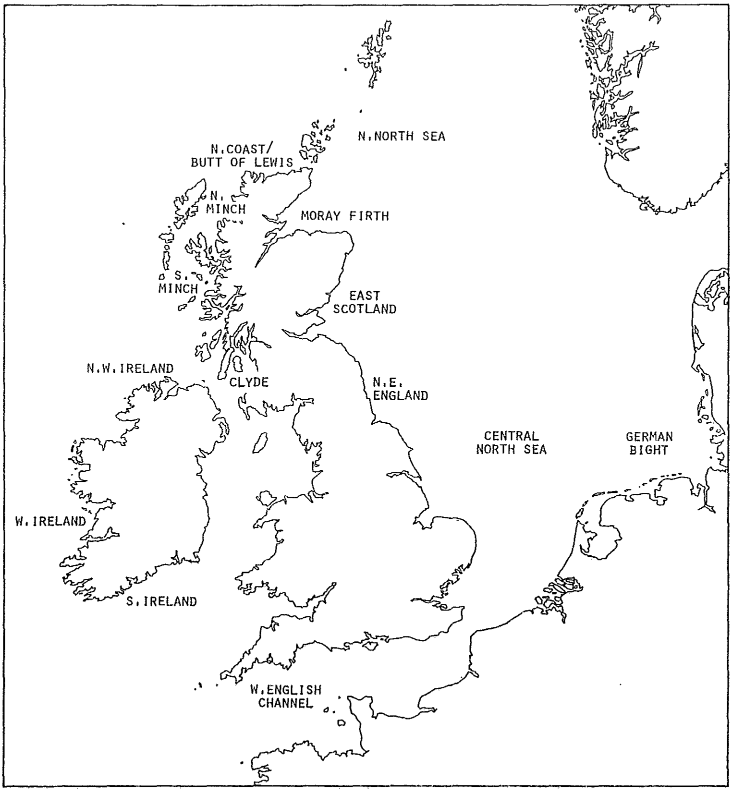


Fig. 2.11 North Sea and West of Britain showing sampling areas related to Figs 2.12 and 2.13

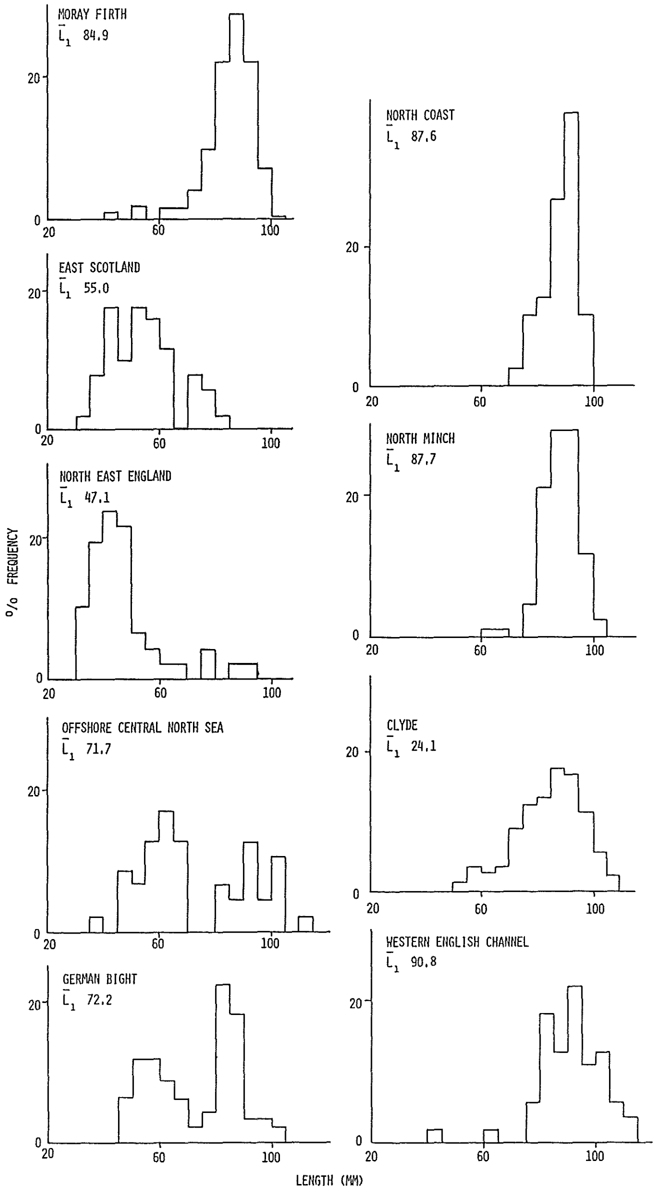
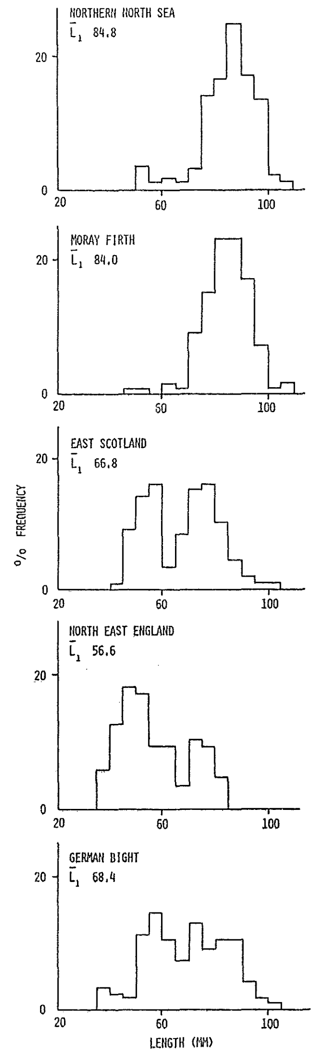


Fig. 2.12 Percent frequency distributions of $\bar{L}_1$'s for 1983 year class during second winter, October 1984 - March 1985.



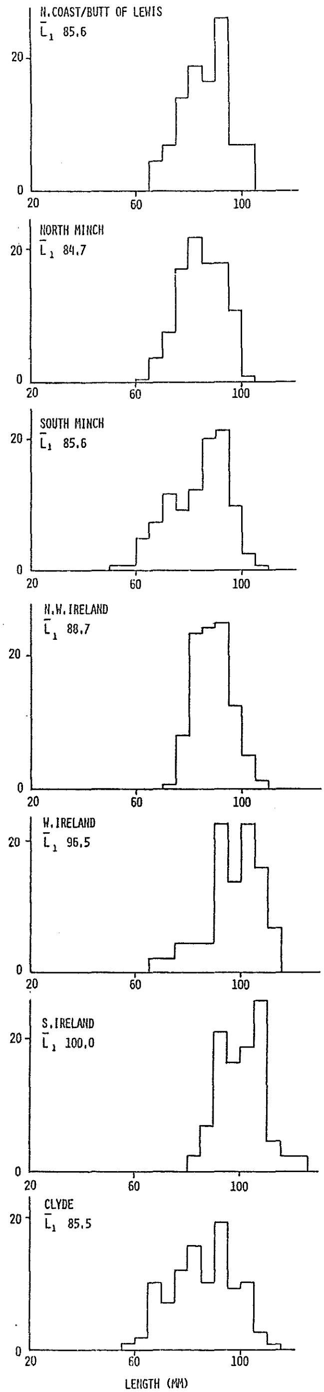


Fig. 2.13

Percent frequency distributions of $\bar{L}_1$'s for 1984 year class during second winter, October 1985 - March 1986.

