PAPER IV

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BIOLOGICAL CHARACTERISTICS OF NORWEGIAN SPRING SPAWNING HERRING (*CLUPEA HARENGUS* L.) SOUTH OF 61°N

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ABSTRACT

In 1989 a fraction of the Norwegian spring spawning herring appeared at the traditionally important spawning grounds south of 61°N for the first time after 1959. In subsequent years this fraction was examined with respect to age and length composition, maturation, meristic characters (vertebral and gillraker counts), component composition (coastal or Barents Sea nursery) and migration behaviour (tagging experiments). The biological characteristics of the southern fraction was also compared with those of the main spawning stock. The herring arrived at the southern grounds in two distinct groups. The first group arrived already in late January from unknown southern wintering areas. The group comprised mainly recruit spawners (age 3-5 years) originating from coastal nurseries. The major group arrived around 20 February and comprised mainly older repeat spawners originating from the Barents Sea nursery. Tag recoveries indicate that these herring were dissenters from the main spawning stock, which fed in the Norwegian Sea, wintered in northern fjords (68°N) and migrated southwards to spawn off the Møre district (62-64°N). Despite different arrival dates, the recruits and repeat spawners spawned simultaneously. The spawning commenced concurrently along the coast, but the spawning period was prolonged at the southern grounds compared with Møre.

KEYWORDS: Herring, age, maturation, migration, meristic characters, nursery.

INTRODUCTION

The spawning of Norwegian spring spawning herring has traditionally occurred along the Norwegian coast from Lofoten in the north to Lista in the south (Fig. 1), but the relative importance of the different grounds has changed with time. RUNNSTRØM (1941a) regarded the grounds south of Bergen, particularly the ones to the west and south off the island of Karmøy, as the most significant in the 1930s and also in former periods of rich herring fisheries. Between 70 and 80 % of the landings during the first three decades of this century came from the southern grounds (RUNNSTRØM 1941b; RØTTINGEN 1990). Spawning grounds off the Møre district were used regularly during this period, whereas grounds north of Møre seemed to be used for few seasons only and were considered insignificant. The southern grounds were also important in the late 1940s and onwards, but gradually the spawning moved more northwards in the last years of the period 1946-1958 (DEVOLD 1963). After

1959 the southern grounds were not utilised, whereas significant numbers of yolk sac larvae north of the main fishing areas at Møre indicated that banks north of Møre and even off the Lofoten islands were important in the early 1960s (DRAGESUND 1970).

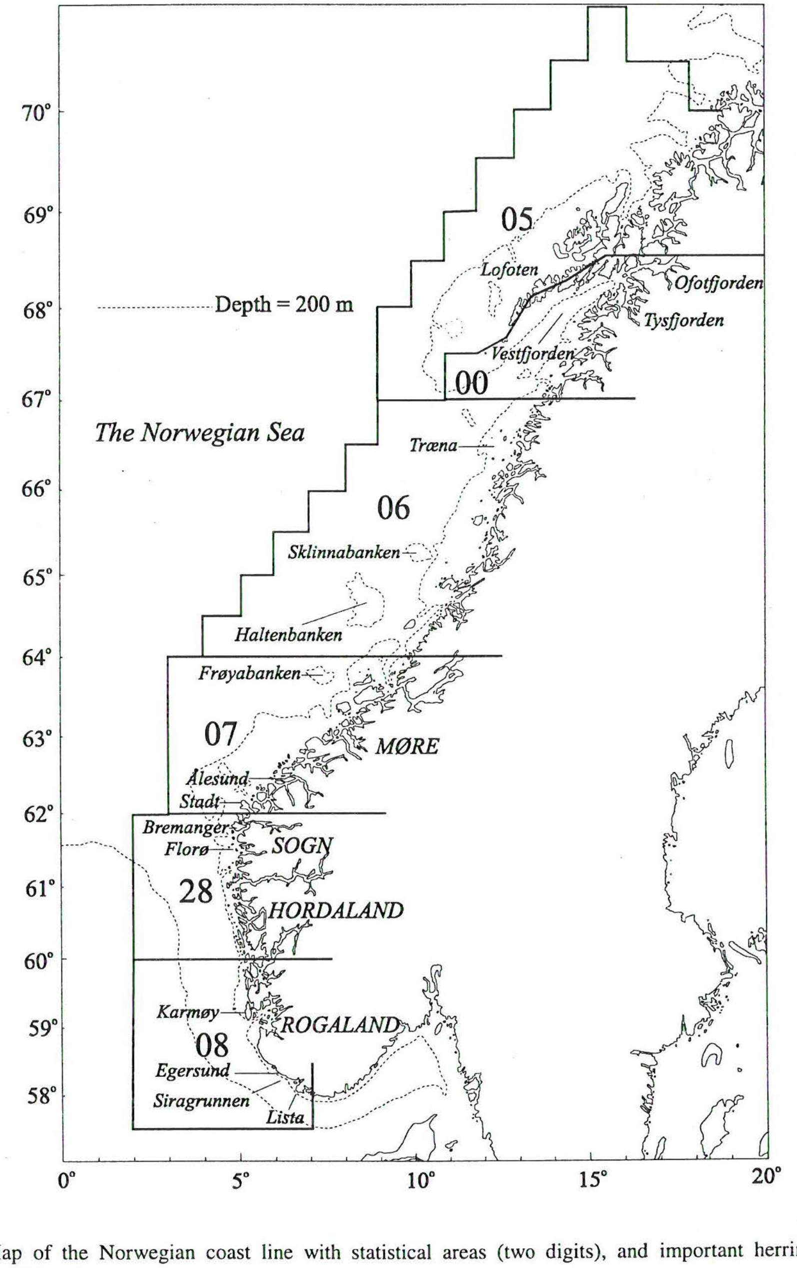

Fig. 1. Map of the Norwegian coast line with statistical areas (two digits), and important herring districts (capitals) and locations.

In the late 1960s a severe decline in stock abundance occurred due to high fishing pressure and low recruitment (DRAGESUND & al. 1980). Simultaneously the stock changed its feeding and wintering areas and hence migrations. Oceanic nursery, feeding and wintering areas were abandoned and the entire life cycle was spent in Norwegian coastal waters and fjords (DRAGESUND & al. 1980; RØTTINGEN 1990; HAMRE 1990). However, the spawning stock recovered to a biomass off approximately 5 million tonnes by the end of the 1980s due to the recruitment of the strong 1983 year class (Anon. 1997). The 1983 year class started to winter in the Vestfjorden area, northern Norway (RØTTINGEN 1992), while the feeding area was extended westwards in the Norwegian sea (DRAGESUND & al. 1997). When spawning for the first times in 1987 and 1988, the 1983 year class mainly utilised the grounds off Møre (RØTTINGEN 1990). However, in 1989 a small fraction of the spawning stock, predominated by the 1983 year class, appeared at the spawning grounds off Karmøy for the first time in 30 years (RØTTINGEN 1989).

A fishing ban for herring was introduced in the areas south of 61°N in1989, as the reappearance of Norwegian spring spawning herring at the southern grounds was considered important with regard to rebuilding of the stock (RØTTINGEN & SLOTTE 1998). At this time there was no knowledge about the biology and migrations of the southern fraction, but it was assumed that this fraction comprised dissenters from the main stock spawning off Møre. In other words it was assumed that they probably had spawned once or twice off Møre in the preceding years, and that they maintained the same seasonal migrations as the main part of the stock with feeding in the Norwegian Sea and wintering in northern Norway, in subsequent years. Due to the general assumption of homing in herring (HOURSTON 1982; WHEELER & WINTERS 1984), it was also expected that the herring would continue to spawn at the southern grounds in subsequent years, and that an increasing fraction could dissent from the main spawning stock off Møre and distribute at the southern grounds as earlier in this century. Furthermore it was assumed that the extension of the spawning area southwards would be of advantage for the stock recruitment and also for the ecology of the spawning grounds. However, these were only vague assumptions, and from a scientific and management point of view there was need for more research of the southern spawning fraction. Therefore, in the subsequent years after the herring reappeared at the southern grounds, this spawning fraction was subject to series of investigations by the Department of Fisheries and Marine Biology (IFM), University of Bergen and Institute of Marine Research (IMR), Bergen, Norway. The southern fraction was examined with respect to abundance, distribution, biological characteristics (JOHANNESSEN & al. 1995a), large scale migrations (tagging experiments by IMR), schooling behaviour (NØTTESTAD & al. 1995), larval drift (JOHANNESSEN & al. 1995b), larval otolith microstructure in relation to hatching origin (STENEVIK & al. 1995) and larval condition (FOLKVORD & al. 1995; BLOM & al. 1997). In addition, ecological investigations were directed towards the effects of herring and herring spawn on the ecology of coastal fish communities (HØINES & al. 1995).

