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Spawning of Norwegian spring spawning herring (*Clupea harengus* L.) related to geographical location and population structure.

by

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ABSTRACT

The catch, distribution, and biology were studied in Norwegian spring spawning herring during the spawning season in 1995. Both the spawning time and choice of spawning grounds were influenced by the size and condition of the fish. The stock wintered in Vestfjorden, northern Norway, and spawning grounds were utilized southwards along the coast within a range of 1500 km. The herring arrived the spawning grounds in a decreasing order of length and condition. This was mainly due to size specific swimming speed and not size specific maturation. Delayed maturation with fish length was only found within the recruits, which spawned in a second wave. In addition, the size and condition of the fish in a spawning area increased southwards, and there was a delayed spawning and prolonged spawning period at the northernmost spawning grounds. We suggest that life-history theory explains the observed spawning distribution. Individuals must consider trade off between migration distance, reproductive output, own survival and larval survival based on their body size and condition.

Keywords: Body condition, fish size, herring, maturation, migration, year class.

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INTRODUCTION

A number of studies on Atlantic (Lambert 1987, see also Table 1; Lambert and Messieh, 1989) and Pacific herring (Hay 1985; Lambert 1987, see also Table 1; Ware and Tanasichuk, 1989) have indicated that the time of spawning is influenced by the age or size of the individual fish. Based on data of Norwegian spring spawning herring collected prior to the severe stock decline in the late 1960s, Norwegian scientists suggested that the recruits spawned progressively later in the season than the older repeat spawners (Lea 1929 b; Runnstrøm 1941 a b; Rasmussen 1939; Dragesund et al. 1980). After reanalyzing data from Runnstrøm (1941 a b), Lambert (1987) studied the maturation more comprehensively and found that the herring spawned in a decreasing order of body size with time. He suggested that there was also a difference in spawning time between age- and/or size groups among repeat spawners. Further, Lambert (1987) suggested that the herring arrive at the spawning grounds in waves, with the largest fish spawning first and subsequently the smaller fish. He also claimed that the appearance of spawning waves is reflected by the relatively large reproductive contribution of dominant year classes. Thus, the number and size of these waves are directly related to the age and size structure of the reproductive population. Lambert (1990) reanalyzed data on Norwegian spring spawning herring from Dragesund (1970), and examined the relation between age structure, spawning waves and recruitment. He concluded that recruitment to the stock is positively correlated with the number of dominant year classes in the spawning population. The conclusions of Lambert (1987, 1990) are consistent with studies on Atlantic herring from the Gulf of St. Lawrence (Lambert and Messieh 1989) and Pacific herring from British Columbia (Ware and Tanasichuk 1989).

In recent years the Norwegian spring spawning herring stock has recovered due to the strong 1983 year class. Since this year class matured in 1988 the spawning stock biomass has increased to about 5 million tons in 1995 (Anon. 1996), and the strong 1991 and 1992 year classes have increased the spawning stock further to about 9 million tons in 1996 (Anon. 1997).

Since 1988 the wintering area of the Norwegian spring spawning herring has been located in the Vestfjorden area, northern Norway (Fig. 1). This situation is different from the period prior to the stock decline, when the wintering took place in oceanic water off East Iceland (Devold 1963). Spawning has traditionally taken place along the Norwegian coast, but the relative importance of the different grounds has changed with time (Runnstrøm 1941a, b; Devold 1963, Dragesund 1970). In recent years main spawning has taken place off Møre and to some extent northwards to Lofoten, whereas only less than 1% of the spawning stock has utilized the spawning grounds off south-western Norway (Johannessen et al. 1995a).

Thus, starting in Vestfjorden, the spawning migration takes place southwards along the Norwegian coast, and the herring may choose between different spawning grounds within varying migration distances. For instance spawning off Møre would demand a 1000 km longer migration distance compared to spawning off Lofoten, and spawning off Siragrunnen would demand an additional migration of at least 500 km. Considering the facts that the spawning migration is energy demanding (Slotte 1996) and that swimming speed increases with fish size (Blaxter, 1969), a direct relationship between the geographical distribution of spawning areas and the spawning population structure (size composition) would be expected.

The purpose of this paper is to test three sets of hypotheses using data representative for Norwegian spring spawning herring in 1995. The first two hypotheses were suggested by Lambert (1987). Firstly, spawning of Norwegian spring spawning herring proceeds consecutively through year classes from the oldest to the younger ones due to differential maturation, and secondly, that spawning occurs in waves related to the number of peaks in the age composition of the stock. We have suggested a third hypothesis, which claims that the age structure of the mature population in a spawning area is influenced by the migration distance from the wintering area.

MATERIALS AND METHODS

Spawning area

A map of the study area is presented in Fig. 1. The area can be divided into 5 sub areas with locations (00 Vestfjorden, 05 Lofoten, 06 Træna-Haltenbanken, 07 Møre, 28 Sogn-Hordaland and 08 Karmøy-Siragrunnen) according to the statistical areas and locations applied by the Institute of Marine Research to report catch statistics (Fig. 2). The biological samples and catch data included in this study all refer to these areas and locations.

Biological sampling and analyses

The sampling was designed in order to test the hypotheses stated above. Herring were sampled in the wintering area in Vestfjorden (00), and during the migration and spawning in the areas off Lofoten (05), Træna-Haltenbanken (06) and Møre (07). A total of 137 samples and 12 553 individuals were collected from 6 January to 9 April in 1995, and the samples were mainly obtained from the purse seine fishery and by trawl catches from research vessels (Table 1). Except for trawl catches, which were analyzed fresh, all samples were frozen at landing. The portion of the stock which migrates past Møre towards spawning grounds off Hordaland (area 28) and Rogaland (area 08) is very small, approximately 1% (Johannessen et al 1995 a). Samples from these southern grounds were collected in the period 1990-1997 and are dealt with in another paper (Slotte and Johannessen in prep).

The following data were recorded from individual herring; total wet weight (g), total length (nearest 0,5 cm below), sex, maturation stage, age (by scales), relative fatness, stomach fullness and gonad weight (g). The maturation stages were classified as recommended by ICES (Anon. 1962): immature = 1 and 2, maturing = 3 to 4, ripe = 5, spawning/running = 6, spent = 7 and recovering = 8.

Based on the data recorded, gonadosomatic index (GSI) (gonad weight/ total weight * 100) and Fulton's condition factor (total weight/ $length^3$ * 1000) (Fulton 1904) were calculated and used as indicators of body condition and maturation respectively. During the spawning period somatic condition factor ((total weight - gonad weight)/ $length^3$ * 1000) was utilized as indicator of body condition, because total condition factor is reduced in spent herring.

The data were analyzed using the computer program *STATISTICA* for Windows (Statsoft inc. 1995). Distance weighted least squares procedure was utilized in curve fittings.

Catch data

All herring catches landed in Norway are recorded with the following: catch size (kg), catch position in terms of statistical area and geographical location (Fig. 2), and date of capture. In addition, catches processed for human consumption are divided into 5 size groups by individual body weights as follows: group 1 (>333 g), group 2 (200-333 g), group 3 (125-200 g), group 4 (83-125 g) and group 5 (<83 g). The proportion of each size group in the total catch (kg) is calculated by taking sub samples of the catch at landing. *The Norwegian fishermen's sales organization for pelagic fish* provided the catch data of Norwegian spring spawning herring for 1995.

Estimation of abundance

RV «Michael Sars» surveyed the spawning areas in the period 14 February - 30 March 1995. Acoustical data were recorded with a 38 kHz SIMRAD EK 500 echo sounder and echo integrator. In addition BEI, Bergen echo integrator system (Knudsen 1990), was applied in the interpretation of the data. Integrator values were scrutinized into herring and «other fish» based on the density and appearance of the recordings, target strength (TS) distribution and data from trawl catches. Based on the age composition of herring in the trawl catches the distribution area was divided into sub areas. Conversion of integrator readings (S_A) into number of herring was achieved by the relation between target strength (TS) and total fish length (L) as recommended by the ICES Working group on Atlanto-Scandian herring (Foote 1987; Anon. 1988):

$$TS(dB) = 20.0 \cdot \log L - 71.9 \tag{1}$$

The number of individuals (N) within a certain area (A) was given by:

$$N = 1/\sigma \cdot S_A \cdot A \text{ where } 1/\sigma = 10^6 \cdot 1.23 \cdot L^{-2} \tag{2}$$

The area A with positive integrator values was delimited after plotting the 1 n.m. integrator values attributed to herring along the survey lines. The mean integrator value (S_A) was the arithmetic mean of all positive values within the area A.

RESULTS

The relation between spawning migration and fishery

Geographical and temporal distribution of the fishery

Information on the fishery is valuable when analyzing the spawning migration of the herring. Fig. 3 describes the distribution of main catches from the fishery during the spawning migration and spawning period by reference to specific areas and locations (see also Fig. 2). The main trend is that the fishery followed the herring as it migrated southwards, and that the main spawning area off Møre was the most important catch area .

In January the fishery was concentrated in the wintering areas in Tysfjorden (location 38) and Ofotfjorden (location 37), but catches of migrating herring were also taken at locations in

Vestfjorden (location 11, 44, 46). In February, however, all catches taken in area 00 were located in Vestfjorden, whereas in March the fishery in this area had come to an end.

In late January a small fishery had started in area 06, and the majority of herring were caught off Træna (location 27, 30, 33). This herring probably belonged to the first portion of the southward migrating herring. During February the fishery was more widespread in area 06. Catches of herring departing Vestfjorden were still recorded in locations around Træna (locations 27, 30, 31, 33), but as the herring migrated southwards, catches were also recorded further south at locations around Sklinnabanken (17) and Haltenbanken (06, 10, 11, 12). During March the fishery in area 06 was located around Haltenbanken and further west (01, 03, 04).

From February through April the main fishery occurred in area 07, and the most important catch locations were close to the shore (from north to south: locations 08, 07, 19, 31, 06, 33, 05), with locations 06 and 33 off Ålesund being most important. In addition, a small fishery took place further south in area 28 (location 04, off Bremanger) in February-March, with a total catch below 2 000 tons.

Temporal patterns of size group composition in the fishery

Temporal patterns in size group composition in the fishery for the areas 06, 07 and 28 are given in Fig. 4. In all areas there was a main trend towards decreasing proportion of group 1 herring with time.

In area 06 the group 1 and group 2 herring predominated until mid March, after which group 2 herring became most common and the proportion of group 1 herring declined in the catches. The proportion of group 3 herring was low during the entire fishing season. Daily catch rates were small, on the average less than 500 tons, and decreased from late January through April.

In area 07 the catch rates peaked at a level close to 3 000 tons/day during mid February. At the same time the proportion of group 1 herring (predominated by the 1983 year class) decreased, whereas group 2 herring (predominated by the 1989 and 1990 year classes) increased. From March and onwards the proportion of group 3 herring, mainly made up by the 1990 and 1991 year classes, also increased.

In area 28 catches were taken from 20 February throughout March, and the proportion of group 1 decreased and group 2 increased during March, while group 3 was low throughout the period. Daily catch rates did not exceed 400 tons.

The relation between spawning migration and population structure

Initial status of the spawning stock

The year class composition of the spawning stock in 1995 comprised two peaks (Fig. 5). One peak was dominated by young spawners of the 1988 - 1991 year classes with the 1990 year class contributing with the highest abundance, while the 1983 year class accounted for the other peak. The intermediate year classes 1984 - 1987 and the year classes older than 1983 were insignificant.

When the spawning migration commenced from Vestfjorden in mid January, a delay in maturation was found among individuals smaller than 32 cm, while those of 32 cm and larger seemed to mature synchronously (Fig. 6). Both length frequency distributions (Fig. 7) and proportion of maturation stages by year class (Table 2) reveal that delayed maturation was more pronounced in the 1991 year class and to some degree in the 1990 year class compared to the older ones. At start of spawning migration the length specific weight varied considerably (Fig. 8), indicating that the initial potential for migration also varied.

Geographical distribution of year classes

RV «Michael Sars» covered the distribution area of the spawning stock by echo survey during the period 19 February-30 March, 1995. In the period 19-27 February the mature herring were distributed as a belt from Vestfjorden to Møre, and later in March also off Lofoten. Due to varying year class composition and abundance the herring distribution belt was divided chronologically into sections 1-17 (Fig. 9, Table 3). The herring migrating southwards followed the slope of the continental shelf (bottom depths below 200 m). However, off Møre the shelf is wide and the herring distributed within the shelf area. During the migration the herring was distributed close to bottom during the day and close to the surface or mid water during night time.

There was a main tendency that the proportion of young spawners (1990 and 1991 year classes) decreased southwards from Lofoten (sections 12-13) to Møre (section 10-11). In Ofotfjorden and the inner part of Vestfjorden (sections 1-2) the numbers of mature herring were estimated to be insignificant. In the outer part of Vestfjorden (sections 3-5) and off Træna (section 6) the biomass estimate reached 283 000 tons, and the 1990 and 1991 year classes were most abundant. The biomass increased further south at Sklinnabanken-Haltenbanken (sections 7-9) to about 1349 000 tons. The 1983 year class dominated in sections 7 and 8 (37 % and 49 % respectively) by numbers of the total spawning stock, whereas in section 9 the 1990 year class was most abundant (35 %). However, it must be emphasized that the estimate in section 8 is not very reliable as it was based on only one sample with 27 individuals. The herring in sections 7-9 were maturing (maturation stages 4-5) and under migration southwards. The biomass of herring which had reached the main spawning area off Møre (sections 10-11) was estimated to 928 000 tons in the period 25-27 February, and the 1990 year class (41 %) dominated by numbers together with the 1983 (24 %) and 1989 (24 %) year classes. Later in the season, during 13-25 March, the biomass of mature herring off Lofoten was estimated to 250 000 tons, of which 205 000 tons were recorded at Røstbanken (section 12). The 1990 and 1991 year classes were most abundant in section 12 with 81 %. Herring in sections 15 - 17 were all immature. It is likely that much of the herring off Lofoten was the same group as recorded in sections 1-5 during 19-21 February.