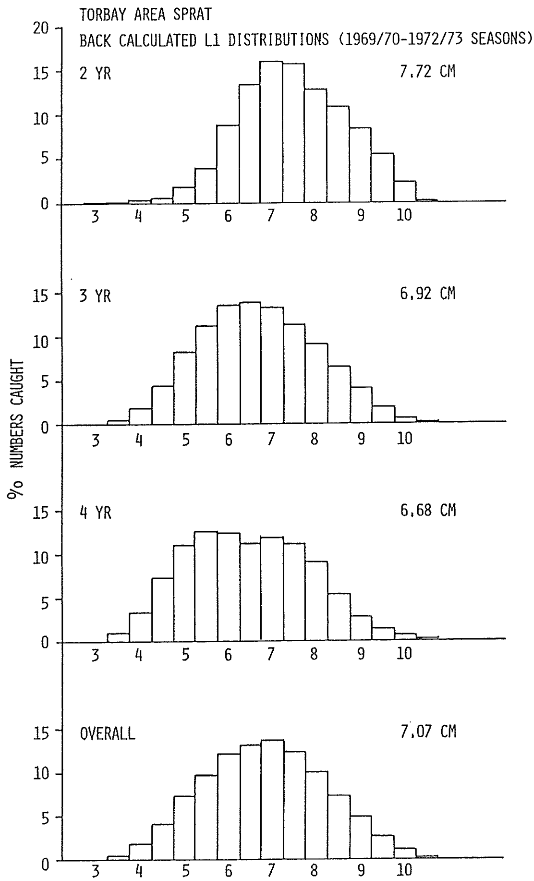


Fig. 2.14 Back calculated length at age one from Western Channel.

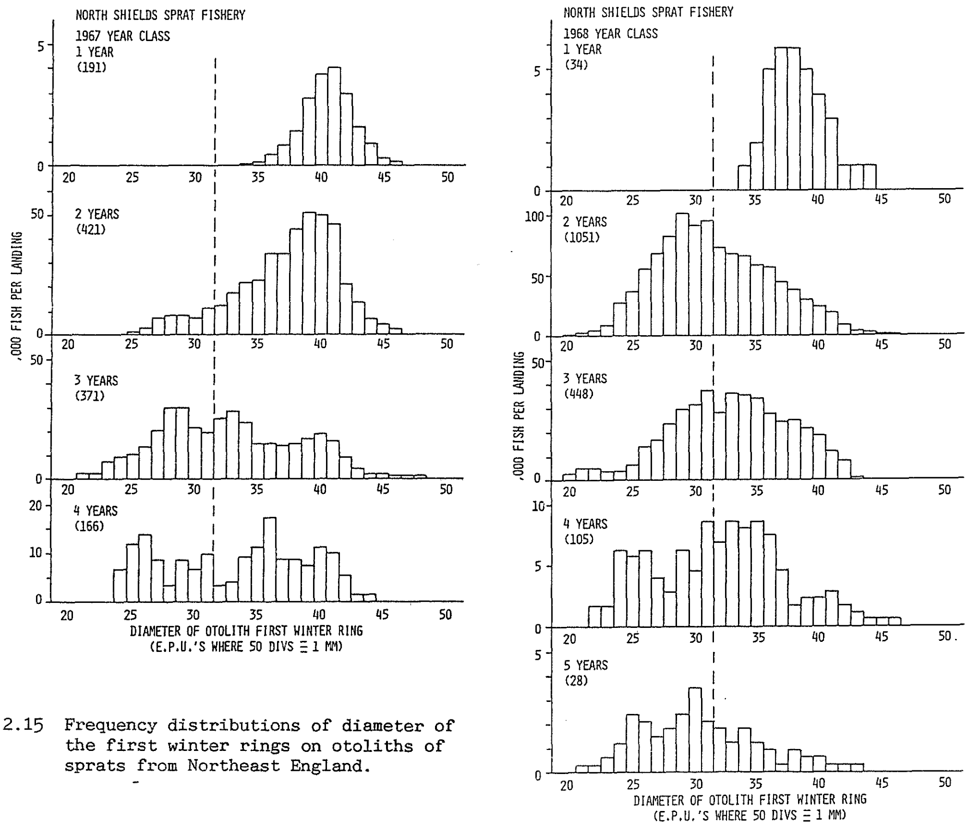
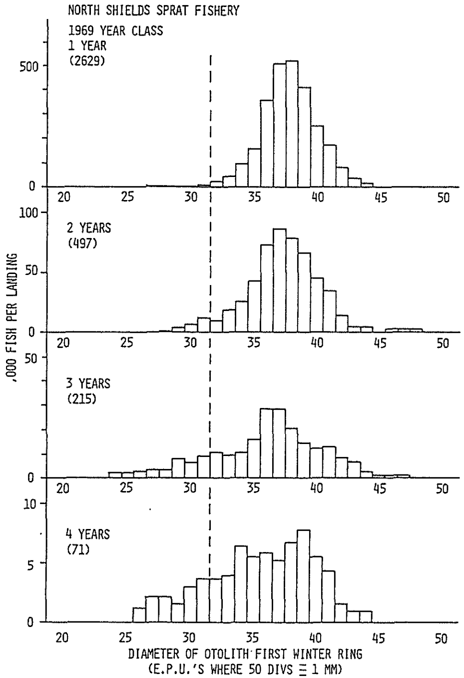


Fig. 2.15 Frequency distributions of diameter of the first winter rings on otoliths of sprats from Northeast England.



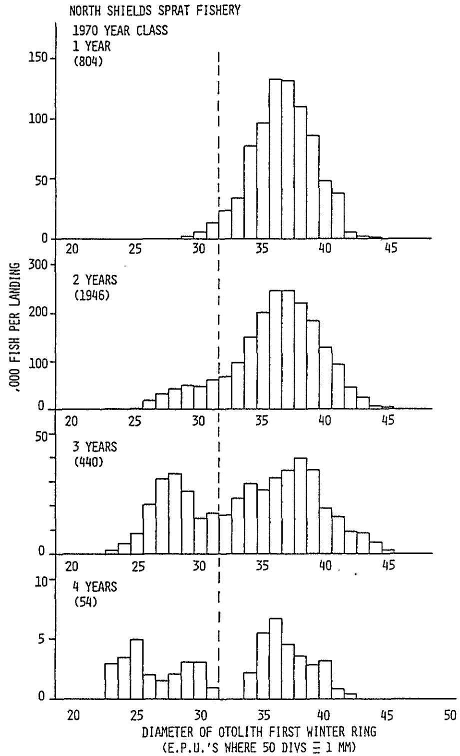


Fig. 2.15 (continued)

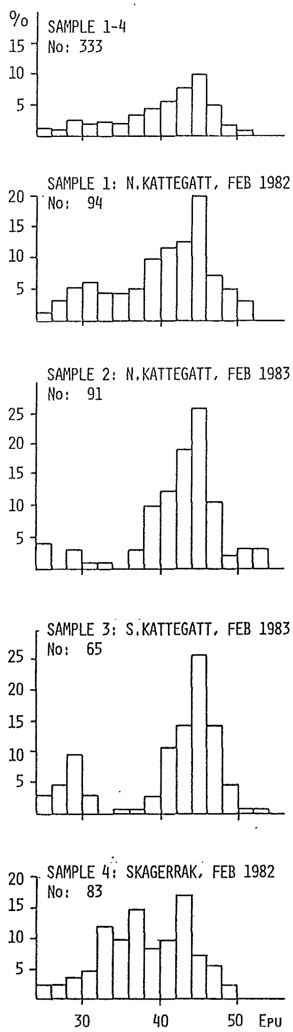


Fig. 2.16 Frequency distributions of diameter of the first winter rings on otoliths of sprats from the Skagerrak-Kattegat area.