The present paper deals in particular with the biological characteristics of the southern fraction, and questions whether it differs from the rest of the spawning stock. Special emphasis is put on analysing the age and length composition, maturation, meristic characters (vertebral and gillraker counts), component composition (coastal or Barents Sea nursery) and migration behaviour (tagging experiments).

MATERIALS AND METHODS

STUDY AREA

The spawning area of Norwegian spring spawning herring was sectioned into five sub areas (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 (IMR), Bergen, Norway (Fig. 1). In this paper the study area was restricted to the southern spawning grounds (areas 08 and 28) and the main spawning area off Møre (area 07) in addition to the wintering areas in Vestfjorden, Tysfjorden and Ofotfjorden (area 00). By definition the southern fraction is spawning south of 61°N. Spawning grounds south of Stadt off the Sogn district (61-62°N), at locations off Bremanger and Florø, are considered to be an extension of the Møre spawning area.

SAMPLING AND BIOLOGICAL MEASURES

The biological data utilised in this study originate from samples collected from research trawl surveys (by IFM and IMR), commercial seine fisheries and from gill net catches of local fishermen. The sampling size of trawl and seine samples were usually 100 herring, whereas the number varied between 20 and 100 in the gill net samples. A large majority of the herring from the southern grounds (area 28 and 08) was sampled from gill net catches, whereas purse seine samples and trawl samples were obtained from the wintering area (area 00) and the main spawning area off Møre (area 07), see also Fig. 3. The sampling on a temporal and geographical scale increased during 1992-94 for comparative studies of biological characteristics within and between areas during the spawning season. The present study includes the following relevant biological variables measured on individual herring during 1992-94 (numbers of fish included are given for the respective analyses in the result chapter): total wet weight (g), total length (nearest 0.5 cm below), maturity stage, age (from otoliths and scales), vertebral count and number of lower gillrakers (only in 1992). The maturity stages were determined by visual inspection of gonads as recommended by ICES (Anon. 1962): immature = 1 and 2, maturing = 3 to 4, ripe = 5, spawning/running = 6, spent = 7 and recovering = 8.

The age composition and maturation (by maturity stages) were compared between the spawning areas 07, 28 and 08 and vertebral counts were compared between and within the southern grounds (area 28 and 08) in all three years 1992-94. In 1992, the vertebral and gillraker counts were also compared between the wintering area and the same spawning areas. Earlier studies have shown that the vertebral (JOHANSEN 1919; SCHNAKENBECK 1931; RUNNSTRØM 1941 a) and gillraker counts (KREFFT 1958; PARSONS & HODDER 1971, MENG & STOCKER 1984; JOHANNESSEN & JØRGENSEN 1990) may be used to distinguish between herring populations or components. These variables were therefore considered relevant when comparing the population structure between the wintering area and spawning areas. The measurements of these meristic characters are very time demanding and due to constraints on staff and time the meristic measures were reduced to include only vertebral counts in the areas 28 and 08 in 1993-94, in order to test for differences between years in the structure of the southern fraction.

ESTIMATION OF COMPONENT COMPOSITION

Another aspect of the population structure is the composition of herring from different nursery areas. In this paper the proportion of herring originating from nursery areas in the Barents Sea, compared to nurseries along the Norwegian west coast, was estimated for the 1983, 1987, 1988 and 1989 year classes by age and area. The estimates were derived from a study by HOLST & SLOTTE (in press) on the effects of juvenile nursery conditions on the geographic spawning distribution in Norwegian spring spawning herring. Based on measurements of the first three annuli they discriminated between individuals originating from the Barents Sea nurseries and coastal nurseries, using the method described in BARROS & HOLST (1995). They estimated the proportion originating from the Barent Sea in the year classes 1930-89, in the spawning areas 06, 07, 28 and 08 using data on herring in maturity stages 4-6. In this study we have utilised the same methods and data as in HOLST & SLOTTE (in press). However, there is one difference: the estimates are presented for each year class separately, instead of blocks of 10 year classes (1980-89) like in HOLST & SLOTTE (in press).

TAGGING EXPERIMENTS

Data from tagging experiments during 1990-94, conducted on individuals of the southern fraction of the Norwegian spring spawning herring stock, were included in order to describe the large scale migrations of herring spawning at the southern grounds. IMR performs annual cruises in March-April for tagging purposes of spent herring. Internal metal tags, which are recognised by metal detectors, were used in the experiments. Tagging was carried out on spent herring only. Individual tags of herring recovered at plants along the Norwegian coast, were returned to IMR with data on catch position and date. At some plants tagged herring were sorted out and frozen, and later analysed with respect to biological characteristics as body weight, total length, maturity stage and age.

RESULTS

AGE COMPOSITION

Geographical variation in age composition was recorded during the spawning season (Fig. 2). The age composition was analysed from samples collected during the entire spawning season (February-April) and pooled by year and area. Although these pooled data were not weighted by abundance, they indicated the age composition of the herring that spawned in the respective areas in 1992-94. Irrespective of year and area, two peaks were prominent in the age composition, one predominated by young spawners at age 3-6 years and another predominated by age-groups 9 (in 1992), 10 (1993) or 11 years (1994), i.e. the relatively strong 1983 year class. In all years the samples from the southern areas 28 and 08 comprised more young herring at ages 3-5 years and less herring of the 1983 year class than did the samples from the main spawning area 07. The proportion of the youngest age groups was particularly high off the Hordaland district (area 28).

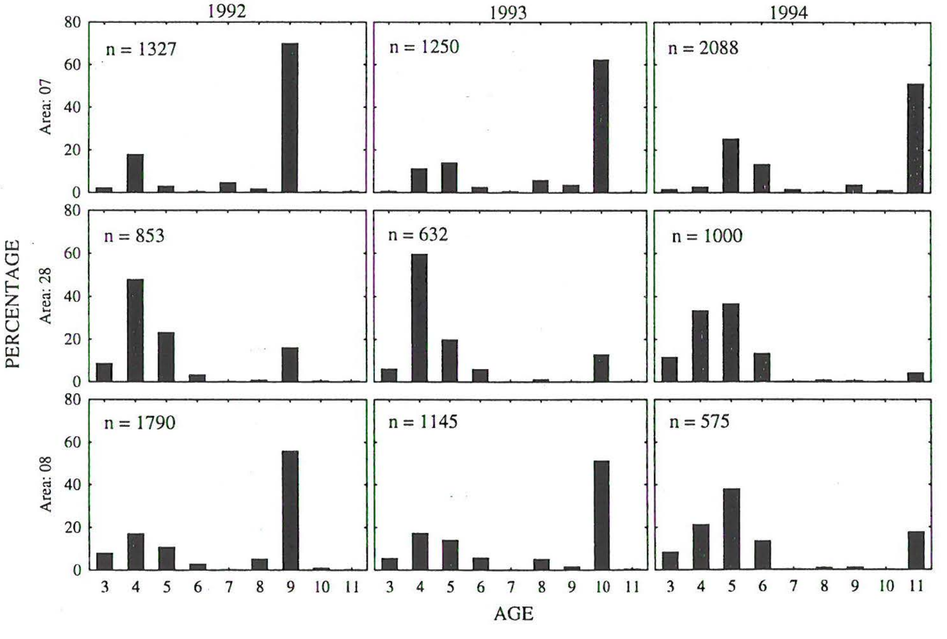

Fig. 2. Age composition for given spawning areas and years, when all samples from February-April were pooled.