Temporal distribution of year classes

Temporal occurrence of the most abundant individual year classes (1983, 1988, 1989, 1990 and 1991) in the spawning areas 05, 06 and 07 are given in Fig. 10. The adult herring (maturity stages 3-4) commenced their spawning migration from the wintering areas in Vestfjorden, Tysfjorden and Ofotfjorden in mid January. Within the second week of February most mature herring had left the wintering areas, aiming for the spawning grounds further south. At about the same time (5-10 February) the first group of spawners were caught off Møre after having migrated a distance of approximately 1000 km.

Off Møre (area 07) the proportion of the 1983 year class, decreased from a level of about 50% during the first arrival around 5 February and stabilized at a level of 20-30% from 1 March and onwards. This was compensated by an increase in the proportion of the 1989 and 1990 year classes. These year classes dominated in March, but after having culminated during the first week, their proportion was reduced and the abundance of the 1991 year class increased slightly. About 12% of the 1991 year class were immature in area 07. The data from area 07 in February were analyzed with respect to temporal variations in length, weight and condition factor (Fig. 11). All these parameters showed a decreasing trend during the period, but the condition factor seemed to be the most important and reliable parameter. In February herring with condition factor in the interval 10-10.5 arrived at mean day 15 while herring with condition factors in the interval 6.5-7 arrived on the average ten days later (day 25).

The 1983 year class comprised about 50% of the first group of spawners in area 06 in late January and February, similar to the first group of spawners arriving off Møre (Fig. 10). However, opposite to the trend at Møre, the proportion of the 1983, 1988 and 1989 year classes decreased during the whole season. The 1990 year class dominated after mid February and culminated in mid March. The subsequent decline in the proportion of the 1990 year class was a result of an increasing proportion and a predominance of the 1991 year class after mid March. However, 18.5% of the 1991 year class was still immature in area 06.

Some herring preferred not to migrate southwards after leaving the wintering area. In March 1995, herring were observed in area 05 (off Lofoten) and the 1991 year class dominated with some contribution also of the 1989 and 1990 year classes, whereas the proportion of the 1983 year class was very low (below 10 %) (Figure 10). However, 75.2% of the 1991 year class was immature in this area.

Temporal variation in maturation by length

Temporal variations in size group composition in the fishery and year class distribution have indicated that the herring arrive at the spawning areas in a decreasing order of size. Whether this is an effect of delayed maturation with decreasing body size, remains to be examined.
The sampling effort was high in the spawning area off Møre (area 07) and the temporal size variations were obvious. Data from this area were therefore used to demonstrate temporal variations in maturation by length.

The trend in maturation by length off Møre was a reflection of similar observations at the commencement of the spawning migration in Vestfjorden. Both mean stage of maturation (Fig. 12) and gonad weight (Fig. 13) by length showed that time of spawning was delayed in herring less than 30 cm, whereas herring equal to and larger than 30 cm spawned synchronously. Although the largest herring arrived at the spawning grounds in early February, they tended to stay and mature until the start of spawning in late February, when also the smaller herring had reached the area.

Latitudinal variations within a year class

The geographical distribution and abundance of herring as observed with RV «Michael Sars» in the period 20 - 27 February, indicated that quite a large proportion of the older year classes (1983 and 1989) were delayed in their spawning migration compared to other conspecifics of

the same age (Fig. 9, Table 3). They were recorded north of Møre at-Sklinnabanken (section 7). Thus, it was interesting to see whether any differences could be observed from north to south within the same year class and time period. Data were analyzed from two time periods when the sampling was adequate on a latitudinal range; firstly, 20 - 27 February representing the spawning migration, and secondly, 11 - 30 March representing the spawning period.

The geographical distribution of a year class during the period 20-27 February, was influenced by three main factors: length, condition factor, and gonadal maturation (Fig. 14). The data on a latitudinal range refer to the sections given in Fig. 9. There was a trend towards an increasing length with lower latitudes (sections 6-9) in the year classes 1989 and 1990. The data in section 8 were excluded because of only one sample with 27 individuals. However, a small decrease was observed in length from Halten (section 9) to Møre (sections 10-11). The condition factor increased southwards from Træna to Møre (section 6 to section 10-11) for all the abundant year classes (1983, 1989 and 1990). Thus, although the length of herring within a year class was somewhat shorter off Møre than further north at Haltenbanken, the condition factor was superior. Data on maturation stages and gonadosomatic indices showed that the maturation within a year class was delayed north of Møre. Though the herring had remarkably low condition factors at Haltenbanken (section 9), the gonadosomatic indices were rather high, indicating a high proportion of energy allocated to reproduction.

The geographical distribution of herring within a year class during 11-30 March was influenced by the same factors as operating during the period 20-27 February (Fig. 15). The 1983 year class was not included in the analyses because of low numbers present in the areas north of Møre. The mean day of catching of the year classes were approximately the same, which tends to eliminate any temporal variations. The frequency distribution of maturation stages by statistical area and year class, showed a trend towards a delay in spawning from south to north and from old to younger herring. This delay in spawning was primarily caused by high numbers of herring in low maturation stages (stages 3-5). In addition both length and somatic condition by year class increased southwards. A result which also emphasizes the latitudinal differences within year classes was the decrease in the proportion of immature herring observed within the 1990 and 1991 year classes from north to south (Fig. 16).

Spawning period

A delay in start of the spawning and a prolongation of the spawning season were observed from off Møre and northwards (Fig. 17). The spawning period was defined as the time lapse between the first and the last occurrence of herring in maturation stage 6. In Area 07 the spawning took place from around 15 February to about 20 March. The data from area 06 were not as good as those off Møre, but they do indicate that the spawning commenced approximately 1 March and lasted until early April. In area 05 the data available do not represent herring during the whole spawning period. High proportions of herring in maturity stages 7 and 8 in early March indicate that the spawning might have occurred from the end of February. About 40 % of the herring were in maturation stages 3 -5 in mid March, indicating that the spawning period lasted probably well into April.

Modeling

Spawning migration determined by condition factor

The assumption that the southward spawning migration for most individual herring do follow a straight line, makes it reasonable to design a simple model of the spawning migration on a latitudinal range. We have emphasized above that the spawning migration is significantly influenced by the condition factor of the fish. Thus, data on catch position on a latitudinal range, day of capture and condition factors of mature herring collected during the period January through February and in the areas 00, 06 and 07 (Fig. 2) were used in order to model the spawning migration. The following second order polynomial equation was fitted to the data after quadratic smoothing to the points in a 3D scatter plot (Fig. 18):

$$\text{Latitude} = 67.681 + 0.081*\text{Cond} + 0.065*\text{Day} + 0.023*\text{Cond}^2 - 0.024*\text{Day}*\text{Cond} \qquad (3)$$
where Cond = total condition factor and Day = Julian day.

The model predicts that all herring start their spawning migration simultaneously around 15 January regardless the condition of the fish. However, as migration progresses the distance between fish with high and low condition factors increases, and consequently resulting in different dates of arrival at the spawning areas.

Length specific migration speed

The condition factor is not preferred to use when calculating size specific migration speed, as it is likely to be inversely correlated with migration distance. Therefore fish length was used in the modeling of size specific migration speed. The mean day of arrival off Møre in February was progressively later with decreasing fish length (Fig. 11), and the following regression equation was fitted to the data:

$$\text{Day of arrival in February} = 49.842 - 0.894*\text{Length} \qquad (4)$$

Assuming that the spawning migration starts 15 January from Tysfjorden or Ofotfjorden and that the migration distance to Møre (62°N) is approximately 1000 km, length specific swimming speed for herring arriving off Møre in February can be calculated as follows:

$$\text{Duration of spawning migration (in days)} = 49.842 - 0.894*\text{Length} + 15 \qquad (5)$$

$$\text{Migration speed (m/s)} = 1000\ 000/(49.842 - 0.894*\text{Length} + 15)*24*3600 \qquad (6)$$

The mean migration speed of the herring arriving off Møre in February varied from 0,29 m/s to 0,37 m/s for 28 cm and 38 cm herring respectively (Fig. 19)

DISCUSSION

Sources of errors

The sampling data are considered representative for the Norwegian spring spawning herring stock during the period investigated. Sources of errors associated with sampling, processing and analyzing of the data are discussed below.

Underestimation of smaller fish compared with their larger conspecifics is not uncommon in pelagic trawls due to a tendency for the smaller herring to leak through the meshes in the upper rear part of the trawl (Larsen 1985; Suuronen et al. 1997). On the other hand, this effect may be counteracted by size specific swimming speed (Blaxter 1969; Wardle 1993) which reduce the impact of trawl avoidance with decreasing size of the herring. Herring infested with *Ichthyophonus hoferi* usually have low condition and are less capable to avoid pelagic trawl (Kvalsvik and Skagen 1995), which indicate that herring with low condition in general may be overestimated by trawling. Swimming speed increases with temperature, and trawl catchability of the herring may therefore be reduced in warm Atlantic water compared to colder water bodies (Mohr 1969). During spawning the trawl avoidance of herring is close to zero (Mohr 1969). After spawning, emigrating and feeding schools are more dynamic in shape, density and movements than prespawning schools and harder to catch (Mohr 1969; Nøttestad et al. 1995). Vertical distribution of the fish may also influence the catchability, as the fish size is shown to decrease with depth in layers of herring (Foote et al. 1996). During the spawning migration trawl selectivity may have affected the year class composition in the catches, but it is unlikely that the selectivity had significant influence on the latitudinal and temporal variations presented.

Purse seines are supposed to be nonselective. However, the vertical distribution of herring by size may affect the composition in purse seine samples, if the net is not deep enough and only catches a portion of the school. More important is the fact that the purse seine fishery itself is selective because there is a commercial motivation for catching the largest, better paid herring (Slotte and Johannessen 1997). Thus, the year class composition as measured by purse seine samples may be biased by having a larger proportion of older fish than actually present in the area. However, this bias is constant and had hardly any significant influence on the latitudinal and temporal variations presented.

There are two main groups of errors in the abundance estimates presented. One concerns the survey design and trawl sampling and another the target strength (TS) of the fish.
Because of limited time acoustic surveys were conducted during both day and night, leading to significant bias in the abundance estimation. During the spawning migration herring were distributed in an upper vertical layer of the water column during night time and close to the bottom in day time. When approaching the spawning grounds the herring was distributed in discrete layers during night time, whereas they tended to form dense schools during day time. These schools were harder to hit acoustically given the present survey design. During the release of spawning products herring keep close contact with the bottom substrate (Nøttestad et al. 1995), and is therefore harder to detect acoustically in the «dead zone» (Ona and Mitson 1995). The reliability of abundance estimates by year class may in some areas be low due to few trawl samples and limited time available to cover large distribution areas. The winter months at sea are also frequently associated with bad weather conditions, which limit the number of days at sea and reduce the recording conditions for echo integration.

Biases in the estimation of abundance are not only concerned with survey and sampling design, but probably more important with acoustic methodology. The swimbladder, which gives the most important contribution to the target strength (TS), increases with fish size, and may also show diurnal variations in accordance with variations in depth, tilt angle distribution and swimming speed of the fish (Foote 1980; Blaxter and Batty 1990; Huse and Ona 1996; Olsen and Ahlquist 1996). Fat content in herring is inversely proportional with swimbladder volume and TS (Brawn 1969; Ona 1984, Reynisson 1993). Ona (1990) found that acoustic abundance estimates of herring could be biased by 30-40%, if the influence of fat content on target strength was not considered. The fact that fat content in Norwegian spring spawning herring decreases from around 20% to around 10% of total weight (a 50% reduction) from start of spawning migration in January until the end of spawning off Møre in March (Slotte 1996), emphasizes that TS may be systematically affected during the spawning run. In addition a positive correlation is found between gonad size and target strength in Norwegian spring spawning herring (Zhao 1996). Attempts to include parameters such as tilt angle, stage of maturation and fat content into modeling of target strength at various depths are planned.

Subjective identification of maturation stages and age of herring were preferably made on fresh samples (Anon. 1962). However about half of the samples were frozen, and because important criteria like color and softness change during the freezing process (Cleary et al. 1982), the likeliness for incorrect staging of maturation increases. However, the technicians performing the processing of samples are skilled, and the variability caused by subjective decisions are probably small and not supposed to affect the conclusions in this paper.

Age is measured from growth rings in scales of the herring. Some scales are unreadable and hence, some individuals are not identified by age. The proportion of unreadable scales increases with body size (see Fig. 20). In 1995 herring of the 1983, 1988 and 1989 year classes were likely to be underestimated in the samples due to this bias. Validation studies of aging are therefore recommended.

When analyzing biological data, Fulton's condition factor (Fulton 1904) and gonadosomatic index (GSI) were used to describe the variability in body condition and maturation. It has been argued that these parameters are inappropriate for such purposes because they are positively correlated with the fish size (Cone 1989; Cone 1990 and deFlaming et al. 1981). This has been accounted for in our analyses, and when testing latitudinal variance in condition factor and gonadosomatic index, the data were pooled by year class, thereby reducing the size effect to a minimum.