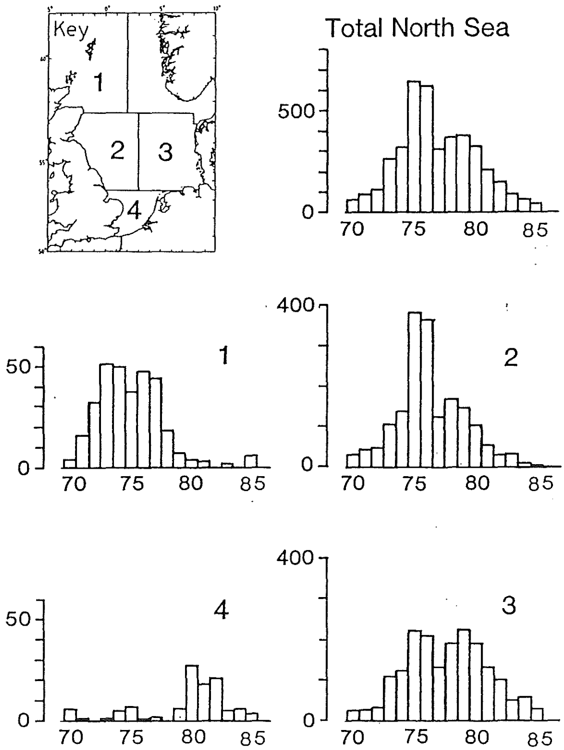


Fig. 3.1. International annual catches of North Sea sprat (scales in thousand tonnes).

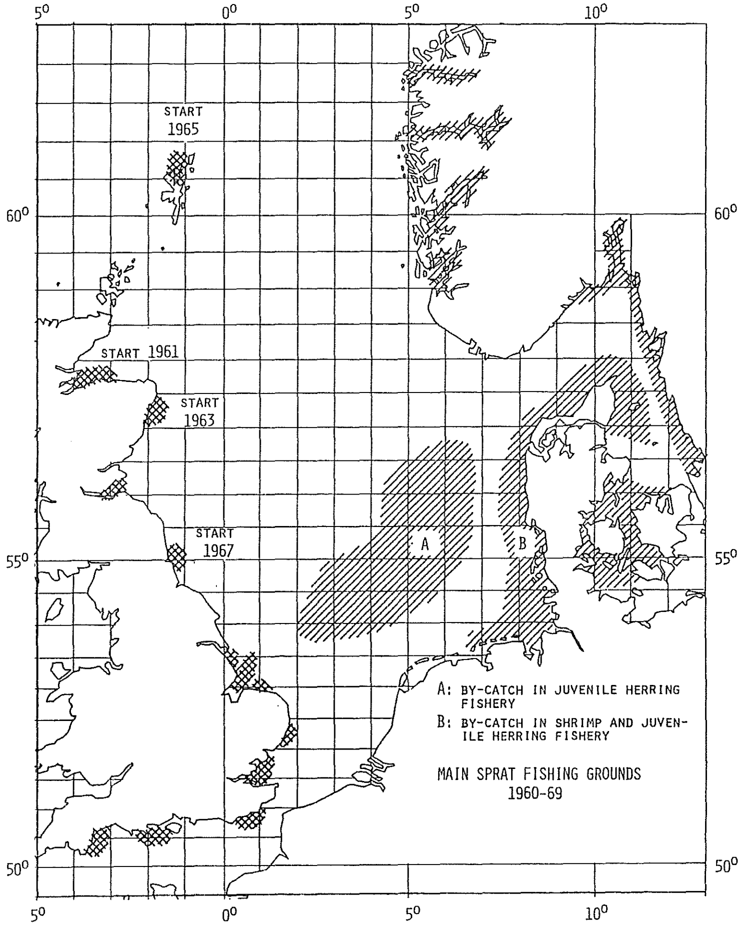


Fig. 3.2. Main sprat fishing grounds 1960 - 1969.

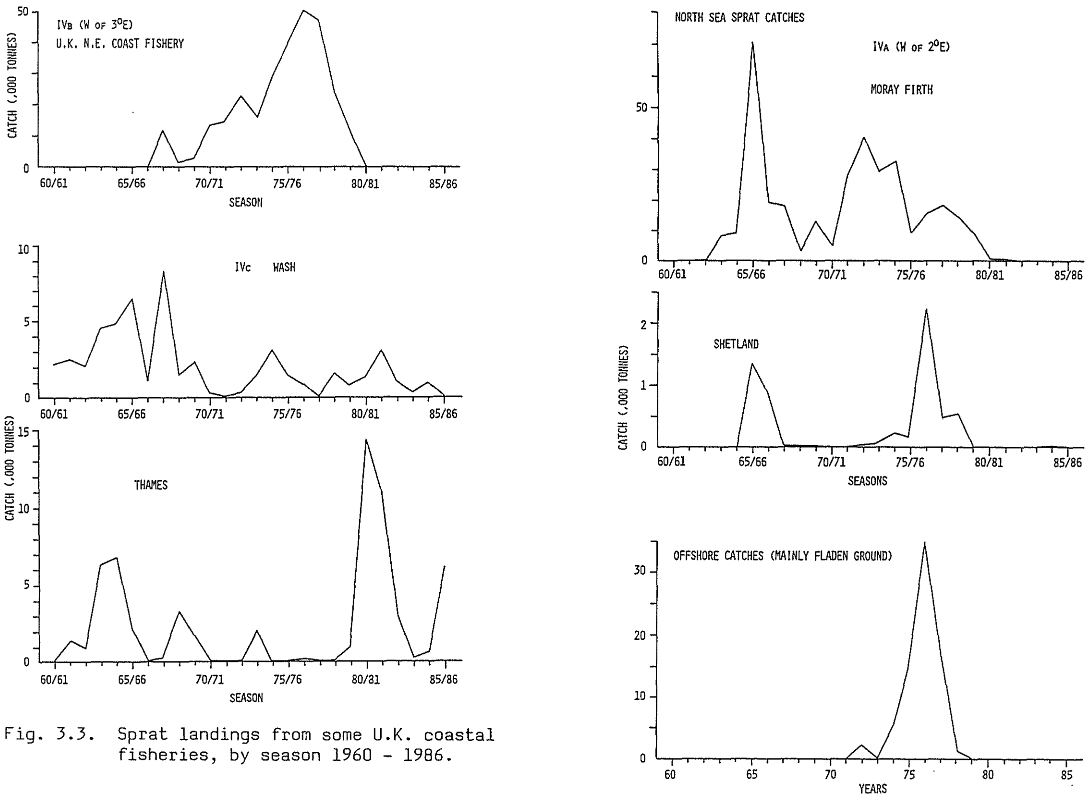


Fig. 3.3. Sprat landings from some U.K. coastal fisheries, by season 1960 - 1986.