The age composition varied on a temporal scale within the specific spawning areas (Fig. 3). In order to describe temporal variations in age composition, the data were presented per calendar day within each area. Only the predominant herring at ages 3-5 years and the 1983 year class were presented. The

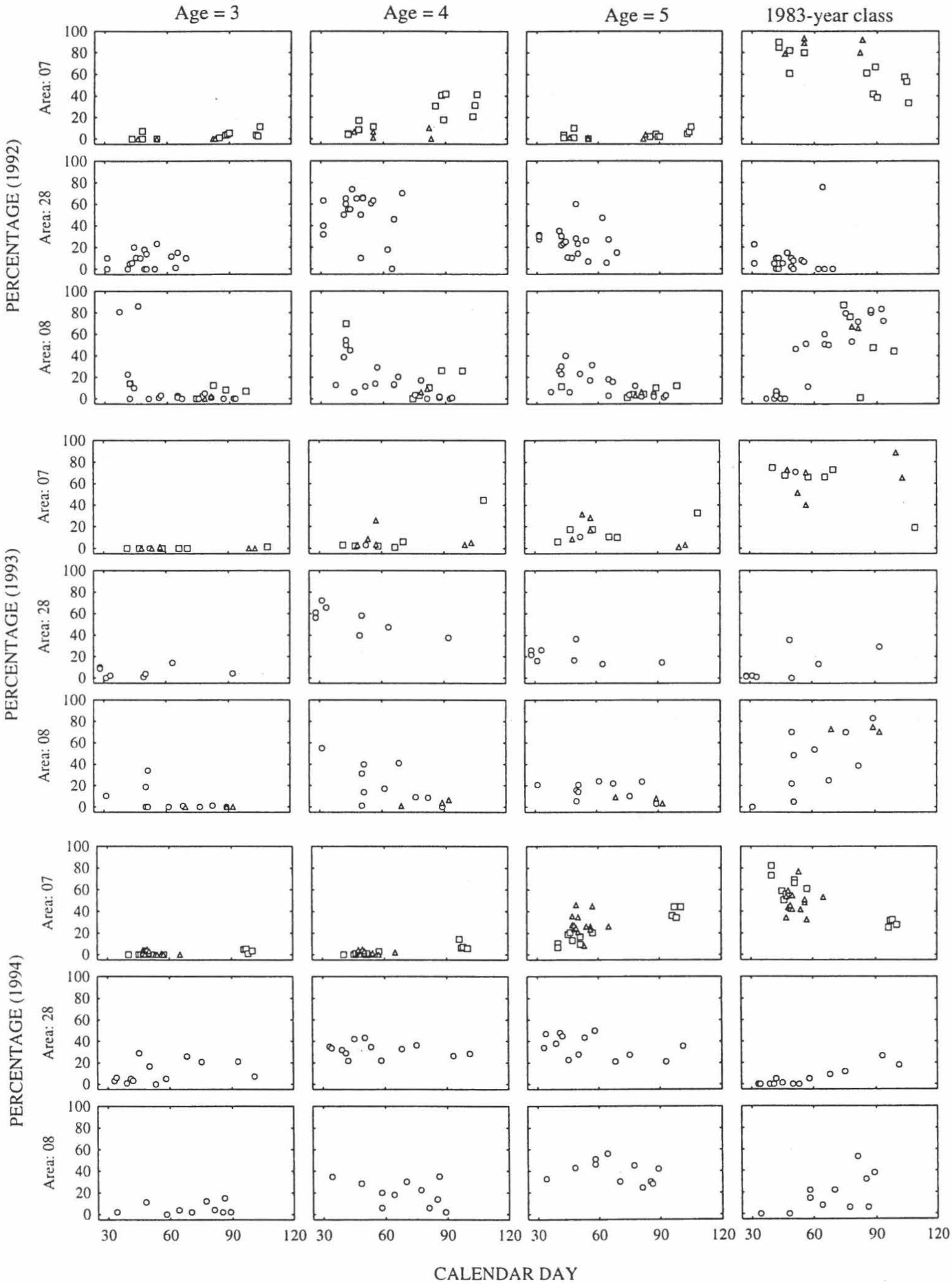

Fig. 3. Comparison of temporal variation in age composition between spawning areas in the years 1992-94. The percentage of young spawners of age 3-5 years is compared with the percentage of the abundant 1983 year class. Symbol definitions: circles = gill net samples, squares = purse seine samples and triangles = trawl samples.

data from the years 1992-94 revealed that 3-5 years old herring occurred already in the last week of January or first week of February along the coast off Hordaland (area 28) and Rogaland (area 08). This was about one week before the first herring was observed off Møre (area 07). The young mature herring predominated off Hordaland throughout the season, whereas off Rogaland the proportion of older spawners, mainly the 1983 year class, increased by the end of February and predominated onwards. The opposite situation was observed off Møre, where the predominant 1983 year class decreased proportionally in the period after first arrival around 5-10 February, whereas the proportion of young, 4-5 years old, herring increased.

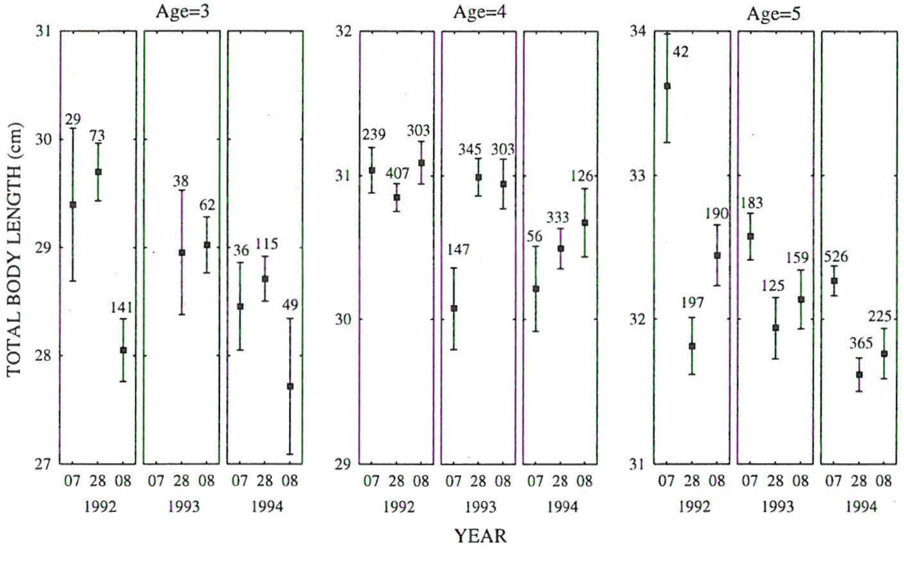

Fig. 4. Comparison of body lengths in 3, 4 and 5 year old herring. between the areas 07, 28 and 08 and the years 1992-94. Mean values ± 95 % confidence limits are given, and number of individuals included is given above each mean. In cases where confidence limits did not overlap, the means differed significantly ($p < 0.001$, t-test). In addition statistical differences were found in some cases with overlapping confidence limits (see the results).

BODY LENGTH AT AGE

The body length of 3, 4 and 5 year old herring differed significantly (t-test) both between areas in given years and between years in given areas (Fig. 4). The geographical differences in body length were not similar in the years 1992-94, with exception of the 5 years old herring. The body length at age 3 years differed between areas 08 and 07 in 1992 ($p < 0.001$), between areas 08 and 28 in 1992 ($p < 0.001$) and in 1994 ($p < 0.001$). The body length of 4 years old herring differed between area 28 and the areas 07 ($p = 0.03$) and 08 ($p < 0.005$) in 1992, between area 07 and the areas 28 and 08 in 1993

($p < 0.001$), and between area 07 and area 08 in 1994 ($p = 0.03$). The 5 years old ones were significantly smaller in the southern areas 28 and 08 than in area 07 in all years studied ($p < 0.001$), and they also tended to be smaller in area 28 than in area 08 in all years, but this difference was only significant in 1992 ($p < 0.001$). Furthermore, in all age groups and areas, with exception of age 3 years in area 07, the body length was significantly smaller in 1992 than in 1994 or 1993 ($p < 0.05$).