An important part of this paper has been to examine whether the maturation rate increases with herring size, leading to differential time of spawning. Maturation stages were preferred parameters to test for such differences. In a similar test of maturation by size Ware and Tanasichuk (1989) utilized GSI trajectories where the size effect had been removed. However, the use of maturation stages was a suitable method, when comparing herring throughout the spawning season. GSI would be less sensitive to distinguish between maturing (stages 3 - 5) and spawning (stage 6), or between early maturing (stage 3) and spent-recovering (stages 7-8) herring. Ware and Tanasichuk (1989) stated the following: «Ovary weight is an increasing function of fish size. Therefore, fish of different size but the same GSI are at different levels of maturity; the smaller fish are more advanced.» This statement is in most occasions true. However, among individuals of the same length, with the same gonad weight, but with

different somatic body weights, the individuals with lowest somatic weight will be in a more advanced state of maturity in terms of GSI units. Hence, GSI may vary with the condition of the fish, even if the individuals are at the same state of maturity (Hay et al. 1988). It should also be taken into account that higher GSI in one individual compared to another, could be caused by differential fecundity or egg size and not state of maturation. Feeding in herring in the prespawning period may increase the egg diameter (Hay and Brett 1988) and/or the fecundity (Wooton 1979; Bradford and Iles 1992). Hay and Brett (1988) suggested that a reduction in the number of maturing oocytes occurs naturally and reflects a mechanism that allows herring to adjust their egg size and egg number according to available energy resources and environmental conditions. Thus, the main conclusion is that GSI may not be an accurate method when testing for size specific maturation. The results gained when plotting individual gonad weight trajectories by body length in the spawning area off Møre did not differ from that of maturation stage versus body length, and emphasize the reliability of the methods utilized.

The relation between spawning distribution and recruitment

Why doesn't the whole Norwegian spring spawning herring stock spawn closer to the wintering area, for example off Lofoten? At the commencement of spawning migration the herring may choose among varying spawning grounds distributed along the coast from Lofoten in the north to Siragrunnen in the south, a range of about 1500 km. If spawning off Lofoten results in similar survival of eggs and larvae as off Møre, the herring should choose Lofoten and instead allocate the energy required for the extra migration distance to Møre into fecundity and improved egg quality. However, if life-history theory accounts for the Norwegian spring spawners, one must assume that spawning further south, for example off Møre, should be beneficial for the stock and for the individual herring.

Considering varying environmental factors influencing survival of eggs and larvae, Dragesund (1970) suggested that the more important factors determining recruitment were: the size and the geographical spread of the spawning area, duration of the spawning period, rate of dispersion of larvae from the hatching grounds and the match or mismatch between available food and hatching of the herring larvae. Thus, the present distribution of spawning areas would improve the probability of recruitment success of the Norwegian spring spawning herring.

What about the effect on the fitness of individual herring? We assume that the larvae hatched at the southern grounds have improved survival potential compared with larvae hatched farther north, because they are dispersed over a larger area with a wider variety of environmental conditions (e. g. temperature, food levels, predator regimes) (Runnstrøm 1934, Dragesund 1970 , Johannessen et al 1995 b). Larvae hatched farther south are more likely to drift through water bodies of higher temperatures leading to higher growth (Stenevik et al. 1996), and they are more likely to drift to nursery areas along the coast and in the fjords, where the growth conditions are better than in the the Barent Sea (Lea 1929 a and b; Ottestad 1934; Runnstrøm 1936, Holst 1996).

Size specific maturation

Our results do not entirely agree with the hypotheses suggested by Lambert (1987); firstly, that spawning of Norwegian spring spawning herring proceeds consecutively through year

classes, from the oldest to the youngest fish, due to differential maturation, and secondly, that the spawning occurs in waves which is reflected by the number of peaks in the age composition of the stock. We have shown that the initial status of the herring at commencement of spawning migration is characterized by a delay in maturation with decreasing body lengths only in fish smaller than 32 cm, while maturation of herring equal to and larger than 32 cm is synchronous. We expect that this is related to an increasing proportion of first time spawners (recruit spawners) with decreasing lengths in herring smaller than 32 cm. The mean length of recruits is rather constant at about 29 - 30 cm in Norwegian spring spawning herring (Toresen 1986, 1990 b). However, the age at maturity in herring varies between year classes as a result of density dependent growth (Lett and Kohler 1976; Hubold 1978; Toresen 1990 a and b; Winters et al 1986; Winters and Wheeler 1994), environmental conditions (Winters et al 1986; Holst 1996) and varying conditions of the maternal stock (Holst 1996). Hence, only peaks which are contributed by recruit spawners may result in subsequent spawning waves.

Considering the present (1995) state and migration pattern of the Norwegian spring spawning herring stock, Lambert's two above mentioned hypotheses are rejected. However, Lambert (1987) reanalyzed data from 1934 (Runnstrøm 1941 a, b), when a different migration pattern occurred in herring with wintering in the Norwegian Sea. Were Lambert's hypotheses really valid during the 1930's? Looking at the original data from 1934 in Runnstrøm (1941a), monthly mean frequencies of occurrence of age groups by maturation stage for the entire Norwegian west coast were converted by Lambert (1987) to mean date of occurrence in maturation stages by age. However, sampling dates and areas listed by Runnstrøm (in appendix table 1, 1941 a), were ignored by Lambert (1987). It is obvious that the samples were taken from various localities along the Norwegian coast, leading to a latitudinal bias in Lambert's results. Runnstrøm also earlier in his paper stated that differences in maturation on a latitudinal range actually occurred (figure 9 in Runnstrøm 1941 a). Thus, we feel that there are several sources of errors in Lambert's analysis, and it is too ambitious to conclude that age groups may reach various maturation stages with an accuracy of only 1-2 days. In addition, the curve fitting procedure and the interpretation of the results (figure 5 in Lambert 1987) are in our view inappropriate. His interpretation of the curves indicate that there is a difference in maturation between herring at ages 7 to 16, while in our view there is no such difference. However, the trend that mean date of peak occurrence of maturation stage 6 increases from ages 6 to 3, seems appropriate. This figure illustrates similar results to those we have obtained for the same stock in 1995, i.e. only recruits spawn with a delay compared to the older age groups. Thus, in our view the data from 1934 show that all herring older than 6 years were repeat spawners, whereas the proportion of recruits increased with decreasing age from 6 to 3.

What about other herring stocks? The study of Lambert (1987) has been supported by other studies on herring (Ware and Tanasichuk 1989; Lambert and Messieh 1989). Lambert and Messieh (1989) studied spawning dynamics of the Gulf of St. Lawrence herring (*Clupea harengus*), which reach similar lengths as Norwegian spring spawners. They reached similar conclusions for this stock as did Lambert (1987) for Norwegian spring spawners, i.e. that the herring spawn in a decreasing order of age and length. However, if we compare figure 4 in Lambert and Messieh (1989) with figure 5 in Lambert (1987), we find that the figures show great similarities. It seems that also within the Gulf of St. Lawrence herring there is little difference in mean date of spawning within herring larger than 30 cm, while within herring smaller than 30 cm the mean date of spawning increases significantly with decreasing body length. This fact, that spawning time occurred consecutively later from large to smaller

herring, may be a result of an increasing proportion of recruit spawners. This could be discussed more comprehensively in Lambert (1987), Lambert and Messieh (1989) and Ware and Tanasichuk (1989).

What are the underlying factors causing delayed spawning in recruits compared to repeat spawners? Hay (1985) discussed the difference in spawning time between recruit spawners and repeat spawners. He suggested that the spawning time of a stock is an adaptive characteristic selected to provide the best match of emerging larvae to available food organisms in spring plankton blooms. He stated that it is not clear how natural selection could promote late spawning in recruits and early spawning among older, repeat spawners. However, the delay in maturation within recruit spawners compared to repeat spawners need not be an adaptive response to natural selection. We suggest that this may be influenced by the difference between the onset of maturation in repeat spawners (from maturation stages 8 to 3) and the onset of first maturation (from maturation stages 2 to 3). The data from the wintering situation of Norwegian spring spawning herring indicate that the onset of maturation is delayed with decreasing lengths among the recruit spawners. The immature herring pass through a period in which it has the option to mature in that specific season or wait until next year, based on its internal state (body length, condition, fat content). Mature herring does not have this option, it normally spawns once every year for the rest of its life time. It seems likely that the «decisions» taken by the immature herring on whether to mature or not, will result in delayed onset of maturation compared with the mature stock. This is the opposite conclusion to that of Ware and Tanasichuk (1989), who found that Pacific herring start maturing at the same time regardless of the fish size, but the instantaneous maturation rate is size dependent leading to faster maturation in larger individuals. We do not reject this hypothesis entirely, but suggest that the delayed spawning among recruits in Norwegian spring spawning herring is influenced by both a delayed onset of maturation and delayed maturation rate with decreasing sizes. This is supported by the fact that fat content are generally lower in immature herring compared with mature conspecifics, and increases with length among the immature herring (own unpublished data; Leim 1958; Hodder et al. 1973). It has been shown both experimentally (Hay et al. 1988, Hay and Brett 1988, Ma 1996) and in nature (Aneer 1985; Henderson and Almatar 1989; Rajasilta 1992) that the maturation rate in herring may increase with improved condition and fat content, or with increased feeding during maturation. In the Baltic herring, Aneer (1985) and Rajasilta (1992) suggested that the fat content determined time of spawning. Rajasilta (1992) found that fish with high muscular fat reserves had reached maturation stage 3 already in December and would thus become early spawners, while those with low fat content were supposed to spawn significantly later. These studies also correspond with the results in our study, where fish with lower condition factors spawned progessively later in the season.

Size specific spawning migration

Based on the facts that the spawning migration is very energy demanding (Slotte 1996) and that swimming speed increases with fish size (Blaxter, 1969), it is reasonable to assume that there is an optimal relationship between the migration distance traveled by specific age groups of herring and the location of their spawning grounds. We find the data presented in this paper to support this assumption. Firstly, the herring arrived at the main spawning grounds off Møre in a decreasing order of body length and condition, and secondly, the proportion of young spawners in the spawning areas decreased and the body condition increased with increasing migration distance.

Although the larger herring swam faster and arrived off Møre prior to the smaller herring, the spawning started rather simultaneously in herring larger than 30 cm. The herring arriving off Møre around 10 February had still not running gonads and when these herring were ready to spawn by the end of February, smaller individuals had also reached the area. The prespawning herring is traditionally called «large herring» by the fishermen (Lea 1929 b; Runnstrøm 1941, a b; Rasmussen 1939). Aasen (1962) found that the time of arrival was correlated with the time of spawning in Norwegian spring spawning herring. In the 1930s the herring arrived as early as 15 December-5 January, whereas the arrival in the 1940s and 1950s was somewhat later (15-31 January). Despite the decadal differences in dates of arrival, the time lag between arrival and spawning did not differ significantly and was on the average 38 days with a standard deviation of one week (Aasen op. cit.). The present (1995) migration pattern with main wintering area in the Vestfjorden is associated with a further delay in arrival. In addition, the time lag between arrival and spawning has been reduced by approximately 50 % in recent years.

We believe that the most likely explanation for the fact that herring arrives at the main spawning grounds off Møre in a decreasing order of body size and condition is the lower swimming speed with decreasing body size (Blaxter 1969). Studies of Ware (1975, 1978) on optimal swimming speed in pelagic fish support this hypothesis. They define optimal cruising speed as the velocity at which the total energy expenditure per unit distance traveled is minimal. It seems therefore likely that the herring migrate towards the spawning grounds at an optimal speed which minimizes the energy used for swimming and maximizes the gonadal growth. In this way the larger herring arrive at the spawning grounds prior to the younger ones.

The fact that first time spawners and herring with low condition factor tended to spawn not too far away from the wintering area in Vestfjorden, could also be explained by a concept of optimal cruising speed in association with a concept of surplus-energy (Ware 1980, 1982 and 1984; Roff, 1983). The surplus-energy concept states that any energy surplus that required for maintenance and swimming can be allocated to growth and reproduction. The main growth of the herring is finished within the spawning season. Thus, in the prespawning period the herring has the option to consider trade off between spending energy for migration and/or gonadal development, probability of own survival and survival of their offspring. We suggest that the Norwegian spring spawning herring have a minimum level of energy reserves, which should not be reduced. Migrating the same distance, the smaller herring or herring of inferior condition are likely to reach this level prior to the larger herring. Therefore it may be deduced that the smaller herring prefer spawning grounds closer to the wintering area, consequently improving their own chances of survival. Considering the long distance from Vestfjorden to Møre and the low optimal cruising speed and the delay in maturation of recruit spawners compared to older herring, it would be more optimal to spend less energy for migration and thus swim a shorter distance and spawn off Lofoten for the first time. In subsequent spawning years, the body size and condition increase and state of gonadal maturation will be synchronized with that of the older conspecifics, and spawning is supposed to proceed farther south. The fact that recruit spawners predominated among the herring spawning off Lofoten also in former periods (Devold 1968), supports our hypothesis.

The herring which spawn in the areas off Karmøy and Egersund, travel an additional distance of about 300-600 km compared with those spawning off Møre. Our hypothesis is that only the

"superior" herring, which by definition should be repeat spawners which have attained a particular body size and are in good condition (large fat reserves), will migrate to the southern grounds. Data for the period 1992-1997 support this hypothesis (Slotte and Johannessen in prep) and may explain why only a relative small portion (less than 1 %, or 30 000 tons) of the total adult stock has hitherto spawned off Karmøy (Johannessen et al. 1995 a).