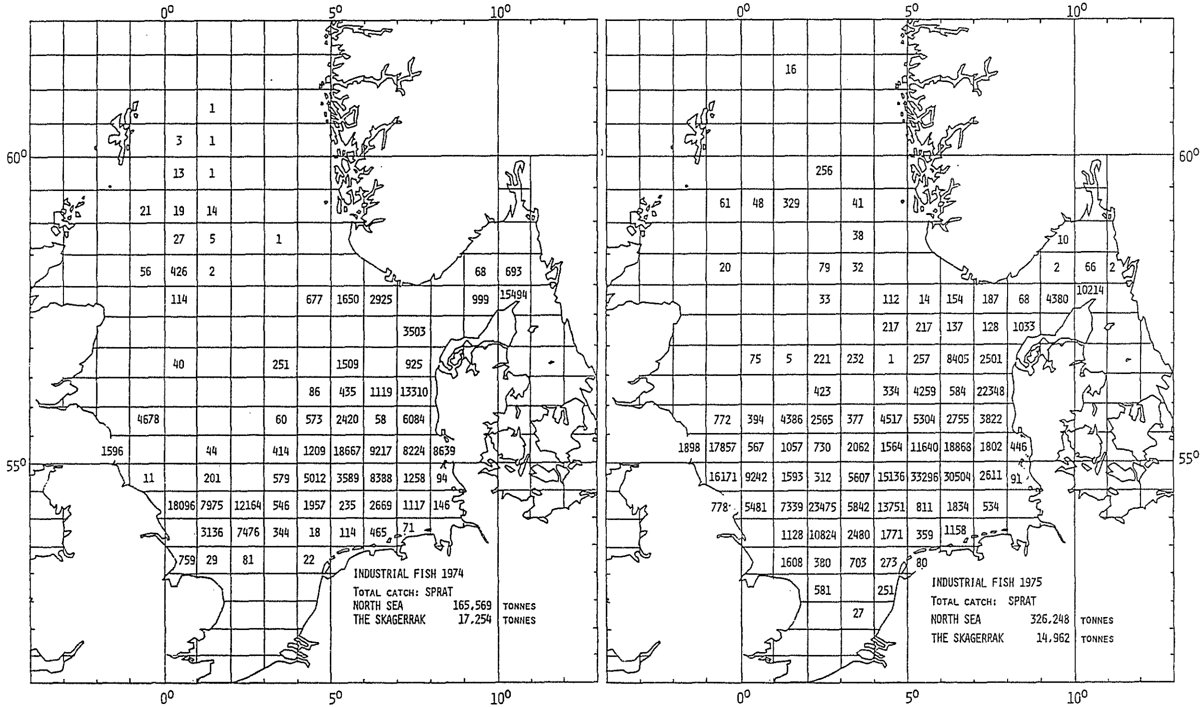


Fig. 3.4. Distribution of Danish industrial catches of sprat 1974 - 1984.

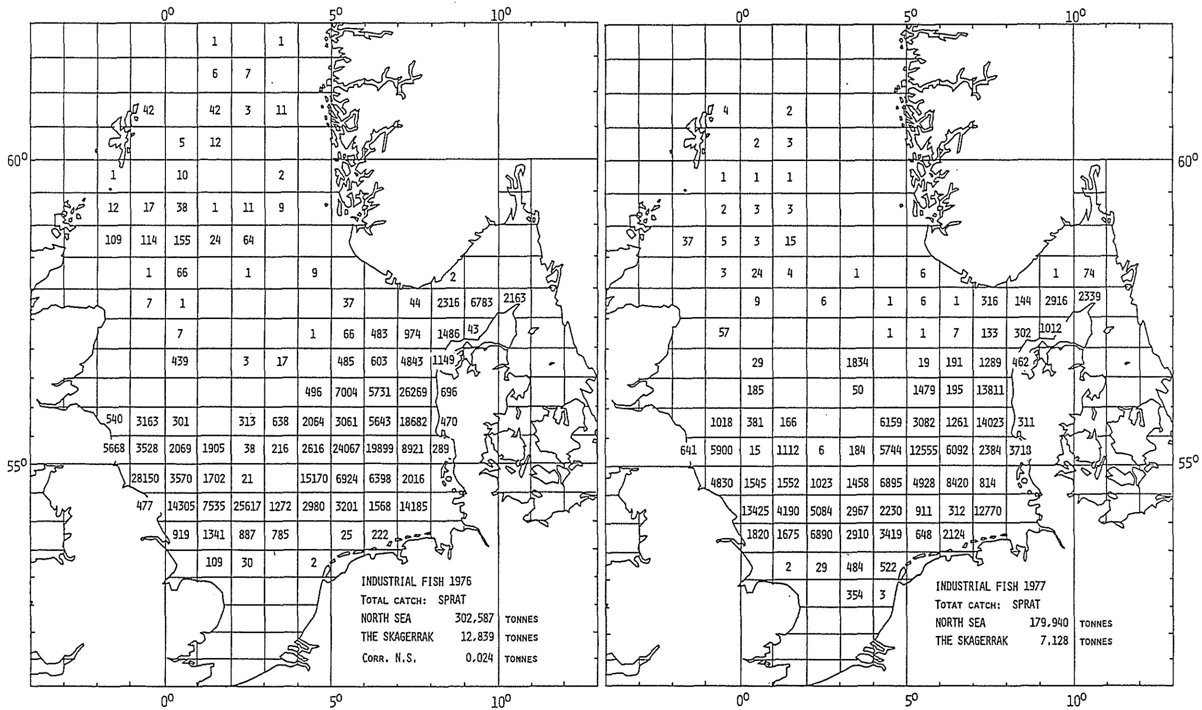
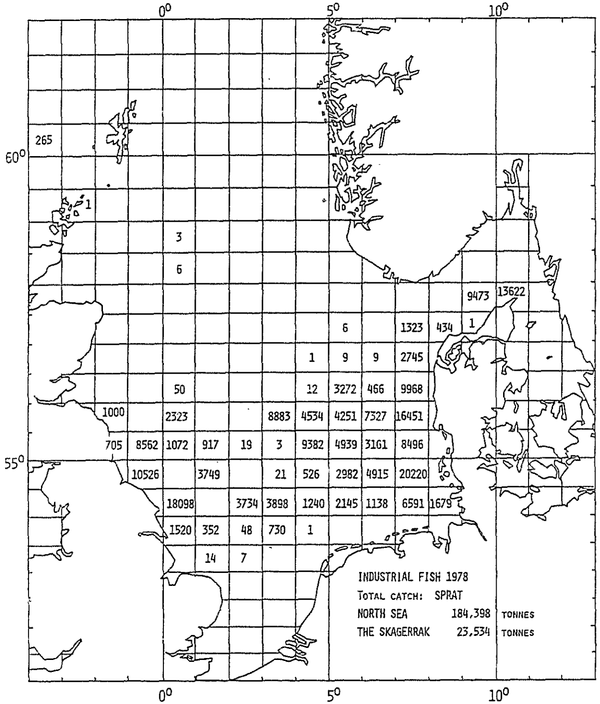


Fig. 3.4. (continued)