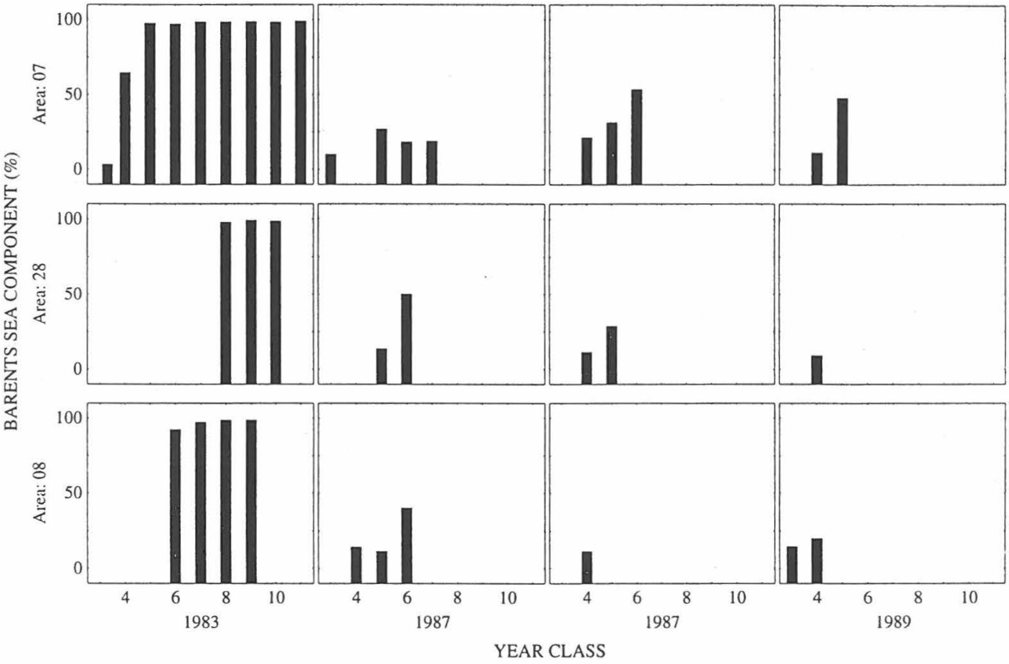

Fig. 5. Proportion of herring originating from the Barents Sea nursery area versus age for given year classes and spawning areas (n>10, data from HOLST & SLOTTE in press).

COMPONENT COMPOSITION

Data on growth history revealed that the estimated nursery areas of origin (coastal areas or Barents Sea) differed between year classes, whereas small differences were found between the spawning areas 07, 28 and 08 (Fig. 5). Close to 100 % of the 1983 year class was found to originate from the Barents Sea. There was a tendency that the proportion of herring originating from the Barents Sea increased with age. However, it was quite clear that among 3-5 years old herring of the year classes 1987-89, a large majority of 70-80 % originated from coastal nursery areas.

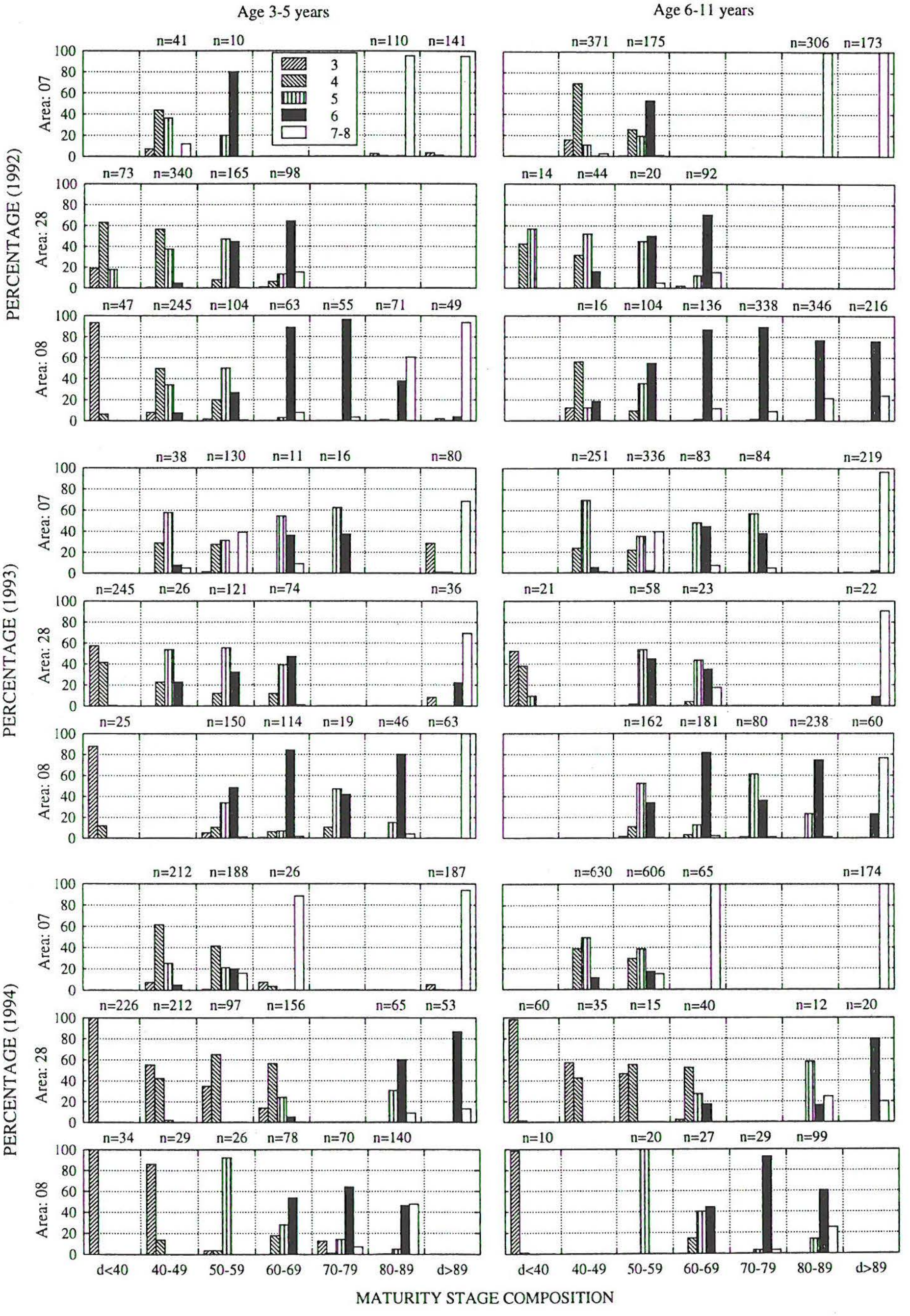

Fig. 6. Temporal variation in maturation between spawning areas in the years 1992-94. The maturity stage composition of young spawners of age 3-5 years are compared with the maturity stage composition of 6-11 year old herring by intervals of calendar day (d) during the spawning season February-April. Number of individuals included is given above each interval. Intervals with less than 10 fish were excluded.

MATURATION AND SPAWNING

The spawning, in this context defined as the occurrence of herring with running gonads (maturity stage 6), commenced at about the same time irrespective of age or area (Fig. 6). Herring at ages 3-5 years were caught with running and spent gonads at the same time as the older fish. The spawning off Hordaland (area 28) and Rogaland (area 08) started at about the same time for all age groups, as the older herring arrived off Karmøy (area 08). This happened around 20 February (day 50) in 1992-1993 and around 1 March (day 60) in 1994. The spawning time at the southern grounds in 1992-93 were similar as that in the main spawning area off Møre, but in 1994 the spawning was somewhat delayed in the southern areas. After mid March in 1992-93 catches of Norwegian spring spawning herring were sparse off Hordaland, indicating that the spawning period culminated and that the herring had left the area. The spawning period off Rogaland appeared to last longer than off Møre, where most herring were spent by the end of March. At the spawning grounds off Karmøy, Egersund and Siragrunnen, herring with running gonads were recorded throughout March and well into April. Maturing (maturity stages 3-5) or spent/recovering (maturity stages 7-8) herring occurred in negligible proportions at the southern grounds after spawning commenced. During this period several herring schools in spawning condition were recorded in the area, and most of these left the area immediately after spawning, whereas off Møre the spent herring tended to stay for some time after the release of gonad products, mainly for feeding purposes.

