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A sonar study of the migration pattern of Norwegian spring-spawning herring (*Clupea harengus* L.) in July

by

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ABSTRACT

About 700 schools of Norwegian spring-spawning herring (*Clupea harengus* L.) were tracked by multi-beam sonar during transect surveys in the Norwegian Sea in July 1995 and 1996. This herring stock usually concentrates in the area west of Lofoten in July-August after its feeding migration in the Norwegian Sea, and the herring were thus expected to swim eastwards towards the coast in July. The survey area was divided into three sub-areas based on distance from the main wintering area in Vestfjorden, habitat and the age of herring. In 1995 a total of 502 schools were classified as migrating, stationary or avoiding, of which 31 % were migrating, 61 % stationary and 8 % avoiding schools. The schools were located shallow (0-60 m) during day and night, suggesting that they were feeding. A high proportion of feeding schools, with high dynamic tendencies, may thus explain the prevalence of stationary schools. Migrating schools had a mean migration speed of 0.66 m s^{-1} , and migrated westwards in coastal areas. Stomach samples from trawl and high acoustic densities of plankton near the continental slope suggested that feeding conditions were better here than in coastal areas, and the schools probably left coastal areas because of sub-optimal feeding conditions. Herring probably track their prey by a flexible combination of predictive (genetic, learning) and reactive orientation mechanisms. By migrating westwards the herring may have improved their feeding conditions, thus extending their feeding season.

INTRODUCTION

The Norwegian spring-spawning herring is both ecologically and economically one of the most important clupeid stocks in the world (Vannuccini 1995; Dragesund & al. 1997; Anon. 1998). In the Barents Sea – Norwegian Sea ecosystem the large-scale migration of herring is an important link in the food web, by making zooplankton in central parts of the Norwegian Sea available for more coastal species (Pavshstiks 1959; Dragesund & al. 1980, 1997; Hamre 1990, 1994; Røttingen 1990, 1992; Skjoldal & al. 1993; Melle & al. 1994). Migrations between spawning, feeding and wintering areas have displayed wide variations in the course of the past century (figure 1, Dragesund & al. 1980, 1997; Røttingen 1992), probably influenced by environmental factors, herring stock size and fishery (Jakobsson 1969, 1980; Dragesund & al. 1980, 1997). In the past decade the main migration pattern has been relatively constant (Røttingen 1992; Dragesund & al. 1997). They spawn in the period February-April along the Norwegian coast, then migrate into the feeding area in the Norwegian Sea and finally, in September-October, reach their wintering areas in Vestfjorden, where they stay until the start of the spawning migration at the beginning of January (Røttingen 1992; Dragesund & al. 1997). The time of migration to the overwintering areas varies, probably depending upon prey availability. Røttingen (1992) observed that herring entered the wintering areas in September, whereas Huse & Ona (1996) state that: “The herring start to enter the fjords in October, when their principal food *Calanus finmarchicus* L. disappears from the surface layers ...”. Feeding herring schools have been observed as late as in September (Pavshstiks 1959; Misund 1993b).

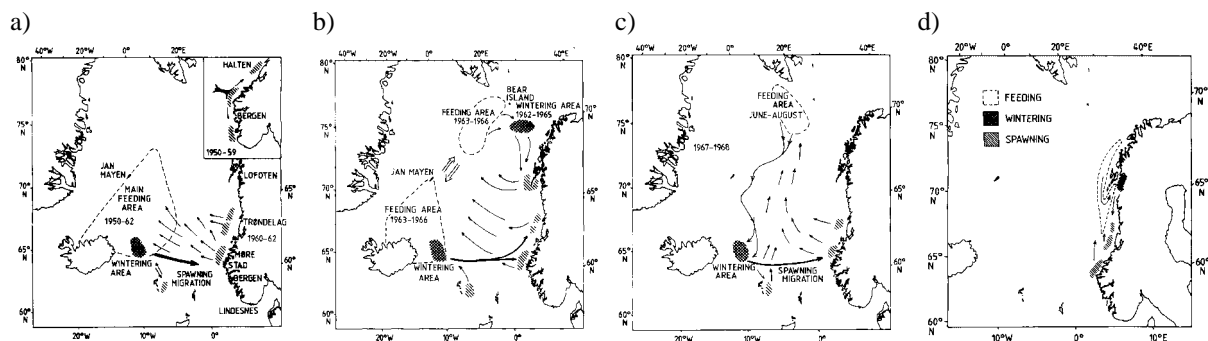


Figure 1 Variations in migration pattern of Norwegian spring-spawning herring (*Clupea harengus*). a) 1950-62. b) 1963-66. Double arrows indicate a separation of the herring stock in two separate areas. c) 1967-68. The two components rejoined and adopted a migration pattern which was a combination of the two earlier ones. d) 1974-86. (from Dragesund & al. 1997).

Herring may use predictive (genetic factors or learning) and reactive (kinesis¹, near-field orientation or comparisons of habitat quality) orientation mechanisms during migration (Harden Jones 1968; Fernö & al. 1998). Predictive orientation mechanisms involve orientation towards areas with supposedly higher habitat quality without the use of information from the near field. A combination of reactive and predictive orientation mechanisms may provide herring with a flexible migration pattern, adapted to both predictable and unpredictable conditions (Fernö & al. 1998).