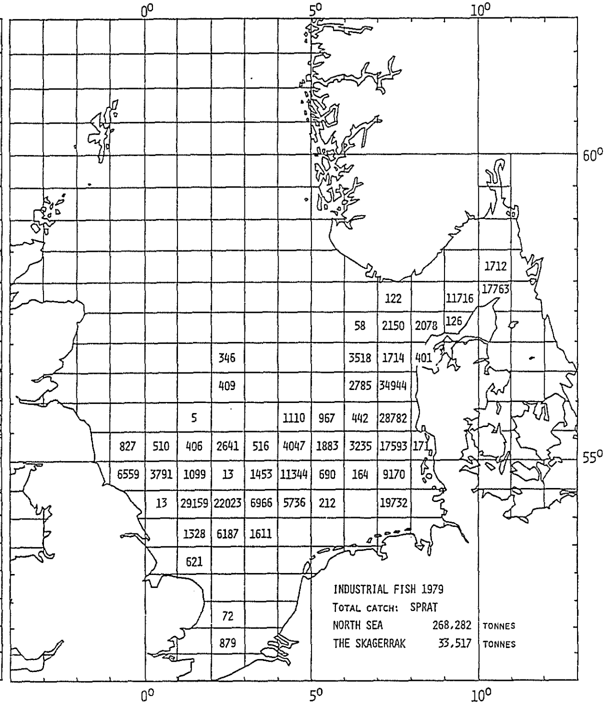
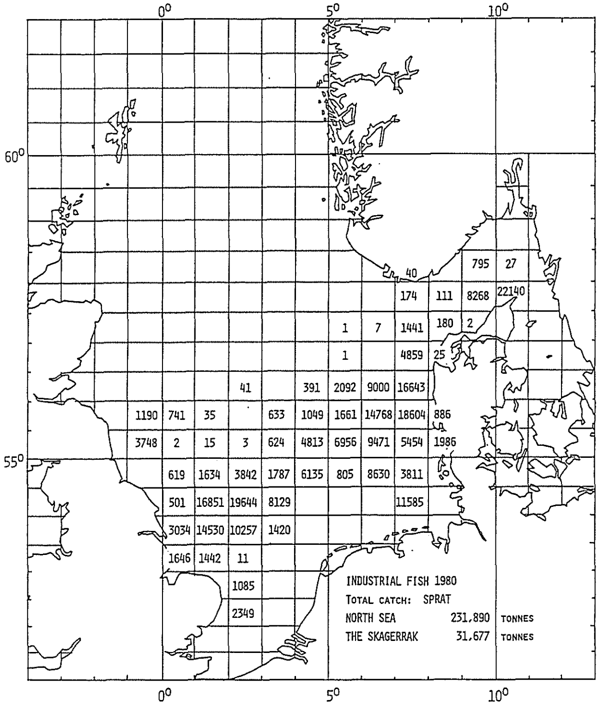
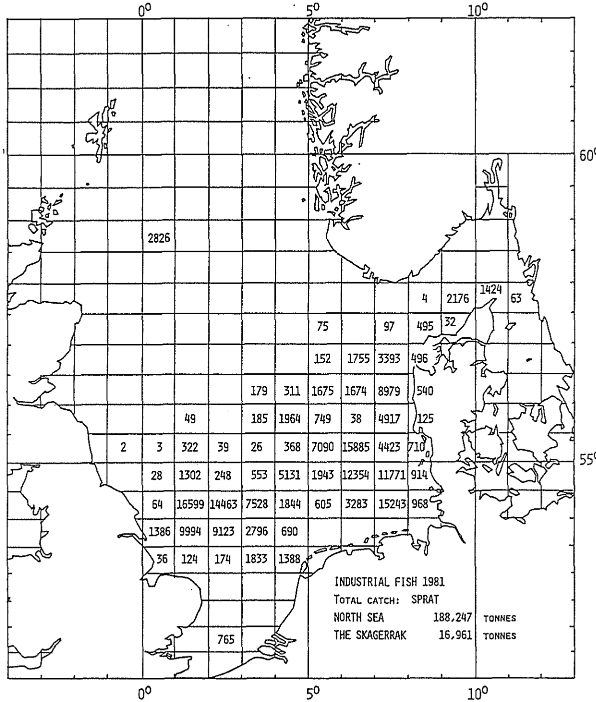


Fig. 3.4. (continued)





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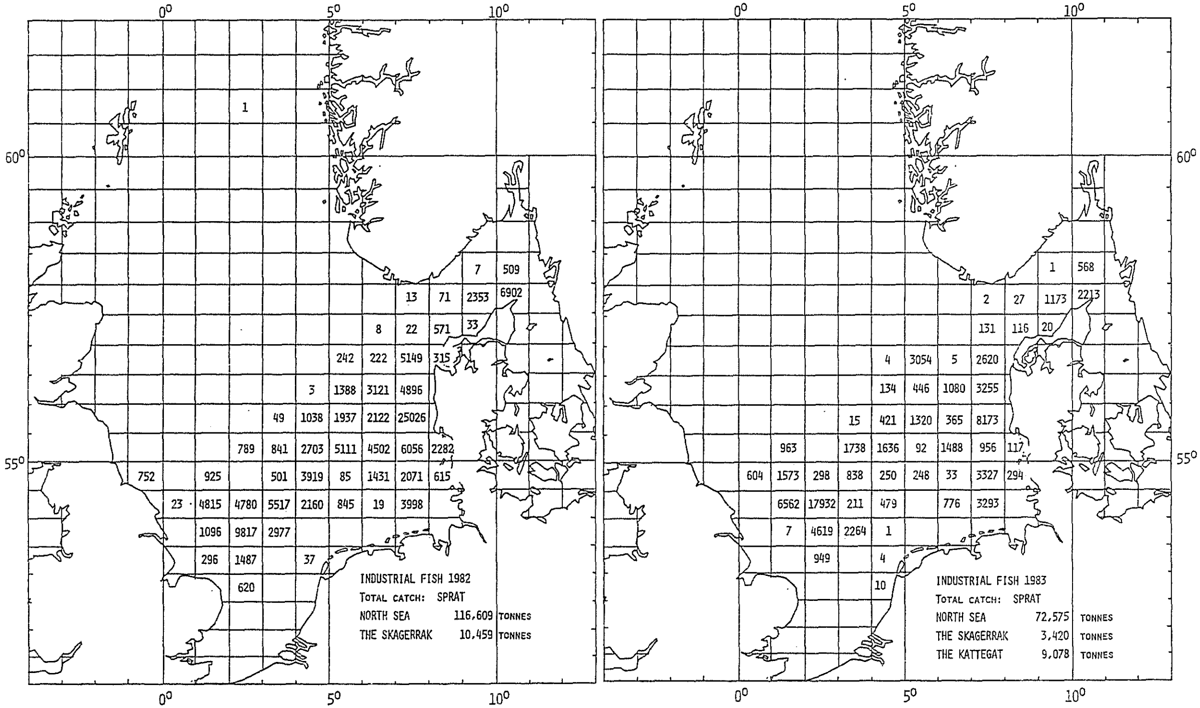


Fig. 3.4. (continued)

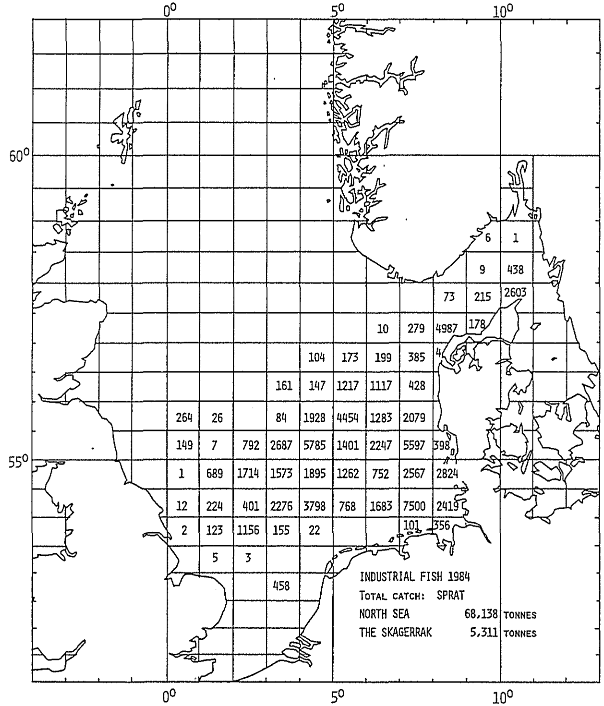


Fig. 3.4. (continued)

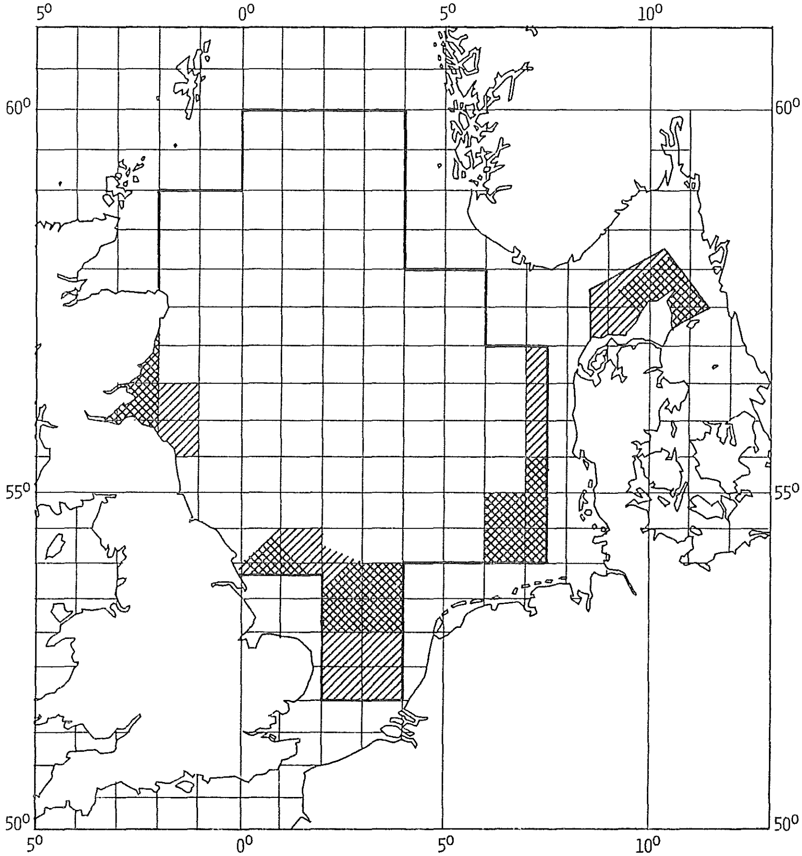


Fig. 3.5. Main distribution of sprat in Danish research trawling within the delimited areas, 1956 - 1957.