The southward spawning migration of herring follows the slope of the Norwegian continental shelf, and the main flow of coastal water northwards follows the same slope (Ljøen and Nakken 1969). Thus, the spawning migration of Norwegian spring spawning herring is «upstream». When comparing the energy costs of spawning migration in anadromous fish, several similarities are found with that of the Norwegian spring spawning herring. Age of maturity in Atlantic salmon is found to increase with the length of the rivers whose water the salmon spawns, which is believed to be an adaptive response to the migration costs (Schaffer and Elson, 1975; Schaffer, 1979). Glebe and Leggett (1981 a and b) found an inverse correlation between the proportion of total energy reserves used for migration and the proportion of fish that are repeat spawners in the anadromous clupeid, American shad (*Alosa sapidissima*). They found that semelpareous shad use 70-80% of their total energy reserves during a spawning run , while iteropareous shad use only 40-60%. A similar pattern was also found in other anadromous species (several salmon and shad stocks), in which semelpareous fish use more than 70 % of their energy reserves, while iteropareous fish use less than 60 %. Semelpareous fish also swim at a rate close to maximum sustainable speed, thereby reducing the duration of the migration to a minimum, whereas iteropareous fish swim at rates near optimum, and thus reduce the energy costs of the migration. There is also a positive correlation between body size and river harshness in Atlantic salmon (Schaffer and Elson 1975) and in American shad (Glebe and Leggett 1981 b). A situation where there are trade off between migration costs and reproductive output is found in the South American characin, *Procilodus mariae*. Females that remain resident in a lagoon devote five times as much energy to egg production as do females that undertake up-river migration (Saldana and Venables 1983). This suggests that migration confers important benefits in survival that compensate for the lower investment in eggs.

Although there are many similarities between the migration strategies of anadromous fish and Norwegian spring spawning herring, the main strategy is different. Semelpareous and iteropareous anadromous fish may spawn 1 and 2-3 times respectively (Glebe and Leggett 1981 b), whereas the Norwegian spring spawning herring may live for more than 20 years and probably spawn up to about 15 times. Hence, the herring is likely to apply a more conservative strategy which secures survival after spawning every year.

Life-history strategy versus «homing»

We have suggested that the spawning migration of Norwegian spring spawning herring is influenced by life history strategy, where the herring consider trade off between energy used for migration (migration distance), reproductive output, own survival and survival of offspring. However, this hypothesis is in conflict with the concept of «homing», which infers that individual fish return year after year to the same spawning grounds as they spawned for the first time, regardless whether they were born there (Wheeler and Winters 1984). Tagging data in recent years indicate that «homing» may occur in Norwegian spring spawning herring (own unpublished data). However, tagging is normally conducted in spent herring (maturity stage 7), and therefore it is difficult to exclude that spawning may have occurred in other

locations. The spawning of 6 years old herring (1983 year class) at the southern grounds (off Karmøy) in 1989 is unlikely to be due to homing because this herring had spawned once or twice off Møre before spawning off Karmøy (Johannessen et al 1995 a). We suggest that «homing» is not important in the case of Norwegian spring spawning herring, taking the present migration pattern into account. If it occurs it is primarily determined by the energetic state of the fish.

Interesting tagging experiments by Jakobsson (1970) and studies by Holst (1996) support our hypothesis that Norwegian spring spawners may shift spawning grounds according to their condition. Jakobsson's results can be summarized in three points: 1) during the period 1963-1968 in excess of 90 % of the herring spawning off the Faeroes were Norwegian spring spawners, 2) individuals spawning one year (1960, 1963, 1964, 1965, 1966) off western Norway spawned off the Faeroes one or several years later (1967) and 3) the herring spawning off the Faeroes during 1965-1968 were mainly contributed by the recruitment of the strong 1959 year class. Growth studies by Holst (1996) show that there was a considerable decrease in body weight at length in herring during the period 1960 - 1968, especially among the smaller herring, which coincided with a decrease in sea temperatures. The herring which spawned off the Faeroes migrated about half the distance from the wintering grounds east of Iceland, compared with the herring which spawned off the Norwegian coast. Considering the results of Jakobson (1970) and Holst (1996), we suggest that the spawning of herring off the Faeroes most likely was induced by the energetic state, thus improving the probability to survive until next spawning.

Conclusions

With the wintering area in Vestfjorden as a starting point, the Norwegian spring spawning herring travel variable distances to arrive and spawn at grounds widely spaced along the coast. In addition, the direction of migration is against the main flow of coastal water, giving a similar «up-stream» migration as in anadromous fish. Based on the facts that spawning is delayed in first time spawners, that the distribution of herring on the spawning grounds is characterized by a predominance of smaller herring closer to the wintering area, that the large herring migrate faster than the smaller ones, that the costs of spawning migration may reduce the individual fat resources with more than 50 %, and the assumption that spawning further south may increase the probability of survival of larvae, we suggest that the spawning migration may be explained by life-history theory. The herring has to consider trade off between migration distance, reproductive output, own survival and larval survival based on its body size (length, condition) and internal state (fat reserves).

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Table 1. Samples of herring in 1995 by statisical area-location (see Fig. 2), date, catch gear (T = trawl, PS = Purse seine) and number (N), which is included in this study.

Area	Date	Gear	N	Area	Date	Gear	N	Area	Date	Gear	N
00-44	06.01	T	100	00-05	21.02	T	100	07-06	09.02	T	100
00-37	06.01	T	100	00-52	21.02	T	50	07-06	10.02	T	100
00-37	06.01	PS	100	00-03	22.02	T	67	07-15	10.02	PS	100
00-37	08.01	T	100	00-09	14.03	T	100	07-05	15.02	PS	100
00-37	08.01	T	100	00-46	26.03	T	50	07-06	18.02	PS	100
00-37	08.01	T	100	00-46	28.03	PS	100	07-06	20.02	PS	85
00-44	10.01	T	100	Total N in area 00=4760				07-06	22.02	PS	100
00-38	12.01	T	100					07-33	24.02	PS	91
00-38	12.01	T	100	05-14	05.03	T	100	07-19	25.02	T	100
00-38	12.01	T	100	05-07	07.03	T	100	07-19	25.02	T	100
00-38	12.01	T	100	05-20	11.03	T	39	07-06	26.02	PS	100
00-38	12.01	PS	100	05-02	16.03	T	100	07-33	26.02	PS	87
00-38	13.01	PS	100	05-08	17.03	T	100	07-06	27.02	PS	100
00-38	14.01	PS	100	05-12	17.03	T	59	07-31	02.03	PS	100
00-37	16.01	T	100	05-06	18.03	T	100	07-06	02.03	PS	90
00-44	17.01	T	100	05-07	18.03	T	50	07-33	03.03	PS	100
00-44	17.01	T	100	05-13	19.03	T	100	07-15	03.03	PS	89
00-38	17.01	PS	100	05-18	21.03	T	100	07-18	04.03	T	100
00-10	19.01	T	100	05-35	24.03	T	100	07-06	04.03	PS	100
00-05	19.01	T	100	05-14	29.03	PS	100	07-06	04.03	PS	100
00-10	19.01	T	100	Total N in area 05=1048				07-06	04.03	PS	99
00-11	20.01	T	100					07-15	04.03	PS	100
00-46	20.01	T	100	06-30	25.01	T	100	07-15	05.03	PS	100
00-46	20.01	T	100	06-26	27.01	PS	100	07-19	06.03	PS	100
00-44	20.01	T	50	06-27	30.01	PS	100	07-33	06.03	PS	100
00-38	20.01	T	100	06-27	30.01	PS	98	07-06	06.03	PS	99
00-44	23.01	PS	100	06-06	07.02	T	84	07-33	07.03	PS	100
00-46	24.01	PS	100	06-17	13.02	PS	99	07-33	07.03	PS	100
00-04	25.01	T	100	06-12	15.02	PS	100	07-33	08.03	PS	95
00-52	25.01	T	50	06-18	16.02	PS	100	07-06	10.03	PS	81
00-11	26.01	T	50	06-31	22.02	T	100	07-19	14.03	T	100
00-44	27.01	PS	100	06-27	22.02	T	100	07-31	14.03	PS	100
00-38	28.01	T	100	06-27	23.02	T	100	07-31	14.03	PS	100
00-38	28.01	T	100	06-23	23.02	T	100	07-18	15.03	T	100
00-44	28.01	PS	100	06-22	23.02	T	50	07-18	15.03	T	100
00-38	29.01	T	50	06-12	24.02	T	27	07-18	16.03	T	100
00-46	30.01	PS	81	06-06	24.02	T	100	07-19	17.03	PS	100
00-46	01.02	PS	80	06-05	24.02	T	100	07-06	18.03	PS	100
00-11	05.02	PS	80	06-15	11.03	T	19	07-31	21.03	PS	100
00-53	06.02	PS	91	06-11	11.03	PS	90	07-31	22.03	PS	100
00-04	07.02	PS	81	06-12	13.03	T	92	07-31	22.03	PS	100
00-46	08.02	PS	90	06-10	17.03	PS	100	07-31	23.03	PS	100
00-44	08.02	PS	100	06-17	25.03	PS	100	07-31	25.03	PS	100
00-05	16.02	PS	90	06-12	30.03	PS	90	07-06	26.03	PS	80
00-37	19.02	T	50	06-31	03.04	PS	100	07-19	27.03	PS	100
00-38	19.02	T	50	06-31	04.04	PS	100	Total N in area 07=4396			
00-46	20.02	T	50	06-23	06.04	PS	100				
00-11	20.02	T	50	06-18	09.04	PS	100	Total number of samples=137			
				Total N in area 06=2349				Total number of herring=12553			

Table 2. Mean length, and percent of herring in maturation stage 3 and 4 by year class during January 1995 in area 00 (Vestfjorden). The year classes 1984-1987 were exluded because of low numbers, and immature herring (maturation stage < 3) and autumn spawning herring (maturation stage > 6) were also excluded.

Year class	Mean length (cm) $\pm$ SD	Number	Stage 3 %	Stage 4 %	Stage 5 %
1991	28.3 $\pm$ 1.7	251	78.5	21.5	0.0
1990	30.7 $\pm$ 1.3	680	21.9	77.8	0.3
1989	33.0 $\pm$ 1.2	630	2.8	96.2	1.0
1988	34.6 $\pm$ 1.2	273	0.0	99.6	0.4
1983	36.6 $\pm$ 1.1	816	0.5	98.9	0.6

Table 3. Abundance and biomass estimates of mature Norwegian spring spawning in different sections along the coast during 20 February - 25 March 1995 (see Fig. 9 for identification of sections and distribution along the coast).