¹ Variation in generalised, non-directional, random movement activity caused by variation in stimuli intensity (Gunn & al. 1937).

The distribution, swimming patterns and dynamics of herring schools may be influenced by internal (condition, swimming capacity, maturation, experience) and external factors, of which the latter may be divided into biological (predators, competitors, prey) and physical (temperature, currents, light, oxygen) factors (i.e. Harden Jones 1968; Radakov 1973; Pitcher & Parrish 1993; Skjoldal & al. 1993; Jakobsson & Østvedt 1996; Fréon & Misund 1999). The herring scarcely feed during wintering and spawning (Nøttestad & al. 1996; Axelsen & al. 1998; Slotte 1999), and the energy-demanding annual migration (Nøttestad & al. 1999; Slotte 1999) thus requires an accumulation of large energy reserves during the feeding period. Consequently, food density is a crucial environmental factor during the feeding migration (Pavshikov 1959; Østvedt 1965; Jakobsson & Østvedt 1996; Dragesund & al. 1997; Nøttestad & al. 1999). In some periods of the year, low temperatures and light levels are factors that limit the spatial distribution of herring (Jakobsson 1969; Blaxter 1975; Melle & al. 1994; Jakobsson & Østvedt 1996), but these factors are probably not very important in July, when the herring are found in the relatively warm eastern part of the Norwegian Sea (Helland-Hansen & Nansen 1909; Røttingen 1992; Dragesund & al. 1997) and there is constant light (Zusser 1958 in Blaxter 1975; Harden Jones 1968). Schooling constitutes a quite efficient defence against predators (Pitcher & Parrish 1993; Nøttestad & Axelsen 1999), making it possible to survive even with high densities of predators. Lack of prey, however, will gradually deplete the energy reserves, reducing spawning success (Slotte 1999) and eventually causing death. Even though factors such as length, maturity, condition, competition, predation, temperature, light and currents are important (Fernö & al. 1998; Nøttestad & al. 1999), the key factor determining the herring's behaviour and migration pattern in the feeding period is thus probably the availability of suitable prey.

The migration patterns in herring have to be studied *in situ*, and acoustic methods (Misund 1997) are suitable for such studies. The herring are mainly located in the upper part of the water column in the Norwegian Sea in July (Harden Jones 1968; Røttingen 1988), and multi-beam sonar is therefore the best available tool for studying behaviour (Bodholt & Olsen 1977). Vessel avoidance (Olsen & al. 1983) has been observed in herring, capelin and mackerel among other species (i.e. Misund 1993a; Hafsteinsson & Misund 1995; Vabø 1999) and may be a problem in such studies. The avoidance may vary with season (Mohr 1969; Olsen 1971; Misund 1994) and sonar conditions (Misund & Aglen 1992; Misund 1994). Hafsteinsson & Misund (1995) classified herring schools as migrating, avoiding or undecided in order to separate vessel-generated behaviour from natural migration behaviour.

The effect of external factors (predation risk, prey availability, light, temperature) on diel vertical migration in fish has been studied thoroughly, both *in situ* (i.e. Munk & al. 1989; Kaartvedt & al. 1996; Torgersen & al. 1997) and by modelling (i.e. Clark & Levy 1988; Mangel & Clark 1988; Hugie & Dill 1994; Rosland & Giske 1994; Giske & al. 1998). To the best of the authors' knowledge, horizontal migration and its influencing factors have received less attention. However, several studies on selective tidal transport (i.e. Harden Jones 1957, 1962, 1977; Arnold & al. 1994; Castonguay & Gilbert 1995) and models of annual migrations (Fiksen & al. 1995; Huse & Giske 1998) have been published. In Norwegian spring-spawning herring the main migration pattern has been studied by tagging experiments (Fridriksson & Aasen 1950, 1952; Røttingen & Røttingen 1991) and acoustic observations of distribution during certain periods of the year (i.e. Røttingen 1992; Anon. 1995, 1996b; Vilhjálmsson & al. 1997; Misund & al. 1998b), whereas few studies have observed the migration pattern of individual herring schools (Hafsteinsson & Misund 1995; Misund & al. 1997). For abundance surveys, knowledge of the migration pattern of a stock is crucial, both in planning the survey and in correcting the resulting abundance estimate (MacLennan & Simmonds 1992;

Gunderson 1993; Hafsteinsson & Misund 1995; Axelsen & Misund 1997). In the present study the migration pattern of herring schools in July 1995 and 1996 were studied using sonar during routine surveys. As the herring schools in July-August concentrate in the coastal areas near their main wintering area, an easterly migration pattern was expected.