MERISTIC CHARACTERS

The vertebral count varied from 55 to 60, whereas the gillraker count varied at a higher range, from 45 to 52 (Fig. 7). No distinct differences were found in the frequency of the different vertebral counts. Fish containing 57 vertebrae were most frequent in all areas, year classes and years examined. An exception was the 1989 year class in area 28 in 1993, which comprised equal proportions (44.1 %) of 57 and 58 vertebrae. The most frequent gillraker count varied between 48, 49 and 50. In general, the frequency of the gillraker counts varied more than that of the vertebral counts.

The vertebral count and gillraker count differed significantly (t-test) between areas for specific year classes (Fig. 8). The vertebral count differed significantly between area 28 and 08 ($p < 0.01$) of the 1987 year class and between the areas 00 and 08 ($p < 0.01$) of the 1989 year class. Otherwise, no geographical differences in vertebral count were found within the year classes examined. However, more geographical differences were found in the gillraker count. Mean gillraker count differed significantly between areas 00 and 07 ($p < 0.05$), areas 00 and 08 ($p = 0.001$) of the 1983 year class; between areas 28 and 08 ($p < 0.05$) of the 1987 year class; between area 00 and areas 07, 28, 08 ($p < 0.001$), between areas 07 and 28 ($p < 0.05$), area 28 and 08 ($p < 0.05$) of the 1988 year class; between area 00 and areas 28 and 08 ($p < 0.001$) of the 1989 year class.

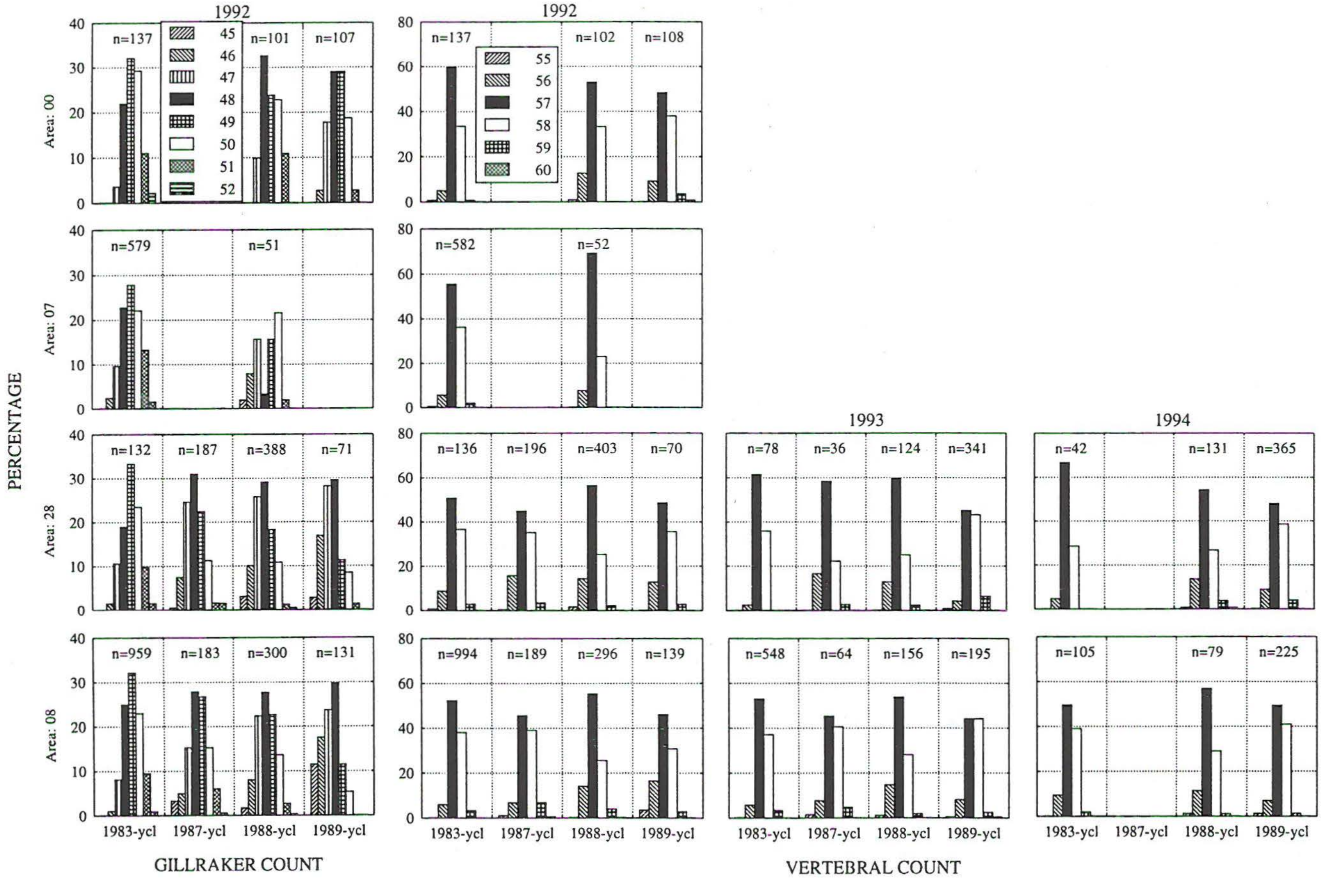

Fig. 7. Frequencies of gillraker count (1992) and vertebral count (1992-1994) by spawning area and year class. Number of individuals included is given above each frequency distribution. Year classes where less than 30 fish were measured were excluded.

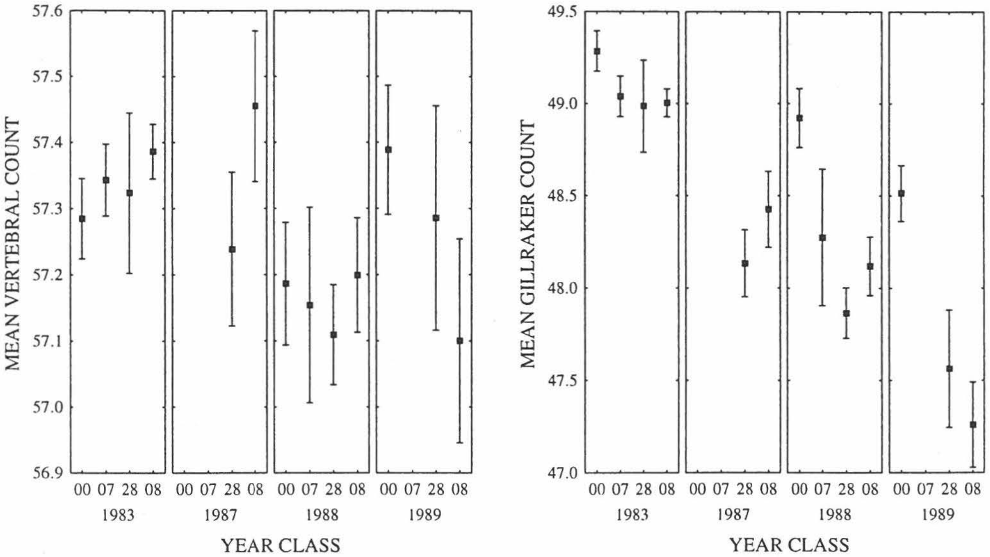

Fig. 8. Mean vertebral count and gillraker count ± 95 % confidence limits by spawning area and year class in 1992. In cases where confidence limits did not overlap, the means differed significantly ($p < 0.001$, t-test). In addition statistical differences were found in some cases with overlapping confidence limits (see the results).