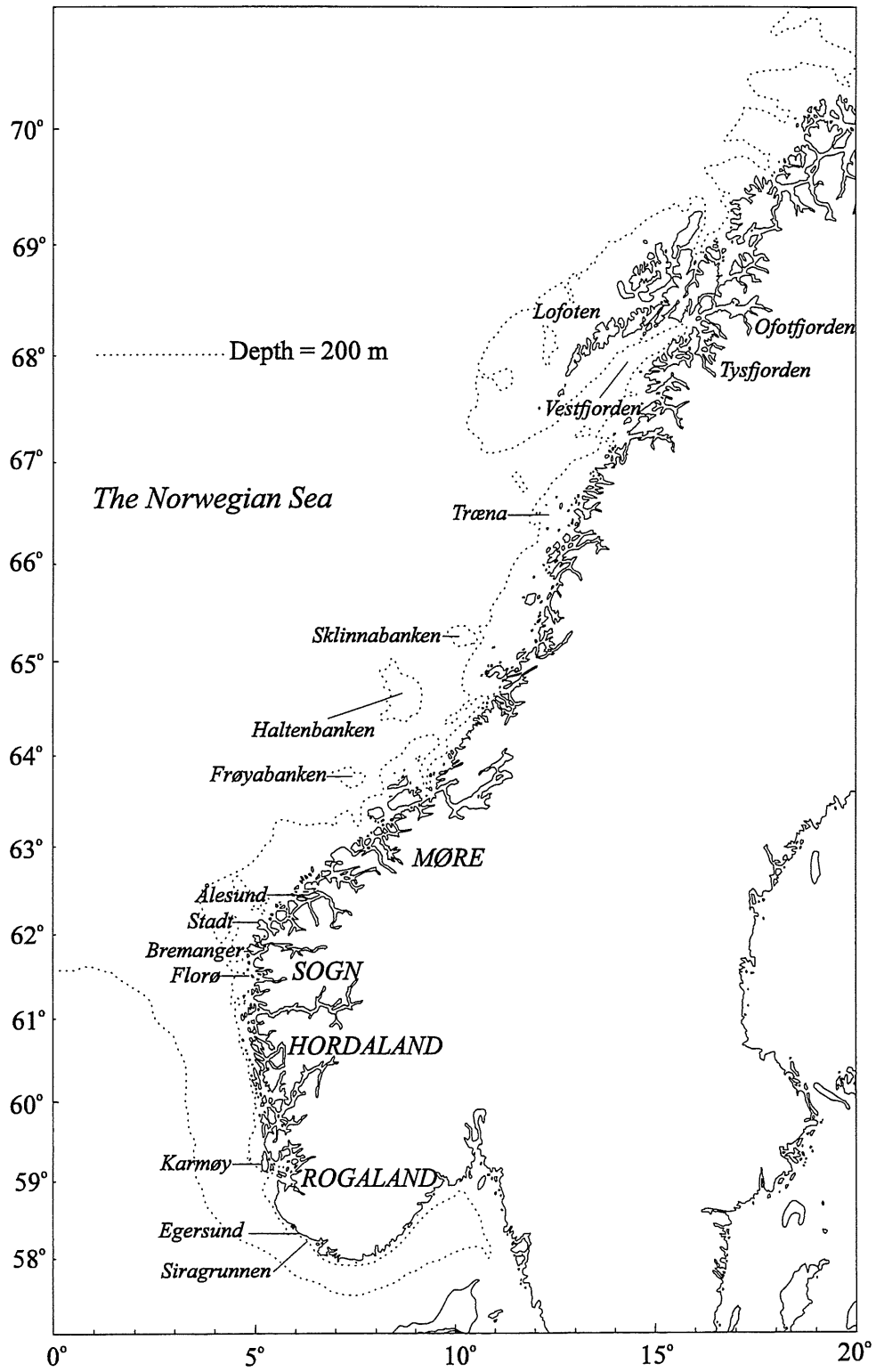|	Section (date)	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983+	Total
Number	1 (19 Feb)	2	10	3	2	0	0	0	0	0	0	17
$N \cdot 10^6$	2 (19 Feb)	1	2	0	0	0	0	0	0	0	0	3
	3 (20 Feb)	0	505	273	73	0	0	0	0	0	21	872
	4 (20 Feb)	0	3	1	0	0	0	0	0	0	0	4
	5 (21 Feb)	0	404	148	20	0	0	0	0	0	10	582
	6 (22-23 Feb)	5	166	220	33	0	9	0	0	0	4	437
	7 (23 Feb)	0	100	600	252	66	11	0	40	19	627	1715
	8 (23-24 Feb)	0	64	296	449	97	0	0	35	10	924	1875
	9 (24 Feb)	11	138	327	244	52	0	0	6	0	159	937
	10 (25-27 Feb)	13	126	821	485	41	0	0	21	21	492	2020
	11 (25-27 Feb)	8	81	519	307	25	0	0	14	13	311	1278
	12 (13-24 Mar)	0	507	490	182	23	0	0	6	0	19	1227
	13 (13-24 Mar)	0	59	48	56	4	0	0	2	0	6	175
	14 (25 Mar)	0	25	12	37	12	0	0	0	0	0	86
	All sections	40	2190	3758	2140	320	20	0	124	63	2573	**11228**
Biomass	1	0.1	1.1	0.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Tonnes $\cdot 10^3$	2	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
	3	0.0	48.8	52.6	15.6	0.0	0.0	0.0	0.0	0.0	8.1	125.1
	4	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
	5	0.0	43.3	28.3	5.1	0.0	0.0	0.0	0.0	0.0	3.9	80.6
	6	0.6	20.5	43.3	8.6	0.0	2.5	0.0	0.0	0.0	1.6	77.1
	7	0.0	16.4	125.1	66.7	21.0	4.1	0.0	14.8	5.2	237.0	490.3
	8	0.0	10.3	64.7	126.0	30.0	0.0	0.0	14.8	3.5	368.0	617.3
	9	1.7	18.0	73.0	67.3	16.2	0.0	0.0	2.2	0.0	62.6	241.0
	10	2.3	23.2	181.9	136.8	13.4	0.0	0.0	8.6	7.9	194.1	568.2
	11	1.4	15.0	115.0	86.7	8.2	0.0	0.0	5.7	4.9	122.6	359.5
	12	0.0	56.6	91.3	42.0	6.7	0.0	0.0	1.7	0.0	6.8	205.1
	13	0.0	7.0	10.4	10.4	1.0	0.0	0.0	0.6	0.0	1.9	31.3
	14	0.0	2.7	2.2	6.9	2.4	0.0	0.0	0.0	0.0	0.0	14.2
	All sections	6.2	263.4	788.7	572.5	98.9	6.6	0.0	48.4	21.5	1006.6	**2812.8**