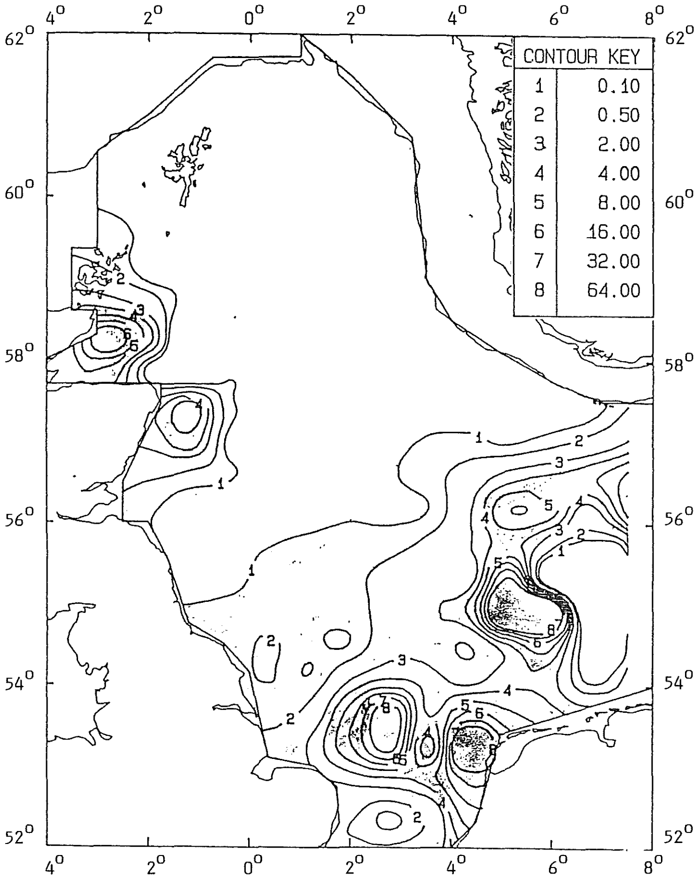
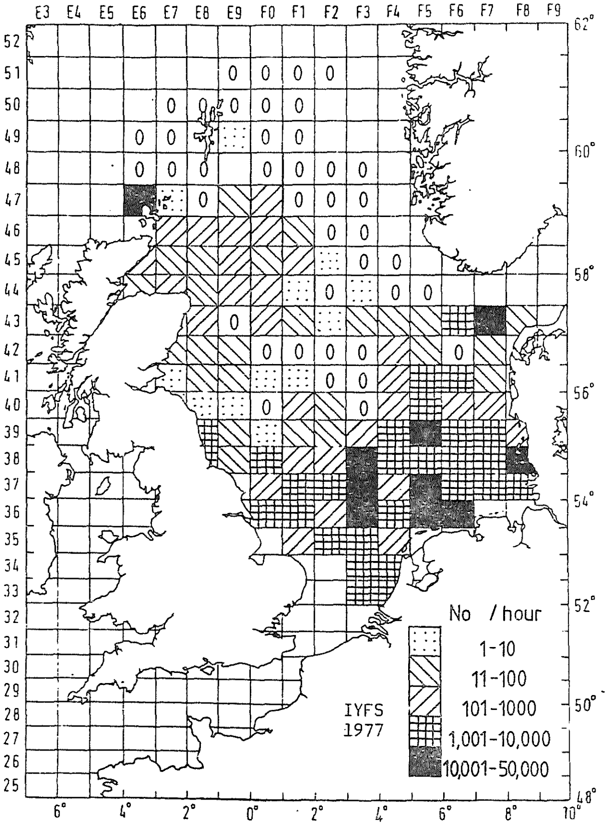


Fig. 3.6. Sprat distribution October - November 1984.
(GOV bottom trawl, kgs/hr.)



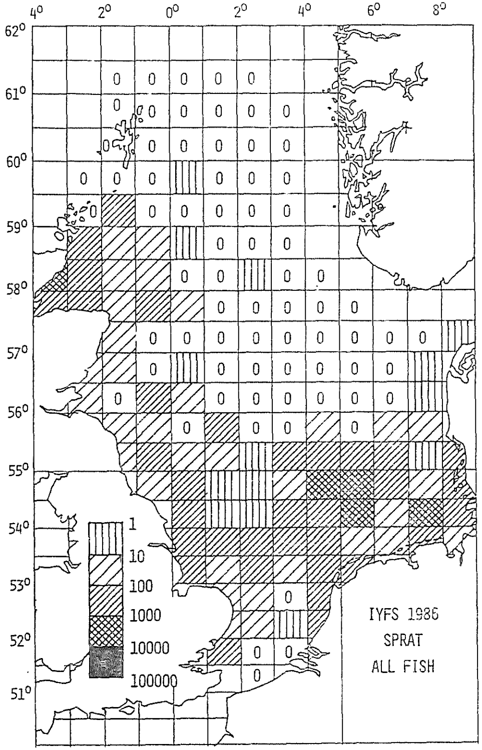


Fig. 3.7. Density distribution by rectangle of sprat all ages taken on the International Young Fish Survey in February 1977 and February 1986.

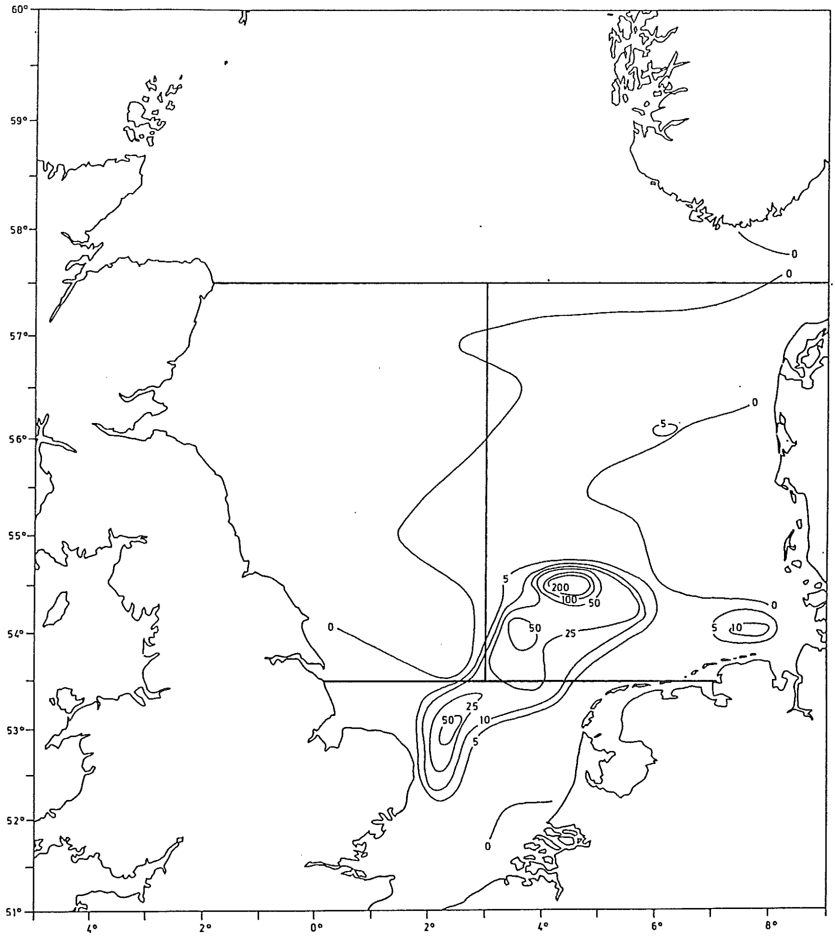


Fig. 3.8 Contoured acoustic densities (tonnes per square nautical mile) of 1-group and older sprat in January 1980 derived from Norwegian investigations.