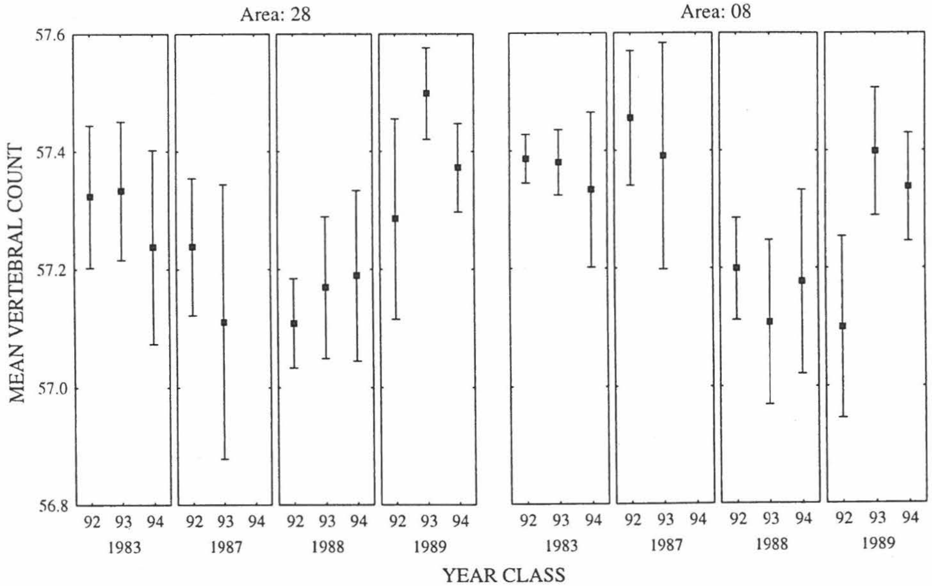

Fig. 9. Mean vertebral count ± 95 % confidence limits by spawning area and year class. A comparison between the years 1992-94. In cases where confidence limits did not overlap, the means differed significantly ($p < 0.001$, t-test). In addition statistical differences were found in some cases with overlapping confidence limits (see the results).

Negligible differences (t-test) were found in vertebral count between years in a given area and year class (Fig. 9). In area 28 the vertebral count of the 1989 year class was significantly higher in 1993 than in 1992 ($p < 0.05$) and 1994 ($p < 0.05$) whereas in area 08 the vertebral count of this year class was significantly lower in 1992 than in 1993 ($p = 0.001$) and 1994 ($p = 0.005$). Otherwise, no significant differences in mean vertebral count occurred between years in the examined year classes in neither of the areas 28 nor 08, which indicates that the mean vertebral count is rather stable within a year class in a given area. The 1988 year class had a particularly low mean vertebral count compared to the other year classes. This was similar in all the years and areas examined. When the data available from all the years and areas were pooled, the vertebral count was significantly lower ($p < 0.001$) in the 1988 year class than in the other year classes examined 1983, 1987 and 1989. Particularly the proportion of fish containing 58 vertebrae was lower in the 1988 year class compared to the other year classes (Fig. 7).

The mean gillraker count decreased from the oldest towards the youngest fish within all examined areas in 1992 (Fig. 8). Further regression analysis revealed a positive relationship between body length and gillraker count in 1992 in area 00 ($r^2 = 0.08$, $p < 0.001$), area 07 ($r^2 = 0.03$, $p < 0.001$) area 28 ($r^2 = 0.1$, $p < 0.001$) and area 08 ($r^2 = 0.17$, $p < 0.001$). In 1992, the mean body length of ages 3 and 4 years old herring was 26.3 and 29.6 cm respectively in the wintering area 00. This was significantly lower (t-test, $p < 0.001$) than in the spawning areas 07, 28 and 08. Nevertheless, as mentioned above the gillraker count was significantly higher in area 00 than in the spawning areas, which indicates that this character also is influenced by other factors than fish size.

TAG RECOVERIES

After spawning, 4.000 - 15.000 herring were tagged annually at the southern grounds during the period 1990-93, and tags were recovered from the feeding grounds in the Norwegian Sea, wintering grounds in the Vestfjorden area, during return migration towards spawning grounds (maturing and ripe herring) and from spent herring heading northwards from the southern grounds (Fig. 10). Individuals of the predominant 1983 year class accounted for a large majority of the recovered tags during the period 1990-96. However, tags were also recovered from individuals of younger year classes, tagged at the age of 3-5 years. Only two individuals of the 1983 year class, one in maturity stage 7 and one in maturity stage 6, were recovered at the same southern grounds in 1992 as they were tagged one and two years before, respectively. Also three individuals tagged in 1992 were recovered one year later (21 March) in fjords to the south and north of Karmøy.

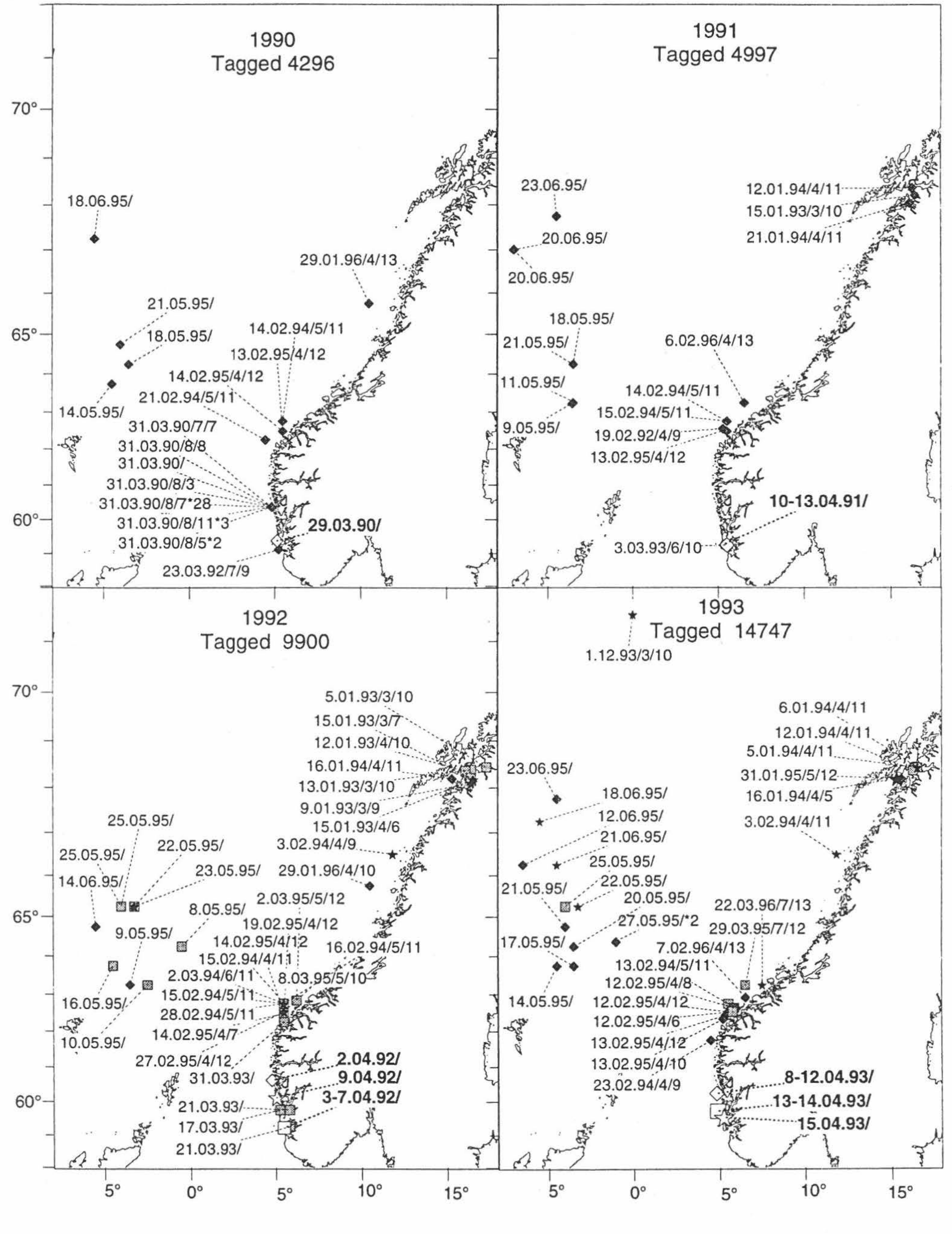

Fig. 10. Results from tagging experiments at southern spawning grounds in the years 1990-93. In cases with more than one tagging position, each tagging position and the tags recovered from that release is marked with different symbols. Open symbols denote the position and date of release, whereas hatched symbols denote position and date/maturity stage/age * number of individuals (only when n > 1) recovered at that particular date, maturity stage and age. Total number of herring tagged at the southern grounds are given in the upper part of each panel.