70°

69°

68° ················Depth = 200 m

67°   *The Norwegian Sea*

66°

65°

64°

63°

62°

61°

60°

59°

58°

Lofoten

Ofotfjorden

Tysfjorden

Vestfjorden

Trœna

Sklinnabanken

Haltenbanken

Frøyabanken

MØRE

Ålesund

Stadt

Bremanger

Florø   *SOGN*

HORDALAND

Karmøy   *ROGALAND*

Egersund

Siragrunnen

0°   5°   10°   15°   20°

Fig. 1. Study area with districts and places referred to in the text.
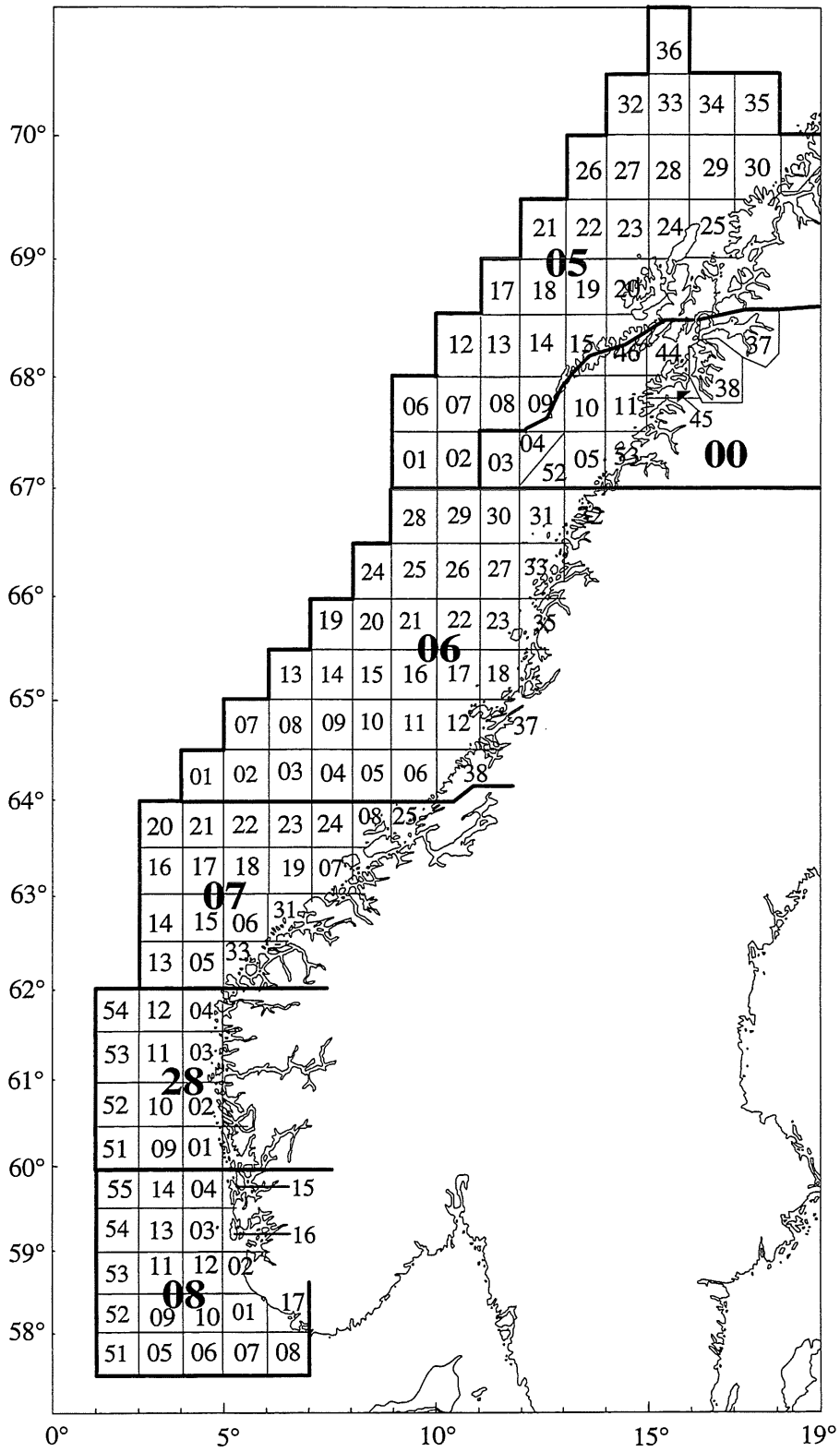
Fig. 2. Statistical areas and locations referred to in the text and graphics.
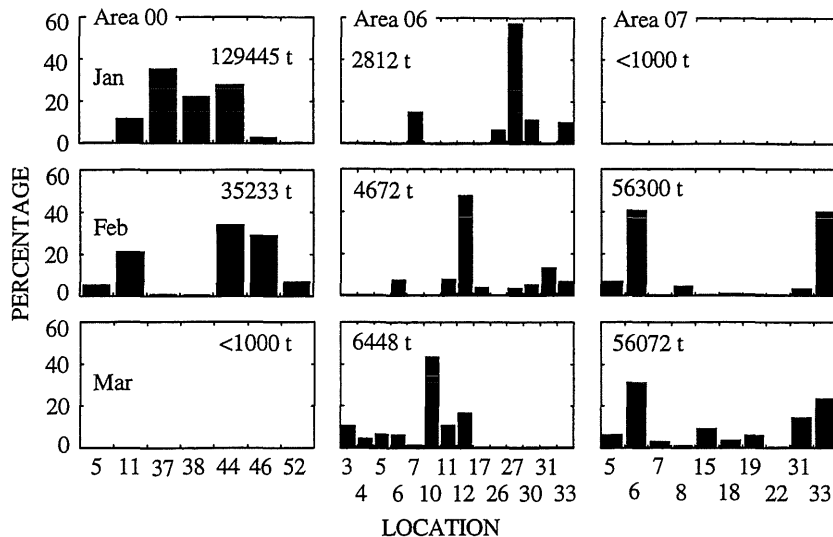
Fig. 3. Distribution of the herring catches by month, statistical area and locations (see Fig. 2) in January - March 1995. Total catch (t) is given for each month and area. The distribution by locations is not given when total catch < 1000 t.
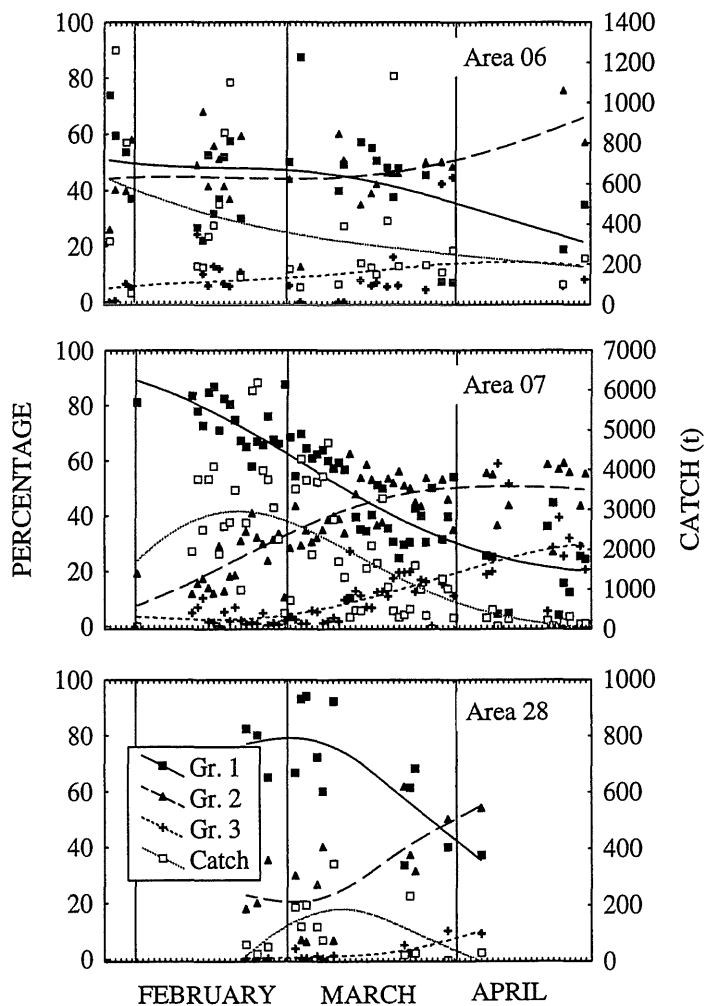
Fig. 4. Variation in size group composition and total dayly catch by time and statistical area during the spawning season 1995.
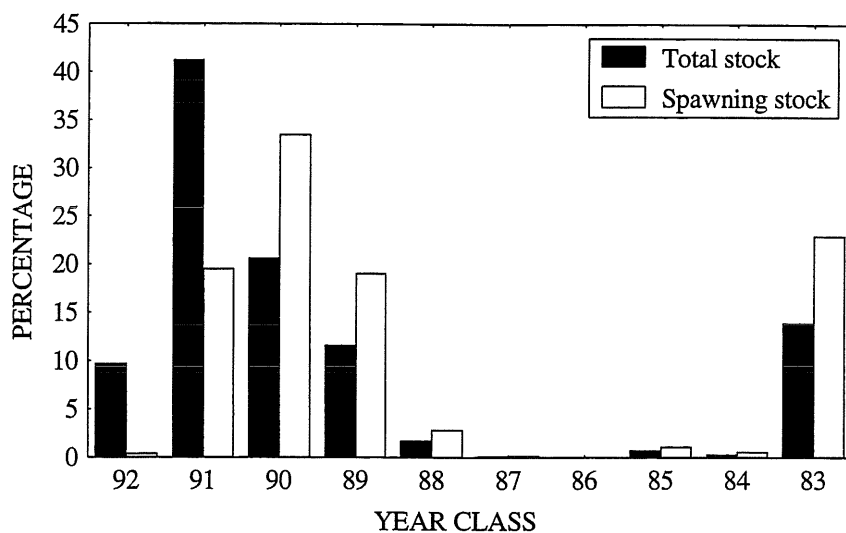
Fig. 5. Year class composition of the total stock and spawning stock (maturation stage > 2) during spawning season 1995, based on an acoustic estimate from a survey with «M/S Michael Sars» 20 February - 25 March (see also Table 3 and Fig. 9).
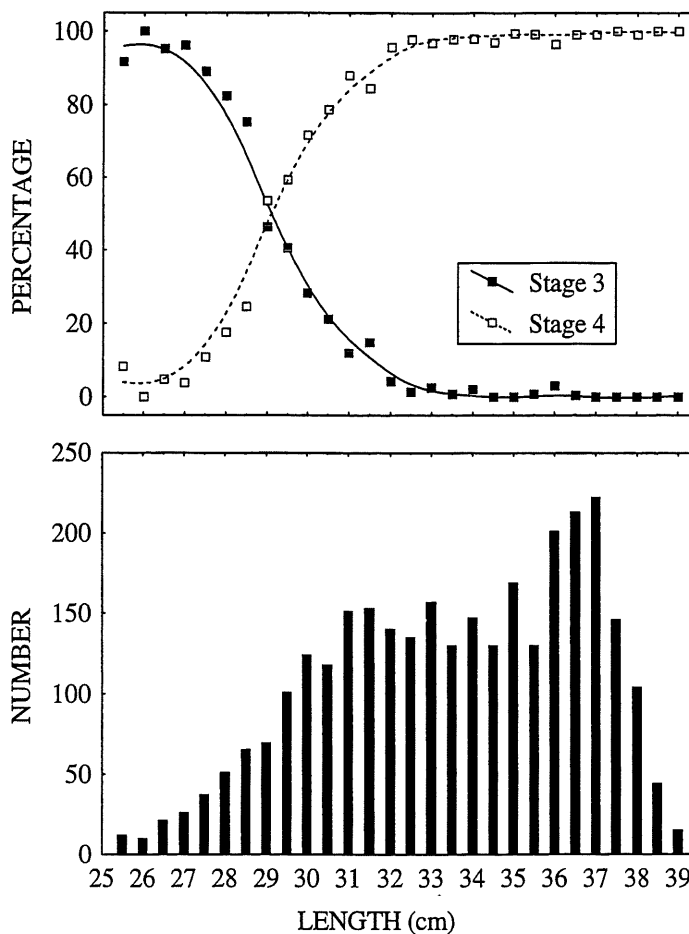
Fig. 6. Percentage of herring in maturation stages 3 and 4 by length (upper) and number sampled by length (lower) in the wintering area in Vestfjorden (Area 00) in January 1995.