MATERIALS AND METHODS

The behaviour of 695 schools of Norwegian spring-spawning herring was studied during surveys in the Norwegian Sea with R/V “Johan Hjort” in the periods 7 July to 2 August 1995 and 9 to 19 July 1996. While the vessel followed a predetermined survey track at 10-12 knots (figure 2), schools within 50 to 400 m distance from the vessel were continuously recorded with the 24 kHz multi-beam sonar Simrad SR 240 (Johannessen 1992). The sonar provided information about the schools’ swimming speed and bearing, distance from the vessel, depth and horizontal area. The sonar beam had a width of 90° and was oriented 45° to the port side, provided the wave direction permitted this (otherwise 45° to the starboard), with a tilt angle of 5-10°. 20 log R Time Varied Gain (TVG) was applied throughout the survey. The schools appearing in the sonar beam were tracked horizontally using the sonar’s target tracking function and vertically by manual adjustment of the tilt angle. The geographical position of the vessel was recorded from the GPS at the beginning of each acoustic registration.

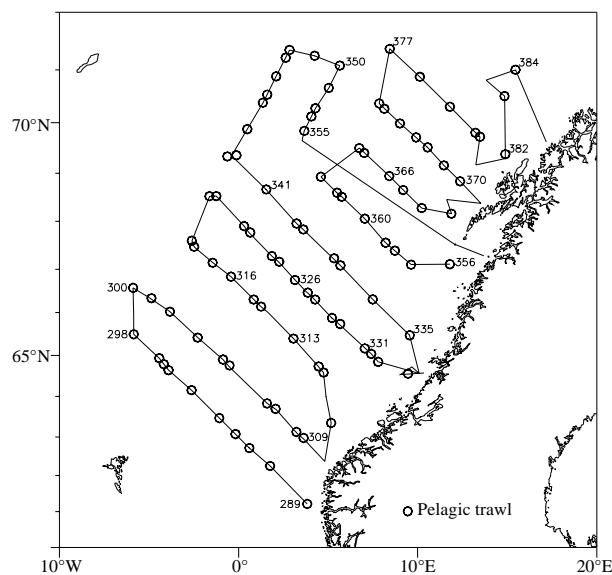


Figure 2. Survey track and trawl stations, R/V “Johan Hjort” 7 July-2 August 1995 (from Anon. 1996a).

Each acoustic school registration was classified as herring, blue whiting (*Micromesistius poutassou*) or mackerel (*Scomber scombrus*) on the basis of pelagic trawl samples and scrutiny of the echo traces. Herring dominated in the survey area. Length and age (fish-scales) of individual herring were measured (Anon. 1996a) and stomach samples collected (Dalpadado & al. 1996) from the trawl catches. MOCNESS was used at several stations for plankton sampling (Anon. 1996a; Dalpadado & al. 1996). A 38 kHz Simrad EK 500 echo sounder connected to the Bergen Echo Integrator (BEI) system (Knudsen 1990) was operated continuously throughout the survey. Wind conditions during the survey period were very

variable, ranging from light air (force 1) to near gale (force 7).

The survey area was split into three sub-areas (figure 3) based on distance to the herring's main wintering area in Vestfjorden, habitat (continental shelf, continental slope or open sea) and the age of herring in trawl samples (young herring: < 8 years, old herring: ≥ 8 years, figure 4). A total of 11 schools recorded outside these defined sub-areas were omitted from the analysis. Sub-area A was situated above the continental shelf and slope, and here the herring had a median length of 24 cm and 3-year-old fish dominated. The eastern part of sub-area B is above the continental shelf, while the northwestern part is in the open sea. The dominant length and age of the herring were 27 cm and 4 year, respectively. Sub-area C is entirely in open sea, and here the median length was 32 cm and 5- and 12-year-old herring dominated.

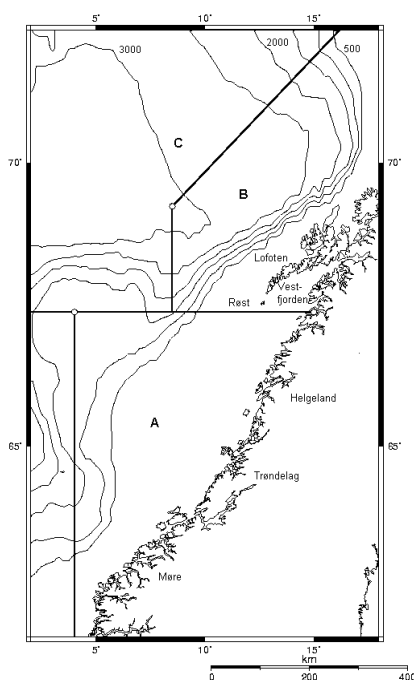


Figure 3. Sub-areas based on distance to the main wintering area in Vestfjorden, habitat (continental shelf, continental slope and open sea) and age of herring in trawl catches (< 8 years, ≥ 8 years, figure 4). Depth (m) is indicated.