DISCUSSION

AGE, BODY LENGTH AND COMPONENT COMPOSITION IN RELATION TO TIME AND LOCATION OF ARRIVAL

Data on age composition in biological samples of herring catches from the west coast of Norway, indicate that the herring arrived at the southern grounds in two distinct groups during the period 1992-94. The first group arrived already in late January and comprised mainly 3-5 years old herring. Based on information from fishermen observing the herring acoustically, the abundance of this group was estimated to be only a fraction of what arrived later. The major group arrived around 20 February and comprised mainly older fish, predominated by the 1983 year class. The majority of samples from Hordaland (area 28) and Rogaland (area 08) were obtained with gill nets and the common mesh size used was 66 mm. According to OLSEN (1959), the optimum length-selectivity of gill nets with this mesh size is 31 cm. Selectivity properties of gill nets may vary also with the maturation and condition factor of the fish (FARRAN 1936; HAY & al. 1986, WINTERS & WEELER 1990). Thus, the selectivity of the gillnets may have affected the age composition of herring in the samples from Hordaland (area 28) and Rogaland (area 08). However, we find the observed geographical and temporal differences in age composition representative, based on two main facts. First, the very same gill nets that caught herring predominated by age groups 3-5 years off Hordaland and Rogaland in January and early February, were later in the season found to catch herring predominated by larger and older fish (mainly the 1983 year class). Second, the age composition was similar in samples taken with gill nets, trawl and purse seine within the same period and area (see area 08 in 1992 and 1993 in Fig. 3). Therefore the gill net samples from the southern areas are considered relevant to detect relative changes in age composition, rather than variations due to selectivity.

Body length of herring at ages 3-5 years differed somewhat between year classes and areas. Differences in mean length at age between year classes are common in this stock due to annual differences in environmental conditions (HOLST 1996). Geographical differences in mean length at age are, however, more difficult to explain. One factor of influence could have been differences in selectivity of sampling gears. Another factor of influence could be interference of local herring stocks in the southern areas, which generally have a lower length at age than the Norwegian spring spawners (own unpublished data). Such a possible interference could explain the low body length in 3 years old herring in area 08 in 1992 and 1994, likewise it could explain why the 5 years old were smaller in areas 28 and 08 than in area 07 in all the years 1992-94. On the other hand, typical 'local' herring samples were not included in the analysis, and the proportion mixed with Norwegian spring spawning herring was probably small.

The data on nursery area of origin and length at age indicated that the 3-5 years old herring at the southern grounds, were recruit spawners originating from coastal nursery areas, whereas the 83-

year class originated from the Barents Sea. In the 3-5 years old herring of the year classes 1987, 1988 and 1989, the coastal component contributed with 70-90 %, whereas in the 1983 year class herring at age 5 years and older comprised close to 100 % of the Barents Sea component. Already early in this century the stock was divided into two types based on variations in growth, a northern type with slow growth and a southern type with rapid growth, with northern and southern nursery areas, respectively (LEA 1929; OTTESTAD 1934; RUNNSTRØM 1936). LEA (1929) found that the herring along western Norway left the coastal waters at an age of 3 years in order to recruit to the adult stock feeding offshore, whereas the age at recruitment was 4 years farther north. RUNNSTRØM (1936) studied the spawning "checks" in herring scales and found that herring of the southern type spawned for the first time at age 3-6 years with the main proportion at age 4-5 years, while the ages of the northern type was 4-8 years and 5-6 years, respectively. This is also in agreement with the present data on component composition, of which negligible differences were recorded between spawning areas, but the proportion of the Barents Sea component tended to increase with increasing age. A similar recruitment pattern was observed from the 1930s to the 1980s (HOLST & SLOTTE in press). They found that nursery area of origin had negligible influence on the geographic spawning distribution of a herring year class, once they were fully recruited. However, in young recruiting year classes there was a tendency that high proportions of the coastal component was present at the southern grounds, due to the asynchronous maturation of herring from the two nursery areas. Furthermore, it has been concluded that the age at maturity in herring varies considerably between year classes, whereas the length at maturity is rather constant for all year classes (TORESEN 1986; 1990). Length at maturity has been estimated to 28-29 cm in the 1930s (RUNNSTRØM 1936), 30.9 cm for the period 1946-62 (ØSTVEDT 1964) and 30.0 cm for the year classes 1973-78 (TORESEN 1986). TORESEN (1986) also calculated mean lengths at maturity for the age groups 3, 4, and 5 years of the southern (coastal) component to be 29.6, 30.5 and 31.9 cm respectively. In the present study the length at age 3, 4 and 5 years old herring varied around 29, 31 and 32 cm respectively. Although significant differences in length at ages 3-5 years were found between years and areas, these data correspond well with the previous investigations on length at maturity. Thus, it seems likely that the herring arriving early at the southern areas were mainly recruit spawners.

The present study also shows that the early arrival of recruit spawners at the southern grounds was in contrast to that observed at the main spawning area off Møre, where the smaller fish tended to arrive later in the season. The fact that the herring arrive off Møre in a decreasing order of size has been further demonstrated for the years 1994-96 (SLOTTE & JOHANNESSEN 1997, SLOTTE 1998a). SLOTTE (1998a) found that the herring migrating southwards from the wintering area in Vestfjorden arrived off Møre in a decreasing order of size mainly due to size dependent swimming speed. Thus, two possible explanations are apparent why the young herring arrived at the southern grounds prior to the older individuals. One explanation is simply that the younger herring aiming for the southern grounds commenced the migration from Vestfjorden prior to the rest of the stock. This is a rather speculative explanation, which is not supported by any other studies or biological reasoning. Instead, we hypothesise that the recruits arrived from other wintering areas closer to the southern spawning grounds. This hypothesis is in agreement with previous studies by LEA (1928) and HARALDSVIK (1968, and references therein). In 1916, LEA (1928) observed a similar pattern as in this study, and found that recruit spawners arrived simultaneously along the south-western coast, from Florø to Siragrunnen, prior to the arrival of old spawners at Karmøy. He further suggested that the recruit spawners came from feeding and wintering areas in the northern North Sea. This was later supported by HARALDSVIK (1968) who found a group of Norwegian spring spawning herring mixed with spring- and autumn spawning North Sea herring in the northern parts of the North Sea, and this group was more similar to the herring spawning south, compared with north of Møre. In the summer of 1991, SIMMONDS & al. (1992) estimated that 23.000 tonnes of Norwegian spring spawning herring was mixed with North Sea herring in the northern North Sea. It is not unlikely that this herring wintered in the same area and entered along the west coast of Norway in late January. Thus, the most probable hypothesis suggests that the herring which occurred along the west coast in late January, came from wintering areas in the northern North sea.

AGE AND BODY LENGTH IN RELATION TO SPAWNING TIME

Although the recruit spawners and repeat spawners arrived at the southern spawning areas at different times, the data on maturity stages indicated that the spawning occurred simultaneously. These findings are not in accordance with investigations on size specific maturation and spawning time in 1994-97 by SLOTTE (1998a). He found evidence that the level of maturity in the wintering population in Vestfjorden (1994-97) increased with increasing body length up to approximately 32 cm, after which it stabilised. This was suggested to be due to an increasing proportion of recruit spawners with decreasing body lengths in herring smaller than 32 cm. He also found that the onset of maturation was delayed in the recruit spawners compared to the repeat spawners, mainly due to differential energetic capacities. However, the length specific differences in maturity level in the data from Møre (1995-96) were not as distinct as in the wintering area (SLOTTE 1998a), similar to that observed off Møre in the present study (1992-94). This was supported by the fact that spawning also was delayed with decreasing condition, and that small herring and herring with low condition tended to spawn later in the season further north than Møre, i.e. closer to the wintering area (SLOTTE 1998a). Thus, the young age groups spawning off Møre and farther south off Hordaland and Rogaland were probably in good condition compared with their conspecifics to the north of Møre, and therefore enabled to spawn at the same time as the older individuals. Since the recruit spawners in the southernmost areas probably originated from a more southern wintering area than Vestfjorden, one cannot rule out that other factors, like differential day length and/or temperature, may have caused a deviation from the size dependent maturation pattern observed in Vestfjorden.