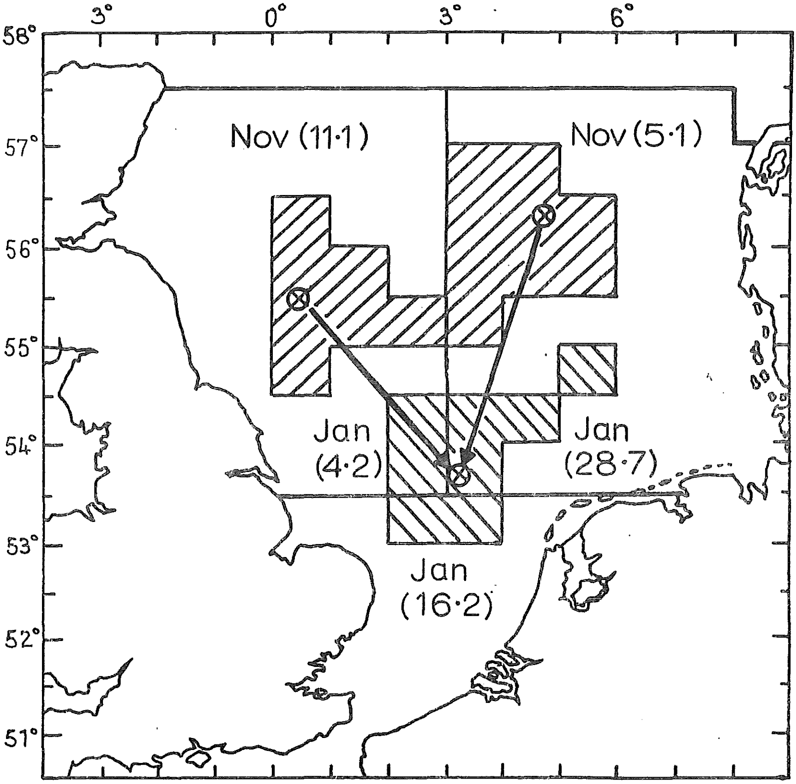


Fig. 3.9 Areas of Norwegian purse-seine fishing for sprat in the North Sea, November 1979 and January 1980. Catches (thousand tonnes) in each ICES sub-division shown in brackets.

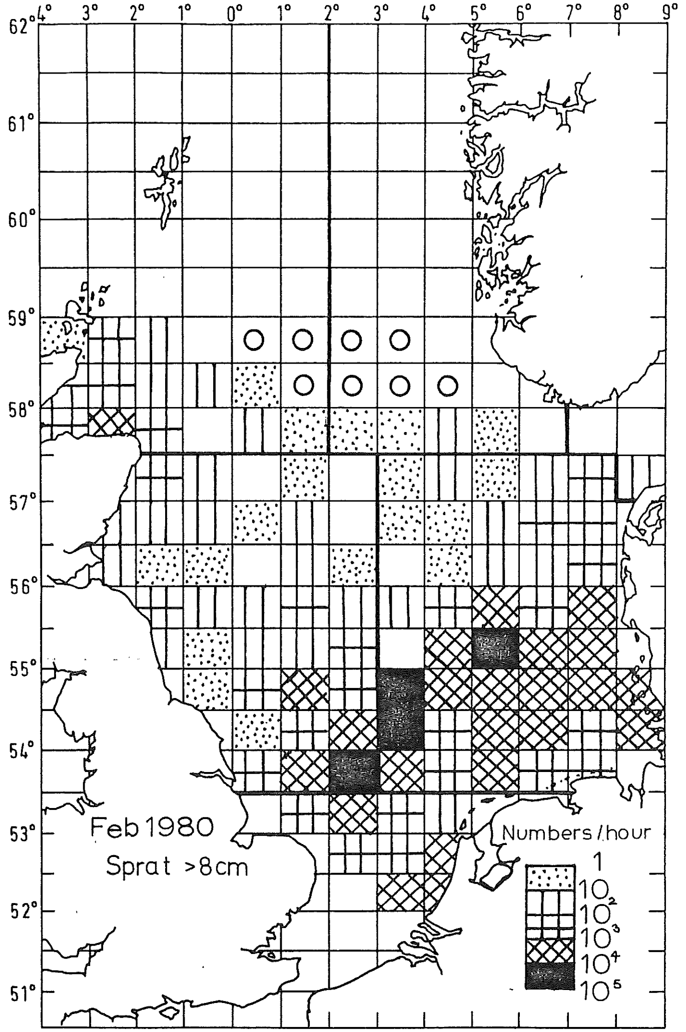


Fig. 3.10. Density distribution of sprat > 8 cm (numbers per hour tow with high headline bottom trawl) in February 1980 determined from IYFS results.

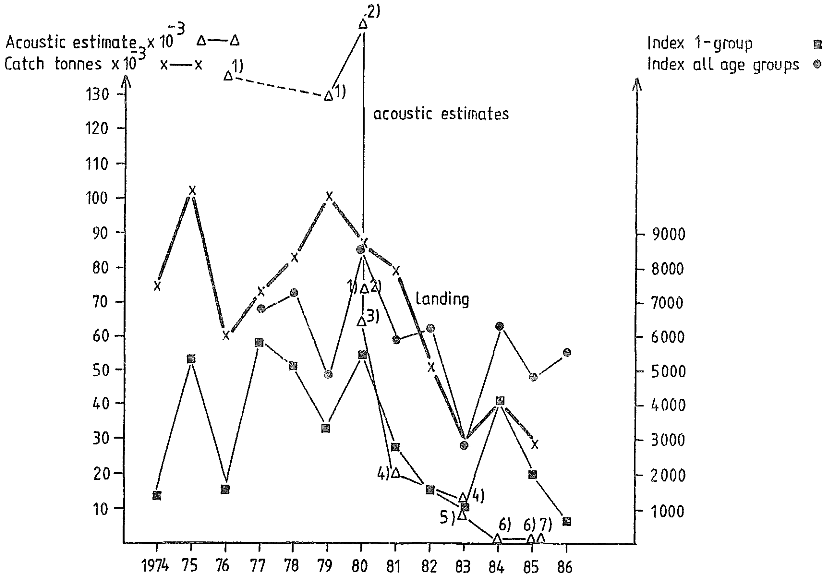


Fig. 3.11 Indicators of sprat stock development in the Skagerrak - Kattegat: Annual landings, acoustic estimates and index of abundance of 1-group from IYFS.