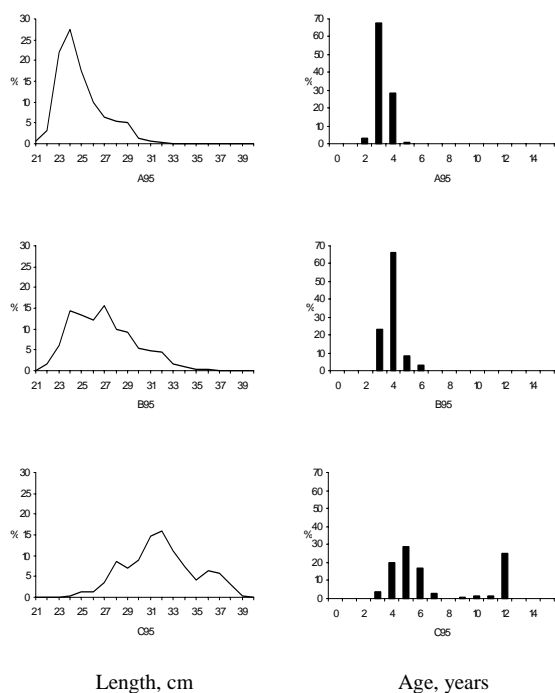


Figure 4. Distribution of length and age of herring by percentage in sub-areas A, B and C in 1995. Trawl stations: A: 329, 331, 333, 336; B: 368-370, 372; C: 350-352, 377. The data are from the survey report (Anon. 1996a). $n_A = 400$, $n_B = 400$, $n_C = 257$.

Some of the registered schools were omitted to reduce bias and ensure high quality of the data material. A possible source of bias was that noise sometimes was interpreted as schools and consequently tracked. In an attempt to exclude such artificial schools, three school types were excluded. Schools with a mean swimming speed above 2.0 m s^{-1} ($n = 43$) were excluded, as the sustained swimming speed of herring of the observed size is below this value (He & Wardle 1988). This may have excluded some avoiding schools, which may have a higher swimming speed than migrating schools (Olsen & al. 1983; Hafsteinsson & Misund 1995). Additionally, some artificial schools with “swimming speed” just below 2 m s^{-1} may have been erroneously included. However, the key issue in this study was to obtain an objective measure of the migration pattern of herring, not the frequency of avoidance. School

registrations lasting less than 21 pings ($n = 76$) were omitted, due to low data precision during short registration periods (Hafsteinsson & Misund 1995). Finally, schools were excluded ($n = 26$) if the vessel heading changed by more than 20° during the recording period, as large changes in vessel direction distorted the school movements (figure 5).

To plot the movement of each individual school in relation to the vessel and to calculate mean swimming speed², mean depth² and direction of migration from the sonar data, a computer program (Kvamme 1999) was developed in SAS 6.03 (SAS Institute Inc. 1988). A behavioural analysis of the movement of each individual school in relation to the vessel, based on the method developed by Hafsteinsson & Misund (1995), classified the swimming pattern as migrating, avoiding or stationary (figure 5). **Migrating** schools were moving in straight lines with a clearly defined direction (less than 45° change in direction). In longer-lasting registrations (> 2 min), large changes in bearing ($> 45^\circ$) were accepted, as long as the schools had defined swimming directions when the trend in direction during the entire recording was examined. **Avoiding** schools were either: **1**) changing their sustained bearing (maintained for a minimum of 10 s) by more than 45° and heading away from the vessel, thereafter maintaining (potential changes less than 45°) the new bearing until the vessel passed or the school disappeared from the sonar beam; or **2**) changing their sustained bearing by more than 45° and approaching the vessel track. When in front of the vessel, the school might subsequently change its bearing by more than 45° in any direction. This latter type of avoiding schools might have been trapped between the lobes of high sound intensity to the sides of the vessel when trying to avoid the noise, thus being driven forwards by the moving vessel (Misund & Aglen 1992; Hafsteinsson & Misund 1995). **Stationary** schools frequently changed bearing and performed irregular or minor movements in the course of the observation period.