The data on maturity stages also indicated that the spawning started at about the same time in the southern areas as off Møre, whereas the spawning period was prolonged off Karmøy and further south compared to that off Møre. This was supported by data on back calculations of larval hatching curves (JOHANNESSEN & al. 1995a, b), which indicated peak spawning in primo March off Møre and ultimo March off Karmøy during 1992-93. The repeat spawners that dissented from the main spawning fraction off Møre, had to migrate an additional distance towards the southern grounds. Due to the longer migration distance the herring would have to remain in a ripe stage (hold maturation) for a longer period. This is probably the reason why the spawning season is prolonged and the peak spawning is delayed at the southernmost grounds compared to that off Møre. This may also explain why the herring off Karmøy in general were either in a ripe or spawning stage throughout March. Hydroacoustical recordings of herring in the Karmøy area also confirmed that the herring arriving at the southern grounds in March, immediately 'settled' at the bottom to spawn, and left the area shortly after the spawning had culminated (NØTTESTAD & al. 1995, SLOTTE 1998b).

MERISTIC CHARACTERS IN RELATION TO YEAR CLASS AND AREA

The differences in meristic characters observed between areas and year classes could be tracked to hereditary or environmental factors. The vertebral count is to some extent found to be affected by some hereditary component (HEMPEL & BLAXTER 1961; LINDSEY 1988). The number of vertebrae is fixed at hatching, but may be modified during the incubation period by variations in environmental factors like temperature (negative correlation), light and salinity, or the amount of oxygen and carbon dioxide (LINDSEY 1988). Thus, vertebral counts may indicate specific environmental conditions under which the fish eggs were incubated. SCHNAKENBECK (1931) and RUNNSTRØM (1933, 1941a) demonstrated both geographical and temporal differences in vertebral count during the spawning season in Norwegian spring spawning herring. SCHNAKENBECK (1931) differentiated between two different herring races. This was, however, refuted by RUNNSTRØM (1933, 1941a) who addressed the observed differences to geographical and temporal differences in age composition, indicating that the vertebral count differed between year classes due to differential environmental conditions at hatching grounds between years. He demonstrated that the vertebral count in 0-group fish and mature year classes of Norwegian spring spawning herring tended to increase southwards from Møre to Siragrunnen. He suggested that the number of vertebrae was inversely correlated with temperature, as the temperature decreased southwards due to stronger influence of the cold Baltic outflow along the south-western coast of Norway in winter and spring. Thus, the present differences in vertebral count between year classes of herring may be attributed to annual differences in temperature. However, negligible differences in vertebral count were found between areas within a year class, which may indicate that the herring were hatched within the same area This is likely, since most of the herring in the 1980s spawned off Møre.

The gillraker count is also found to have a hereditary component (SVÄRDSON 1952). On the other hand, the number of gillrakers is not fixed at hatching as is the vertebral count. This number may increase with fish size, but the fish size at which the final gillraker count is reached, may vary (MCHUGH 1954; KREFFT 1958; LINDSEY 1981; MACNEILL & BRANDT 1990). This is in accordance with the positive relation found between gillraker count and herring body length in the present study. However, the gillraker count may also be subject to environmental modifications due to variations in available food (ANDRAU 1969, LINDSEY 1981). This may explain the differences in gillraker count observed between herring in the wintering area in Vestfjorden and the herring at the spawning grounds. In 1992 the gillraker count of herring at age 3 and 4 years were significantly lower at the southern grounds than in the wintering area in Vestfjorden, although the individuals from the southern grounds had larger mean body length. Thus, these differences in gillraker count may indicate differences in conditions under which the herring have grown up during their first years after hatching.

LARGE SCALE MIGRATIONS AND HOMING

Data on tag returns during the period 1990-96 from tagging experiments at the southern grounds in 1990-93, clearly show that the herring spawning at the southern grounds had similar migration pattern as the rest of the spawning stock, i.e. feeding in the Norwegian sea, wintering in Vestfjorden and southward spawning migration towards Møre and even further, in subsequent years. Since the herring were not tagged in Vestfjorden, one cannot be certain that the herring at the southern grounds arrived from Vestfjorden. However, for repeat spawners, which were predominated by the 1983 year class, this seems likely given the late arrival at the spawning grounds, and given information from fishermen of southward migrating schools off the Sogn district. For the recruit spawners arriving early at the southern grounds, we find it more likely that they came from other wintering areas than Vestfjorden. However, some herring tagged at the age of 3-5 years were subsequently recovered in Vestfjorden, off Møre and during post-spawning migration from the southern grounds towards Møre. These were probably recruit spawners at the time of tagging, which could have wintered in the northern North Sea prior to first spawning, and subsequently copied the migration pattern and wintering area of the repeat spawners in consecutive years.

A frequently accepted statement in herring biology concludes that individual fish return year after year to the same spawning grounds as they spawned for the first time (HOURSTON 1982; WHEELER & WINTERS 1984). However, the tag recovery data were not sufficiently supportive to conclude that herring returned to the southern grounds. Only two tags from the 1983 year class were recovered from the southern grounds. In addition, three tags were recovered from herring catches in fjords to the south and north of the release sites off Karmøy. We suggest that these tag recoveries came from specimens of local coastal or fjord herring populations. Furthermore, many recovered tags were found one or more years later in maturing herring in February off Møre or farther north, and it is inconclusive whether these individuals would continue migration farther south. The Norwegian spring spawning herring fishery to the south of 61°N was closed during 1990-96, due to conservative regulatory actions (RØTTINGEN & SLOTTE 1998), which consequently reduced the potential to calculate any homing rate.

There are, however other factors, which could prevent high homing rates of herring to the southernmost grounds. During the period 1989-1998 the fraction spawning at the southern grounds was very small, estimated to be less than 4 % of the spawning stock (JOHANNESSEN & al. 1995a; RØTTINGEN & SLOTTE 1998). This could be due to low competition for suitable spawning sites at Møre. Also herring could choose not to migrate to the southernmost grounds due to migration constraints. There are data that indicate that herring at the southern grounds comprise 'elite' herring, being larger and/or in better condition than the average individuals of the stock: (1) The herring migrating to spawn at Siragrunnen/Lista undertake a migration distance up to 1 500 km longer than the herring spawning off Lofoten; (2) Data on energy loss show that the non-feeding herring migrating southwards from the wintering area have 3-4 times higher relative weekly energy loss than during the wintering period, and the relative energy loss decreases with fish size (SLOTTE in press); (3) In 1995-96 the herring body length and condition increased with increasing migration distance from the wintering area, from Lofoten in the north to Møre in the south (SLOTTE 1998a); (4) This relationship between fish size/condition and migration distance was supported with data from 1997 (SLOTTE & DOMMASNES 1997) and 1998 (SLOTTE & DOMMASNES 1998), when adequate data were recorded also at the southern grounds.

SLOTTE (1998a) demonstrated that the larval survival would increase at the southernmost grounds due to higher temperatures during the larval stage. Furthermore, it was argued that there also are three other main benefits with spawning at the southern most grounds. First, there is an increasing probability southwards that larvae will drift into coastal areas and fjords, i.e. larva will stay at higher temperatures through the juvenile stage. Second, by spawning farther south the larvae will also be dispersed to a wider range of environments along the coast and in the Barents Sea through differential retention and drift routes with the coastal current. Thus, by spreading the larvae from nursery areas in the south towards north, the progeny may overcome the variations in environmental conditions, which may ultimately increase the overall survival. Third, by migrating southwards the herring could avoid competition from other herring, and thus reduce density dependent mortality of eggs and larvae. However, spawning at the southern grounds involves significant migration costs, and Slotte (1998a) demonstrated by a model that optimal spawning ground was farther south with increasing fish size. Spawning at the southernmost grounds was only predicted in the largest fish, given high larval mortality rates, i.e. larval stage should be shortened. Thus, potential homing towards the southernmost grounds, or potential migration to the southernmost grounds to increase the survival of progeny, is limited by the state of the fish (size, condition or energy storage). In other words, an individual does not home to or visit these grounds if this diminishes the probability of survival until next spawning, or more specifically, decreases its future fitness. Since the spawning grounds at Karmøy, Egersund and Siragrunnen are within an extended distance from the wintering area, it is likely that the spawning fraction and homing rate is lower in this area compared to the main spawning area off Møre. Thus, the main factors that could increase the southern fraction, given wintering in the Vestfjord system, would be an increasing population size, increasing fish lengths and/or increasing fish condition in the population.

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