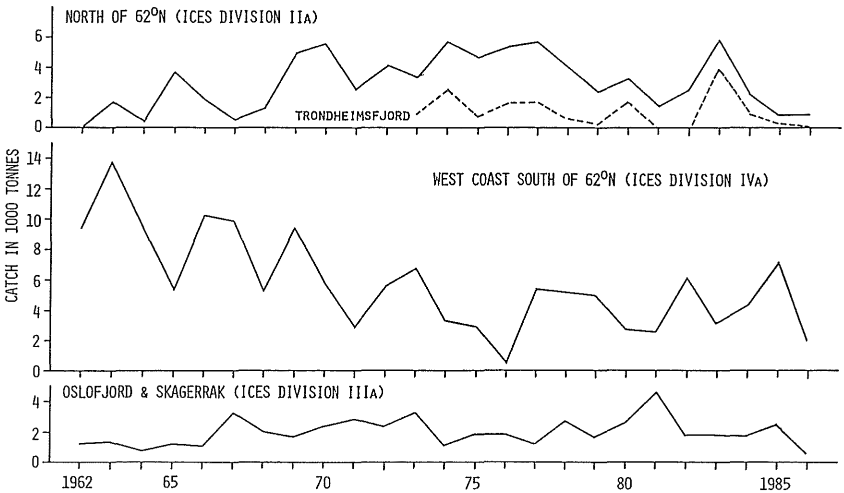


Fig. 3.12. Catches of sprat in Norwegian fjord areas 1962 - 1986.

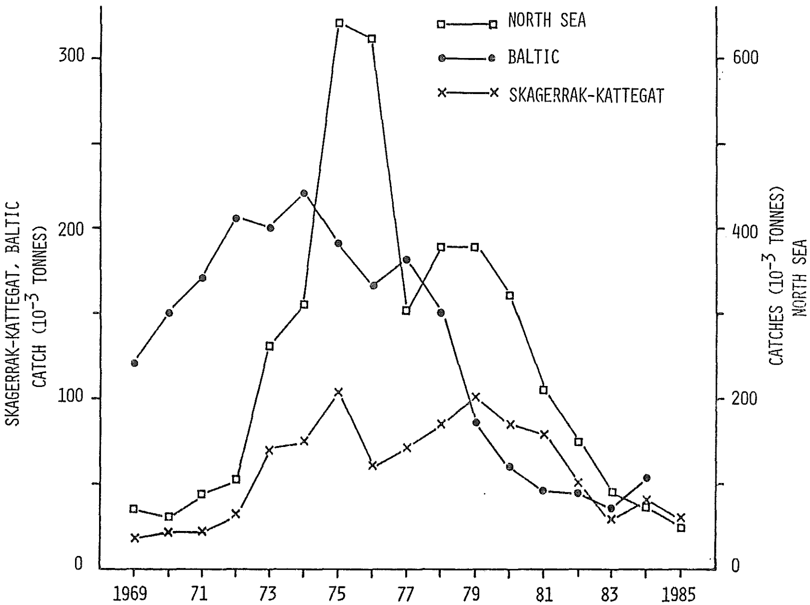


Fig. 3.13. Landings of sprat 1969-1985 from major fishing areas in northern Europe.

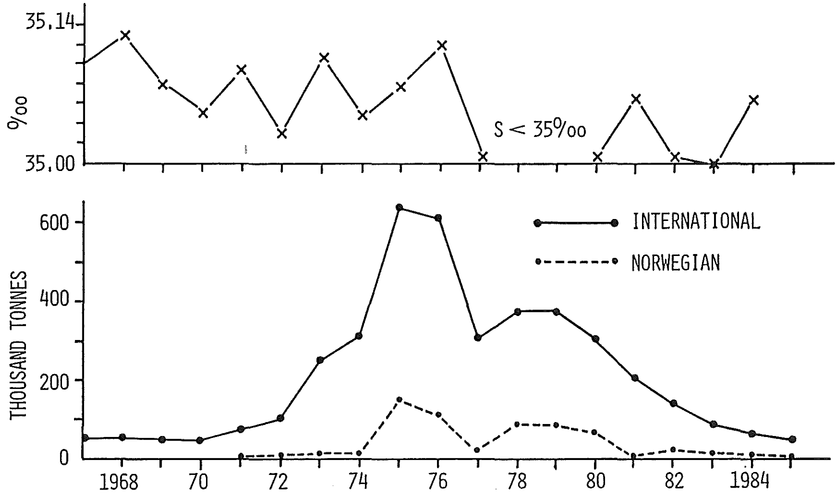


Fig. 3.14 The average salinity (°/oo) in summer at the hydrographical section along 57°N in the North Sea and the international and the Norwegian sprat catches.

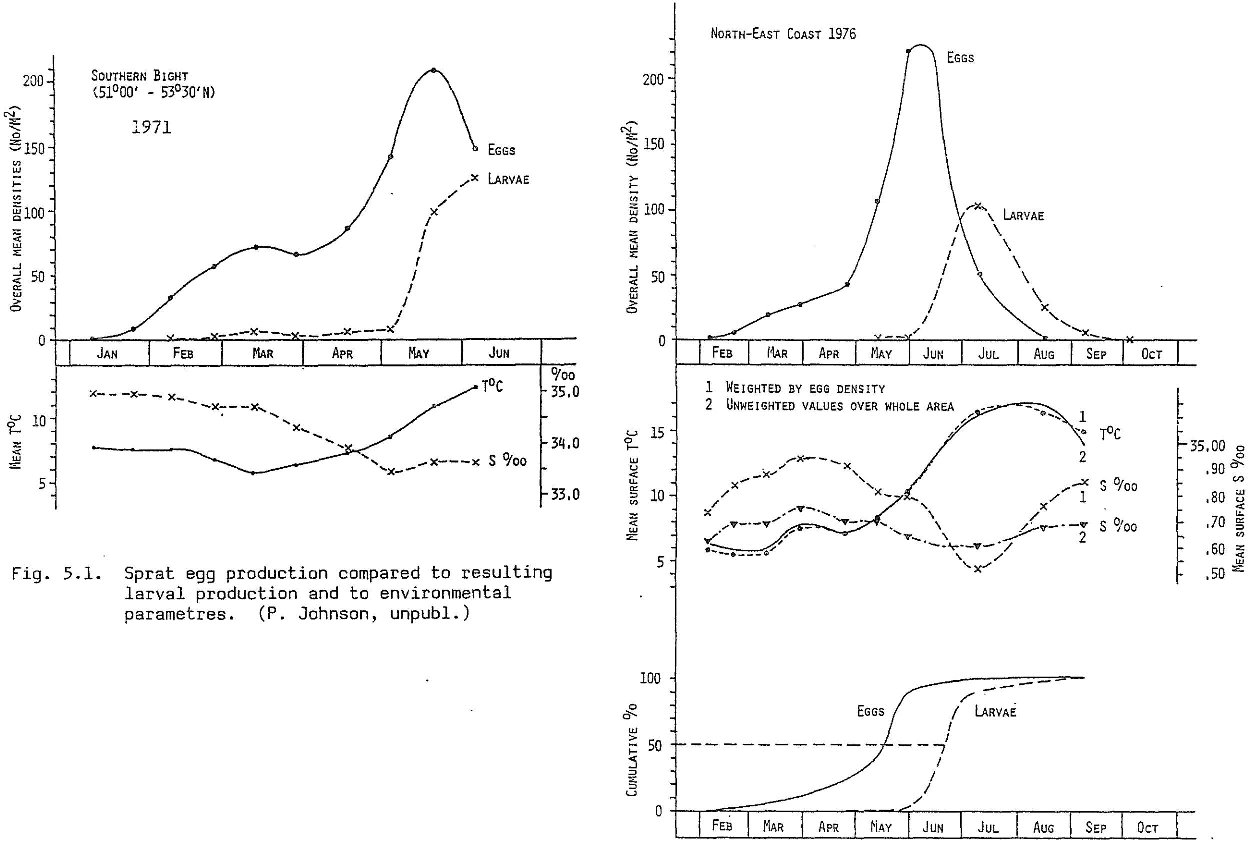


Fig. 5.1. Sprat egg production compared to resulting larval production and to environmental parametres. (P. Johnson, unpubl.)