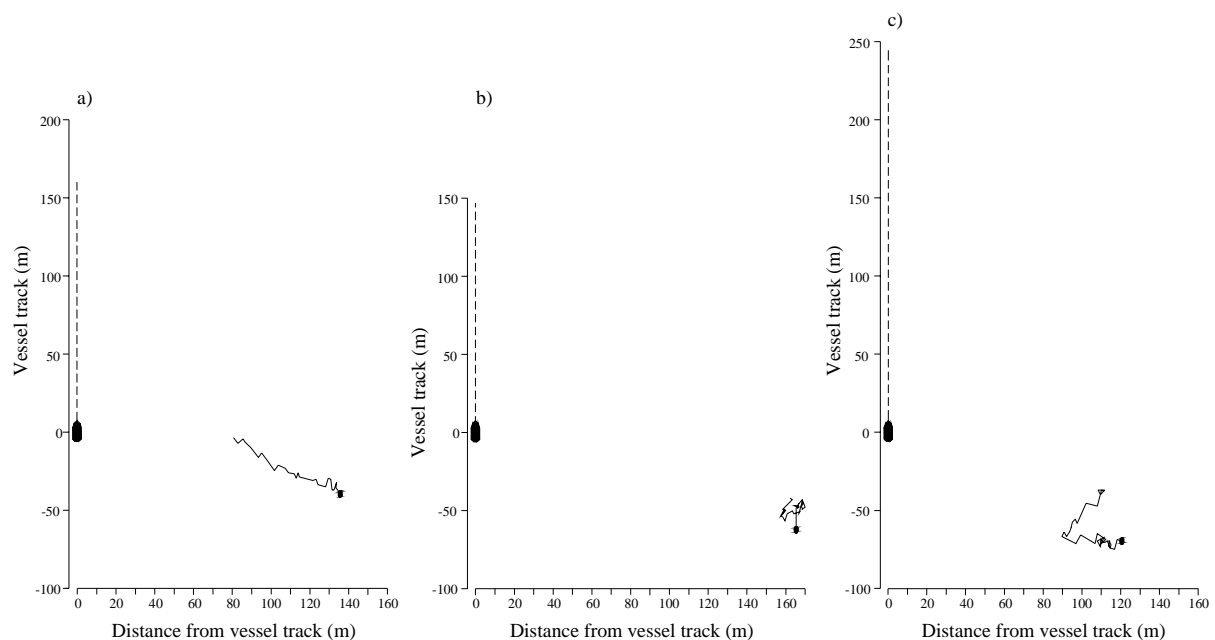


Figure 5. Examples of each behavioural category. Vessel movement is parallel to the y-axis. Starting points for both school and vessel are indicated. a) Migrating school. b) Stationary school. c) Avoiding school.

² Only from 1995. In 1996 the swimming speed and school area was measured by a different method, making the estimates non-comparable to the 1995-estimates (Kvamme 1999).

Swimming speed was measured as the movement of the school's acoustic centre of gravity in relation to the earth's surface, which gives an estimate of the distance covered by a school per unit time. In a study of migration patterns this is a more relevant parameter than the actual speed at which an individual herring within the school is swimming. The sonar produced estimated swimming speed in knots for each ping. The SAS program converted these values to m s^{-1} and calculated the means. Swimming speeds in body lengths s^{-1} were calculated by dividing the mean swimming speed by the corresponding sub-area median length of the school (A: 0.24 m, B: 0.27 m, C: 0.32 m, figure 4). The sonar also provided estimated school depth as $\{[\text{school-vessel distance} * \sin(\text{tilt angle})] + \text{transducer depth}\}$. Due to the sonar's inaccuracy in measuring depth, this is not an absolute value but rather an index.

Each school's (j) migration speed, S_{M_j} (m s^{-1} , rate of movement in the direction of migration), and direction of migration, β_{M_j} ($^\circ$, direction of movement during the acoustic registration), was calculated from the swimming speed, S_{ij} , and bearing, α_{ij} (Hafsteinsson & Misund 1995).

School j's rate of movement in northern ($S_{N_{ij}}$ [m], 0°) and eastern ($S_{E_{ij}}$ [m], 90°) direction for each ping i was calculated as:

$$S_{N_{ij}} = S_{ij} \times \cos(\alpha_{ij}) \quad (1)$$

and

$$S_{E_{ij}} = S_{ij} \times \sin(\alpha_{ij}), \quad (2)$$

respectively.

The migration speed was calculated as:

$$S_{M_j} = \sqrt{\left(\frac{1}{N} \sum_{i=1}^N S_{N_{ij}}\right)^2 + \left(\frac{1}{N} \sum_{i=1}^N S_{E_{ij}}\right)^2} = \sqrt{S_{N_j}^2 + S_{E_j}^2} \quad (3)$$

The direction of migration was determined according to:

$$\beta_{M_j} = \arccos\left(\frac{S_{N_j}}{S_{M_j}}\right) = \arcsin\left(\frac{S_{E_j}}{S_{M_j}}\right) \quad (4)$$

A rough estimate of each school's horizontal area was calculated from its length along the sonar beam on the sonar display (lw , cm), measured by ruler during the survey. The school's length along the sonar beam (LW) was calculated as:

$$LW = (lw \times s \times \cos\alpha) - (c \times t_s/2) \quad (5)$$

In this equation s is the sonar converting factor (ratio between the vessel-school distance and the corresponding distance on the screen, $s \approx 30 \text{ m cm}^{-1}$ with a range of 400 m), α the tilt angle ($\alpha \approx -7^\circ$), c the sound speed ($c \approx 1500 \text{ m s}^{-1}$) and t_s the pulse length ($t_s \approx 2 \times 10^{-3} \text{ s}$). During the survey, there was no time left to measure the width of the school on the screen

across the sonar beam (cw), as required in the formula for school area used in Misund (1990). A constant ratio of 3:2 between CW (the school's real width across the sonar beam) and LW was therefore assumed (Misund 1990), and the school area (m²) was hence calculated as:

$$A = \frac{\pi(CW \times LW)}{4} \approx \frac{3\pi(LW)^2}{8} \quad (6)$$

Due to the assumption made, this parameter is not an accurate absolute measure of school area, but should be a valid index to compare school sizes between different sub-areas or behavioural categories.