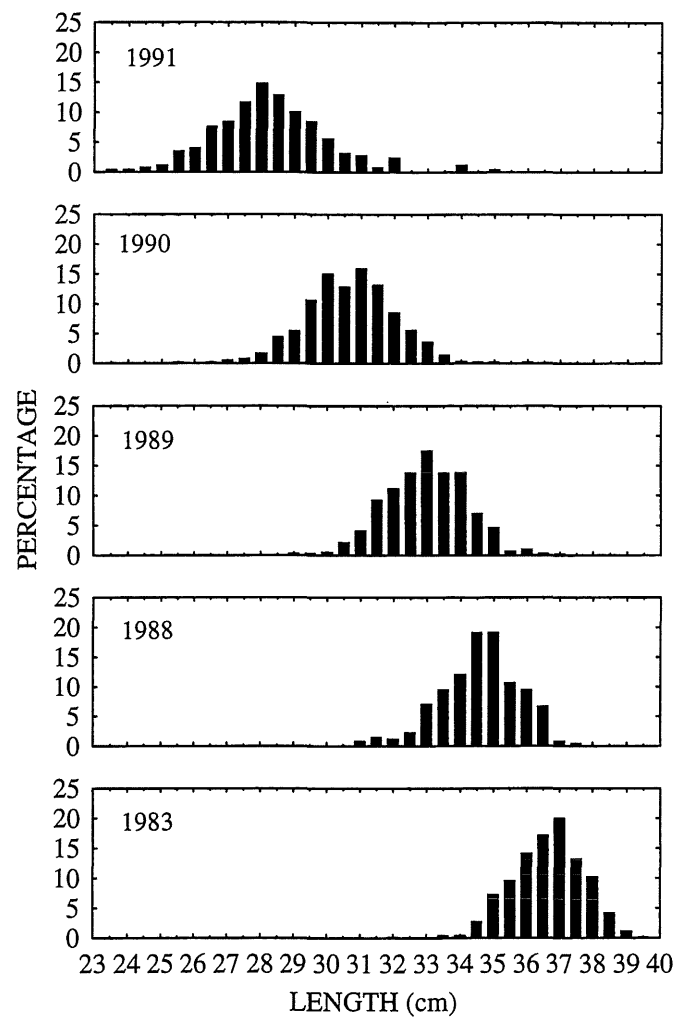
Fig. 7. Length distributions of mature herring (maturation stage > 2) by year class in the wintering area in Vestfjorden (Area 00) in January 1995.
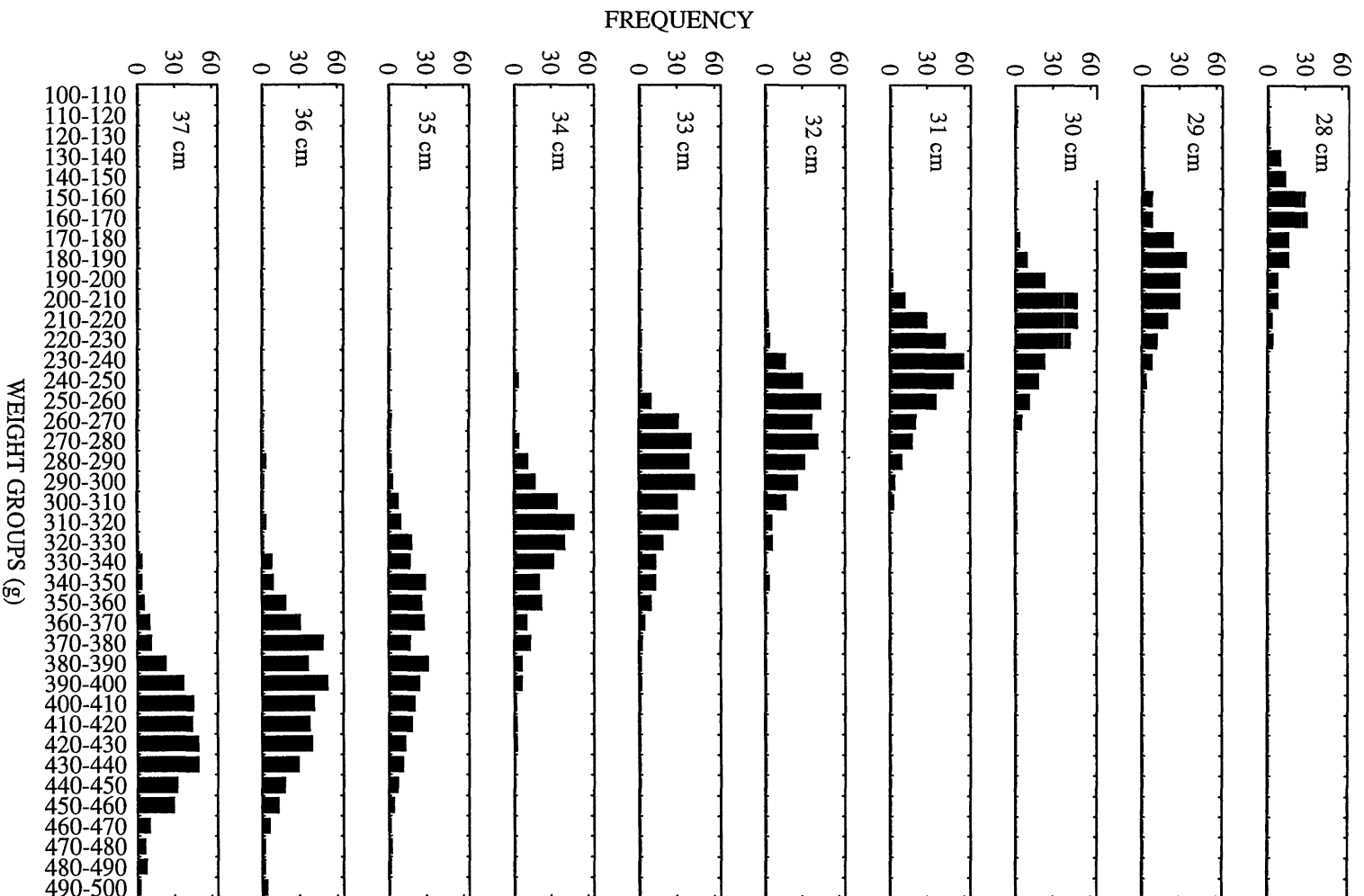
Fig. 8. Weight distributions of mature herring (maturation stage > 2) by length group in the wintering area in Vestfjorden (Area 00) in January 1995.
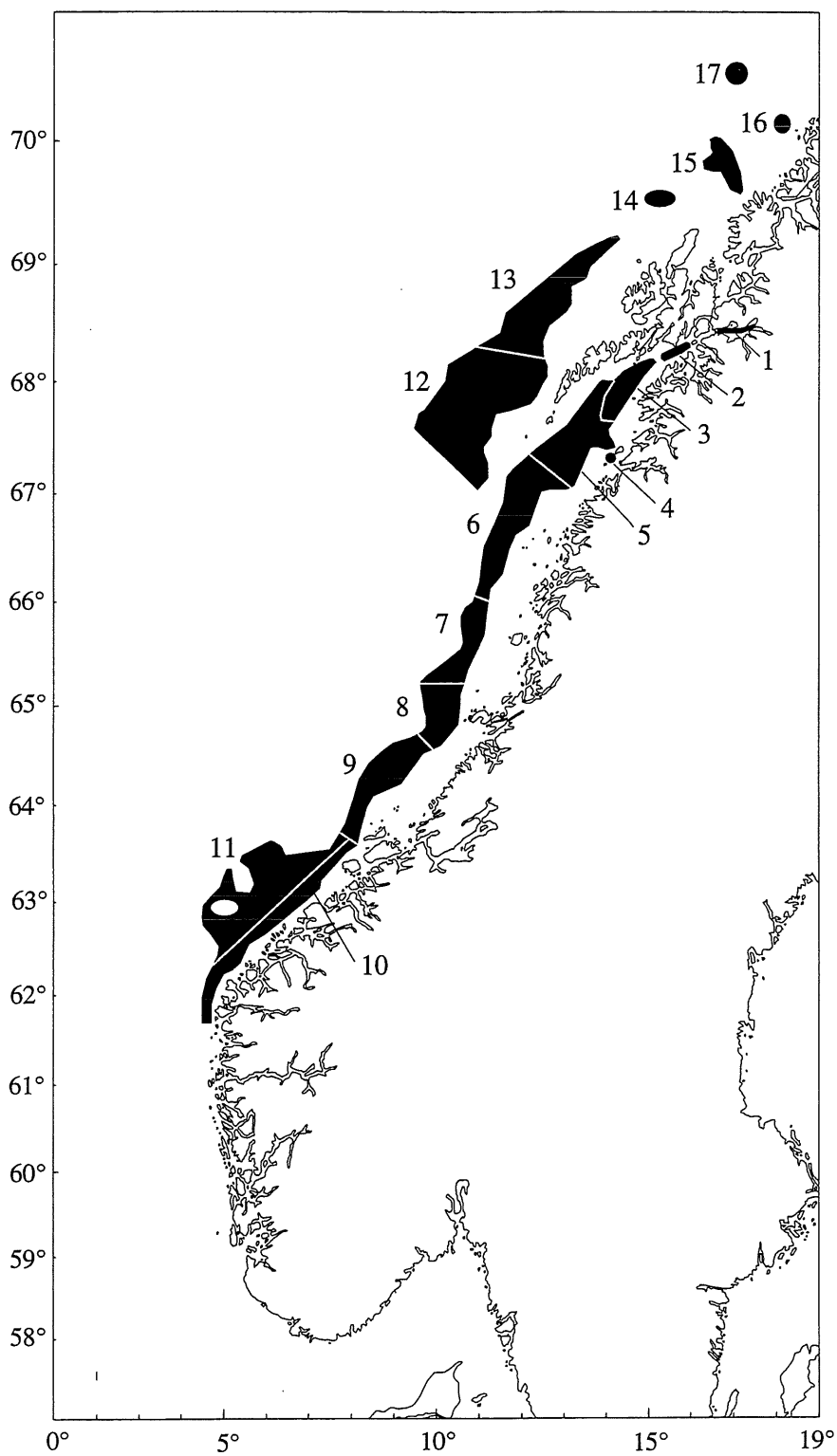
Fig. 9. The distribution of herring along the coast during the spawning season in 1995 as observed during a survey with «M/S Michael Sars» 20 February - 25 March. The distribution area was devided into smaller sections (1-17) according to varying year class composition, before abundance estimates were calculated (see Table 3).
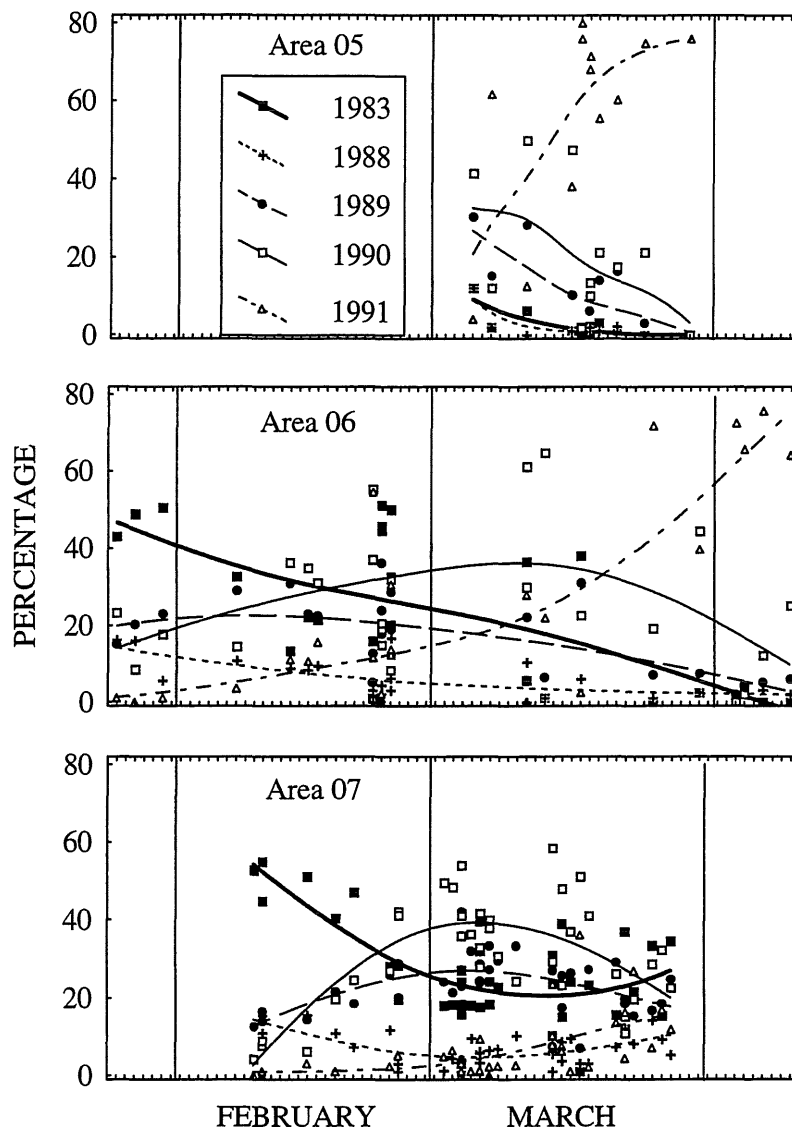
Fig. 10. Variation in year class composition by time and statistical area during the spawning season 1995.
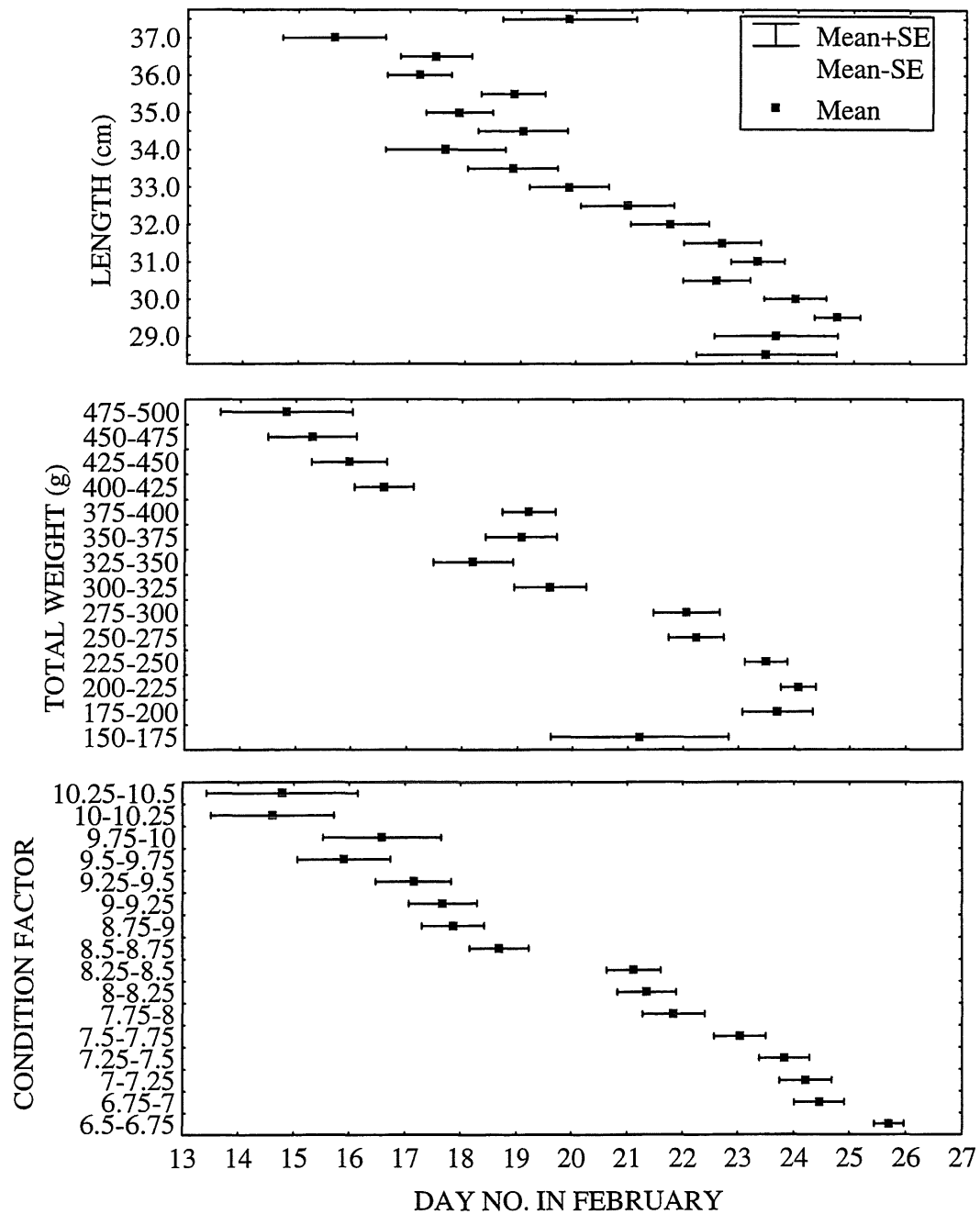
Fig. 11. Mean day for arrival of herring off Møre in February by length, total weight and condition factor. Only the data collected in february were used in the analysis.
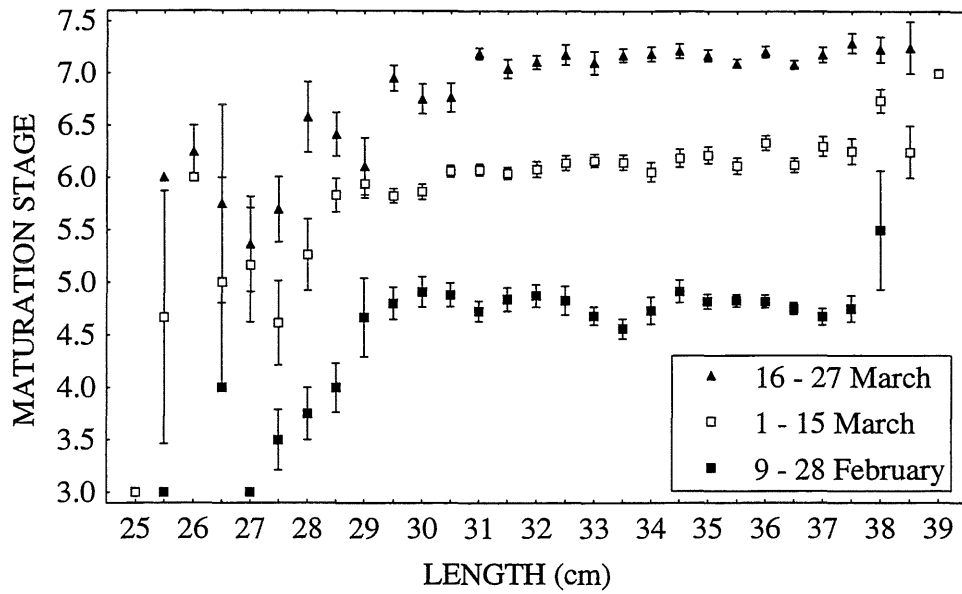
Fig. 12. Temporal variation in maturation stage (mean value ± SE) with length in mature herring (maturation stage > 2) in the main spawning area off Møre (Area 07).
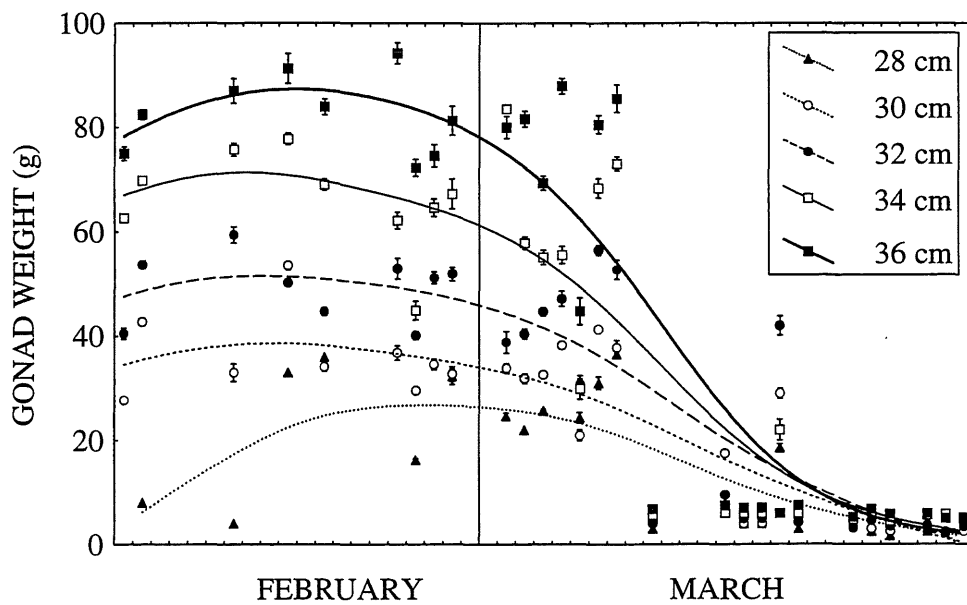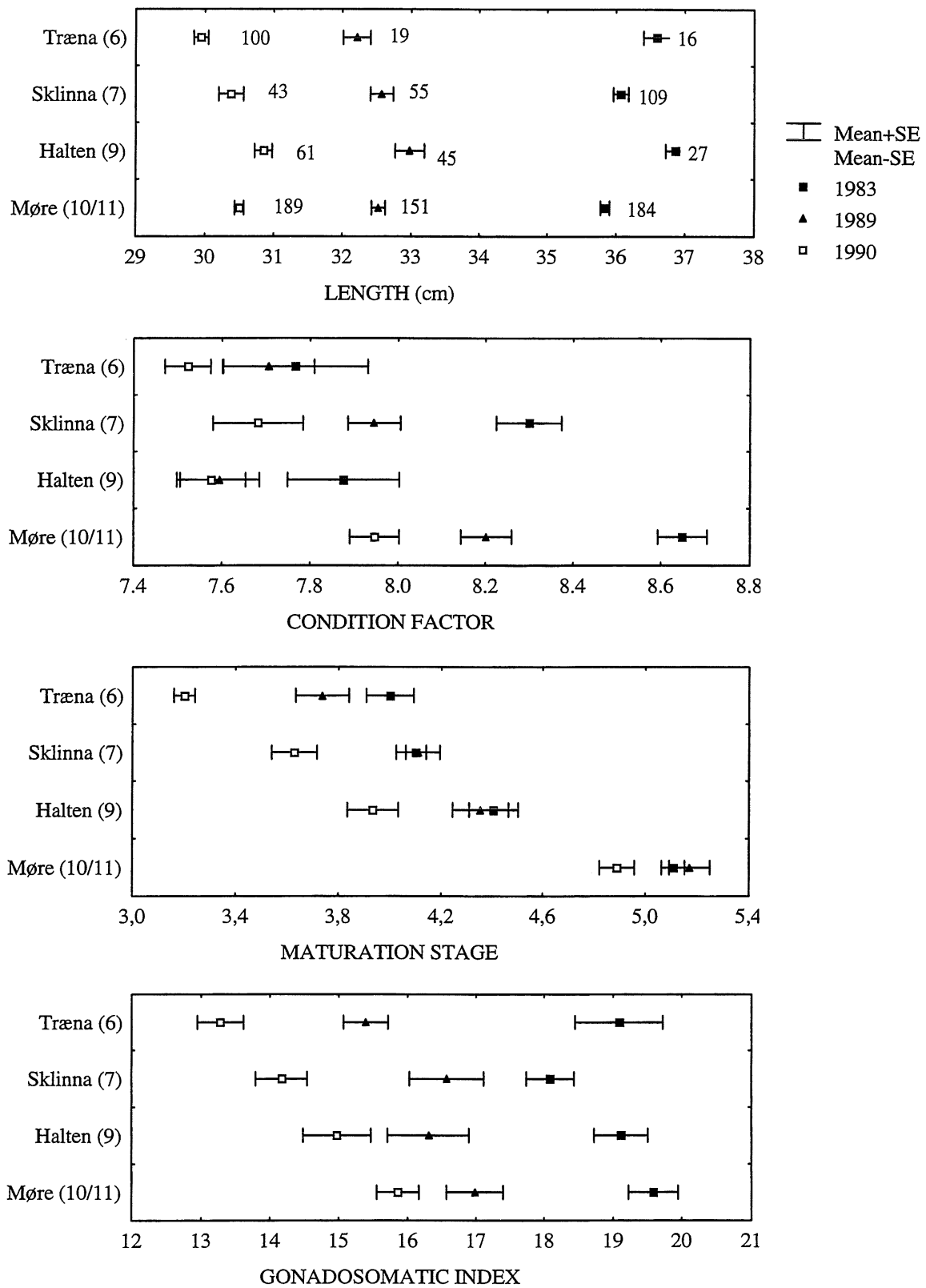