Mean, standard deviation, maximum and minimum values were calculated for all parameters. Statistical tests assumed a significance level of 0.05 unless otherwise stated. Most of the parameters had nonparametric distributions, and nonparametric tests were therefore applied. Potential differences in the distribution of behavioural categories between the sub-areas were tested by a chi-square test (Zar 1996). The migration directions in the different sub-areas were compared by studying the rose diagrams (see figure 6). Kruskal-Wallis rank tests (Zar 1996) were used to test for differences in swimming speed, migration speed, school area and depth between sub-areas and behavioural categories. Where significant differences were found, a post-hoc comparison by a Mann-Whitney U test was made in order to compare two and two groups. The significance level was set to $\alpha^* = 0.05/c$ (Bonferoni's method, Howell 1987), where c is the number of tests in the *post hoc* comparison. Statistically significant differences are indicated in the text as * for p-values less than 0.05 ($[0.05/3] = 0.0167$ with three *post hoc* tests, as for comparisons of sub-areas and behavioural categories), ** for p-values less than 0.01 (0.0033) and *** for p-values less than 0.001 (0.0003).

RESULTS

As expected prior to the survey, the herring were concentrated relatively close to the coast in July. The schools were patchily distributed, with the highest frequency of recordings in sub-area A and the lowest in sub-area C (table 1). South of 67.5° N schools were mostly recorded east of 4°E, and mainly in the northern part of sub-area A (figure 7). North of 67.5°N schools were only registered east of 5.5°E. In mid-July, the largest distance between a school and the innermost parts of the main wintering area (Vestfjorden) was about 930 km, observed in sub-area A. At the end of July the maximum distance observed was about 560 km.

The prevalence of the observed behavioural categories differed among the sub-areas ($\chi^2 = 10.70$, *). Sub-area A differed the most, with a higher prevalence of migrating and avoiding schools and fewer stationary schools than in the other sub-areas. Migrating schools were relatively common in sub-areas A and C, but stationary schools dominated in all sub-areas, with a total of 60.8 % stationary schools. There were generally few avoiding schools.

The dominant direction of migration among migrating schools was westerly (figure 6). The mean directions of migration were south-westerly in sub-areas A (231°) and B (229°), whereas no dominant direction could be detected in sub-area C. This means that the schools did not swim towards the coast, as had been expected. When we studied the direction of migration with a finer resolution, within the sub-areas (figure 7), differences between the

Table 1. The relative occurrence of behavioural categories in the sub-areas in 1995 as percentages (numbers in parentheses).

Sub area	Behavioural category			Total
	Migrating	Stationary	Avoiding	
A	35.6 (94)	54.9 (145)	9.5 (25)	52.6 (264)
B	24.1 (40)	68.1 (113)	7.8 (13)	33.1 (166)
C	31.9 (23)	65.3 (47)	2.8 (2)	14.3 (72)
Total	31.3 (157)	60.8 (305)	8.0 (40)	100 (502)

eastern and western parts were found within sub-areas A and B. Near the coast, a westerly or southerly direction dominated in both sub-areas. However, in the western part of sub-area A (west of 8°E) an easterly migration direction was dominant. In the western part of sub-area B (west of 12.5°E) there was wide variation, similar to sub-area C. The results from July 1996 showed that in that year the dominant direction of migration near the coast was westerly (figure 6). Stationary schools displayed much the same direction of movement as migrating schools, although the variation among the former group was higher. The direction of migration among avoiding schools mainly corresponded to the vessel's heading, and differed from migrating and stationary schools.

The overall mean swimming speed was 0.73 m s^{-1} ($\text{sd} = 0.40 \text{ m s}^{-1}$) or $2.85 \text{ body lengths s}^{-1}$ ($\text{sd} = 1.63 \text{ bl s}^{-1}$), and the mean migration speed was 0.51 m s^{-1} ($\text{sd} = 0.38 \text{ m s}^{-1}$) or 2.00 bl s^{-1} ($\text{sd} = 1.56 \text{ bl s}^{-1}$). Migrating schools had mean swimming and migration speeds of 0.83 m s^{-1} (3.24 bl s^{-1}) and 0.66 m s^{-1} (2.57 bl s^{-1}) respectively, whereas the mean speeds of stationary and avoiding schools were generally lower and higher, respectively (figure 8). A high degree of bias in school area resulted in a large mean school area ($8\,890 \text{ m}^2$, $\text{sd} = 8\,548 \text{ m}^2$). However, in July 1996, a more objective method for measuring school area was used, and the results showed that the herring schools in this period usually were small (mean = 434 m^2 , $\text{sd} = 269 \text{ m}^2$). The recorded school area in 1995 should be treated as an index. All the schools recorded by the sonar and echo sounder were positioned from the surface down to about 60 m (mean depth about 20 m).

Swimming and migration speed, school area and depth were compared between sub-areas within each behavioural category (figure 8). The mean swimming speed was generally highest in sub-area A and lowest in sub-area B. Migrating schools had a higher swimming speed in both sub-areas A (***) and C (***) compared to sub-area B. For the migration speed there was a trend in the direction of higher mean migration speed in sub-areas A and C compared to B. Sub-area A generally contained larger schools than B and C. The sub-areas differed only marginally concerning school depth.

Swimming and migration speed, school area and depth were compared across the behavioural categories within each sub-area (figure 8). Avoiding schools had generally the highest and stationary schools the lowest mean swimming speed. The mean migration speed was generally lower for stationary schools than either migrating or avoiding schools. There were no significant differences between the behavioural categories regarding school area, and only small differences in school depth.

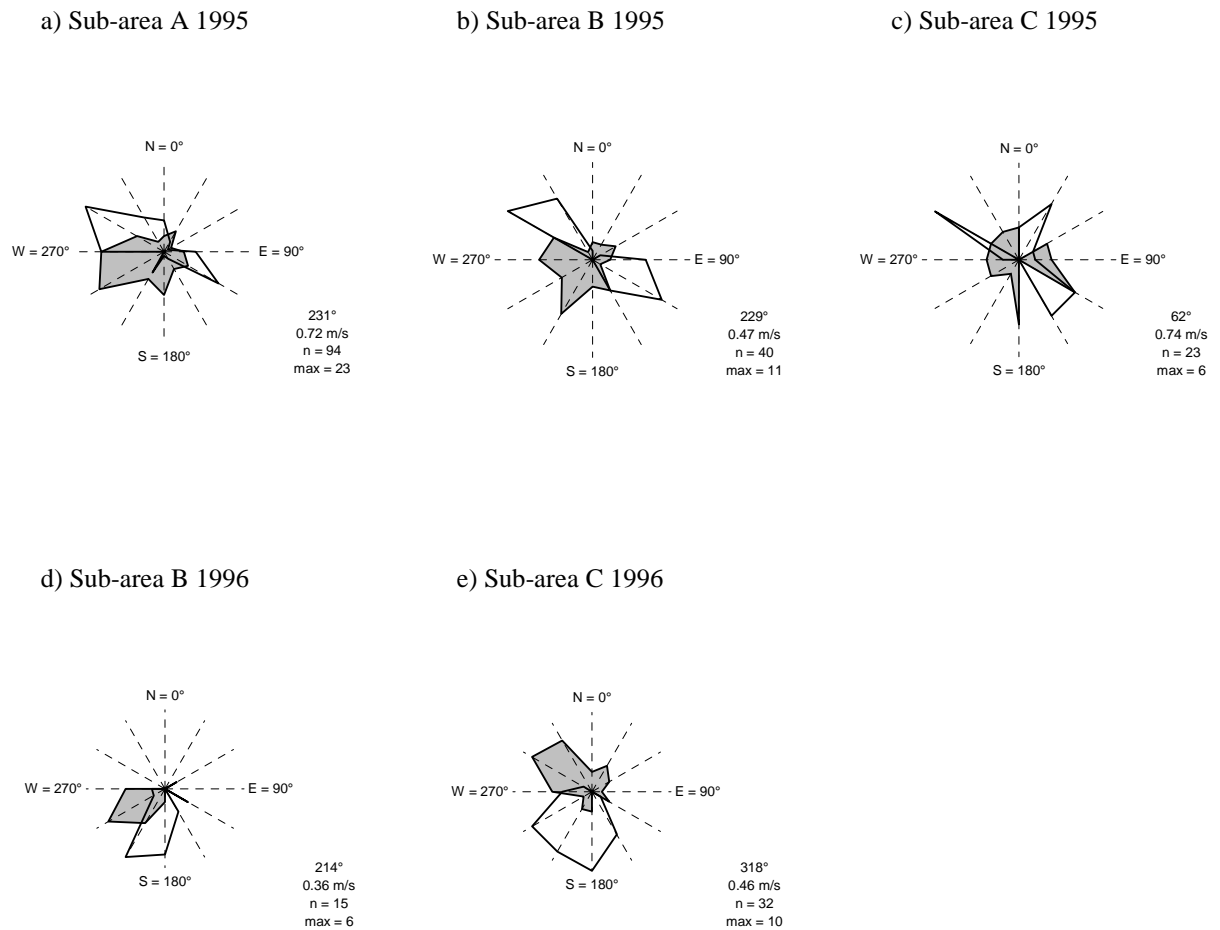


Figure 6. The direction of migration (grey) of migrating herring schools and the vessel heading (white). The class intervals are 30°. Mean direction of migration, mean migration speed, number of observations and maximum axis value (length of the axis) for the different sub-areas are given.