Fig. 13. Temporal variations in gonad weight (mean value ± SE) by length groups in mature herring (maturation stage > 2) in the main spawning area off Møre (Area 07).

Fig. 14. Variation in length, condition factor, maturation stage and gonadosomatic index with different sections on a latitudinal range (see Fig. 9 and Table 3) as recorded during the period 22 - 27 February. The values in the plots are given as means ± SE.
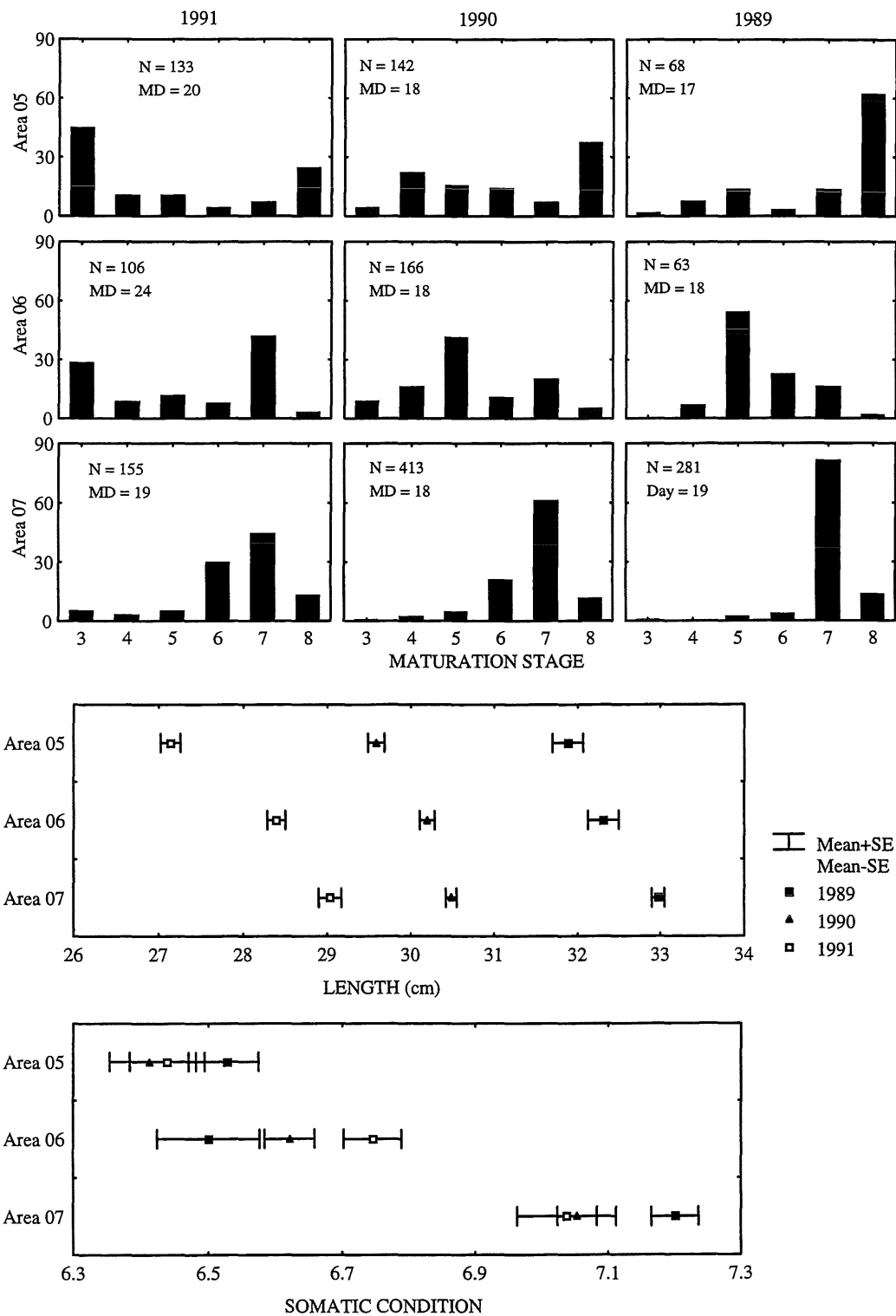
Fig. 15. Variation in maturation stage composition, length and somatic condition factor with year class and statistical area, during the period 11- 30 March 1995. The values in the plots are given as means ± SE. N=Total number and MD=mean day of catch.
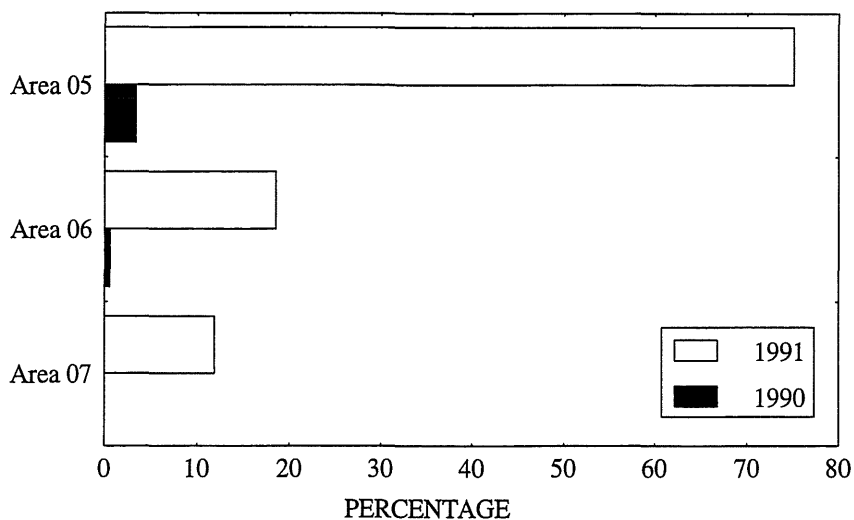
Fig. 16. Percentage of immature herring (maturation stage < 2) by year class and statistical area during the period 11 - 30 March. There were no immature herring in year classes older than 1990.
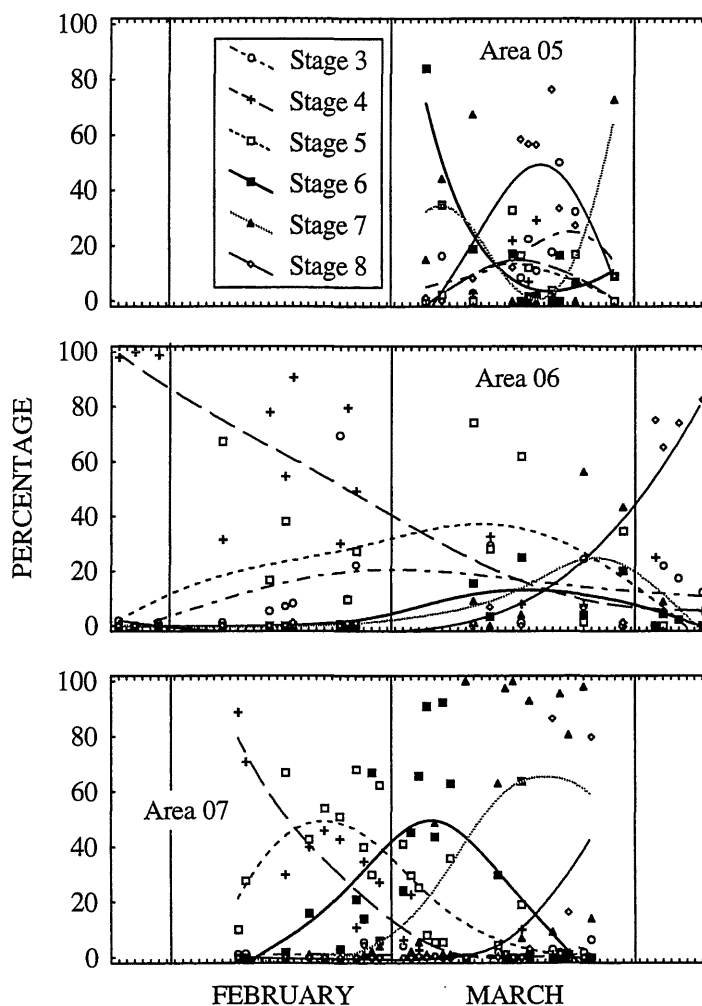

Fig. 17. Temporal variations in percentage of maturation stages 3 - 8 in areas 05, 06 and 07 during the spawning season 1995. Spawning period is defined as the period between first and last occurrence of herring in maturation stage 6.
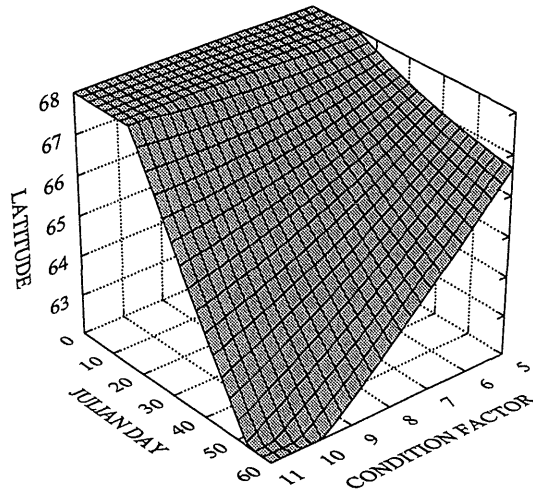
Fig 18. Southward spawning migration in January-February 1995 (Julianday 1-60) by condition factor.
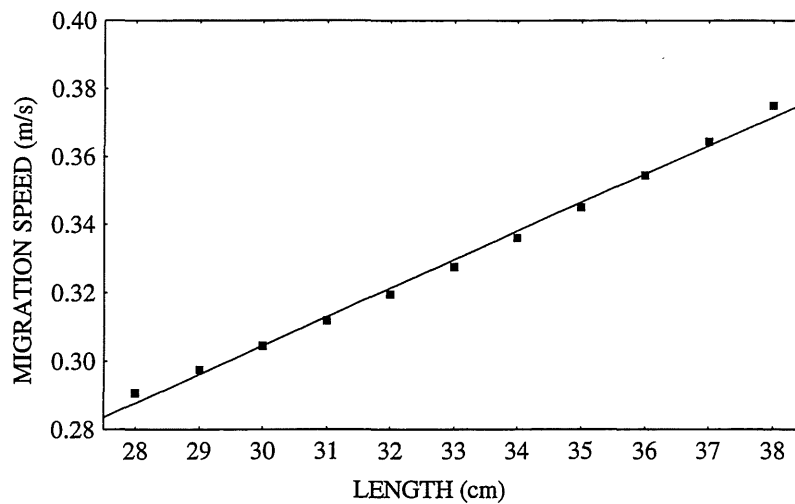

Fig. 19. Mean swimming speed by length during spawning migration in herring arriving off Møre in February.
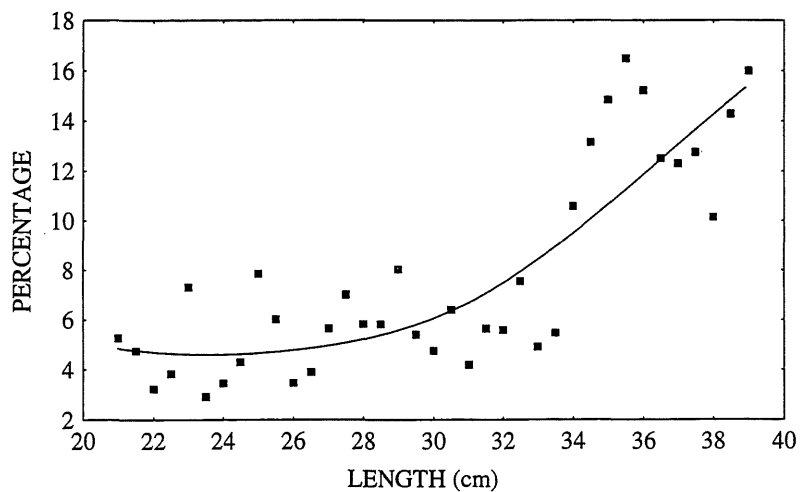

Fig. 20. Percentage of herring with unreadable scales related to the length of the fish included in the data material (see Table 1).