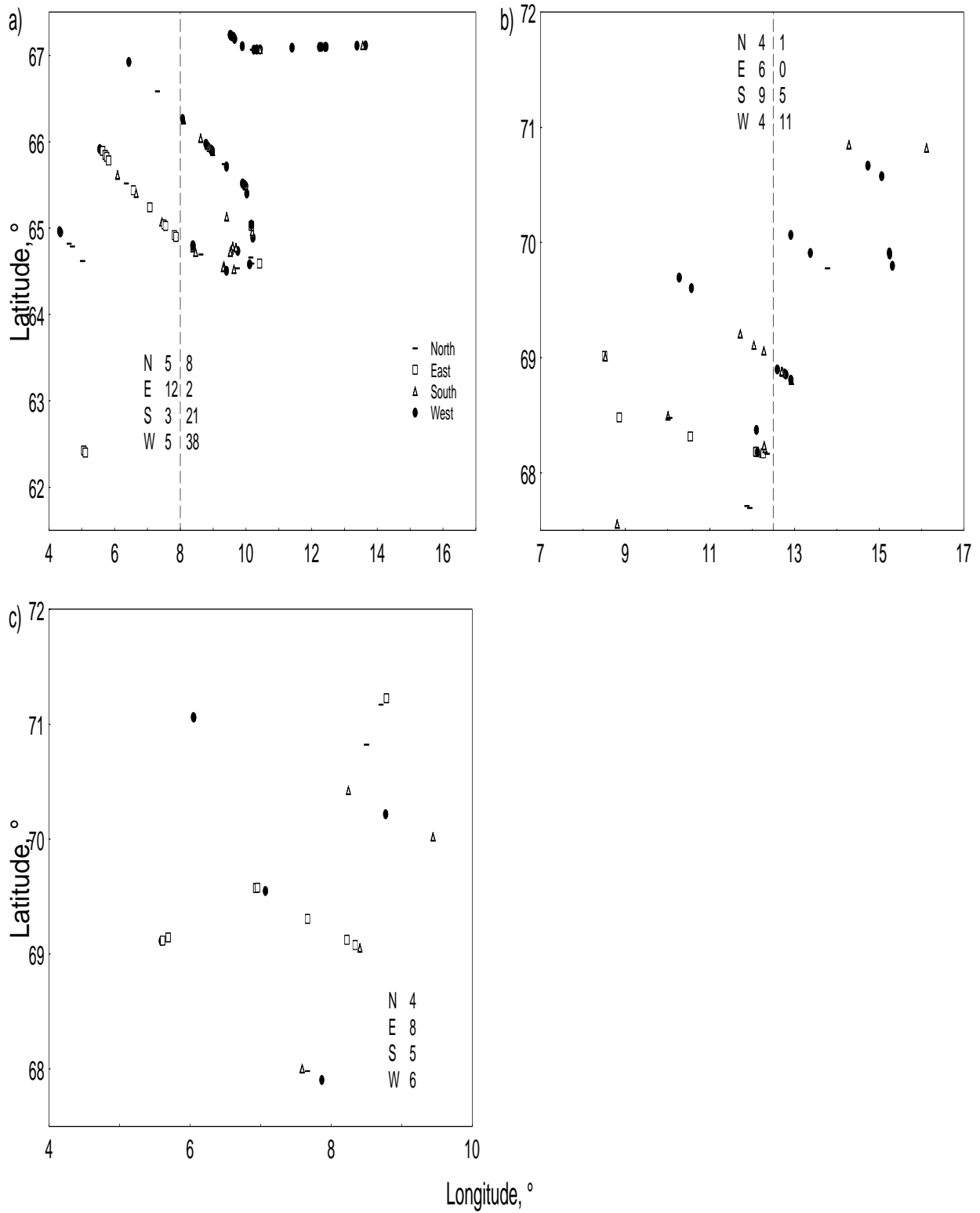
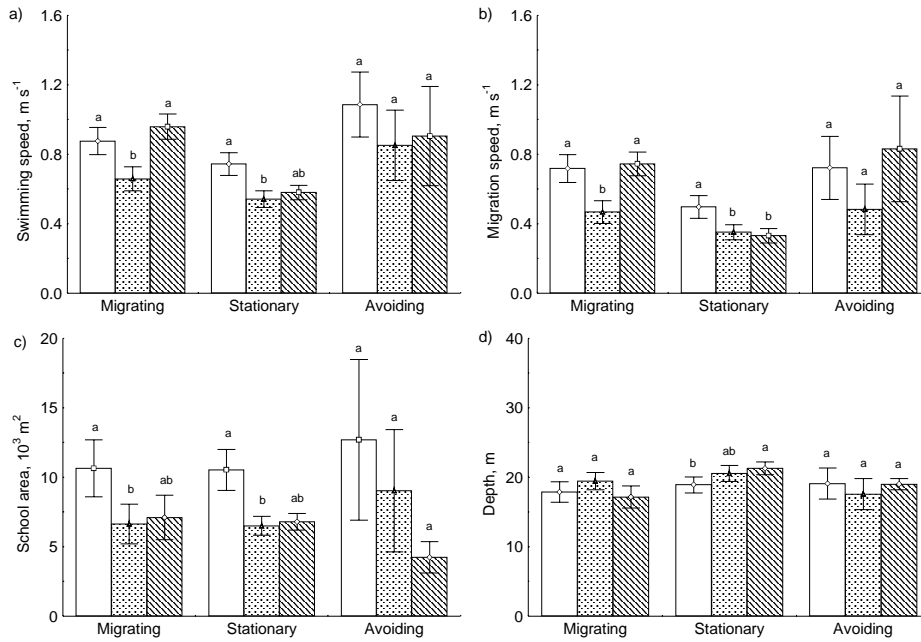


Figure 7. The geographical position ($^{\circ}$) of migrating schools and their direction of migration ($^{\circ}$). North : [315° , 360°) or [0° , 45°), east: [45° , 135°), south: [135° , 225°) and west: [225° , 315°). The number of schools within each category is given. a) Sub-area A, n = 94. The sub-area is divided into a western and eastern part. b) Sub-area B, n = 40. The sub-area is divided into a western and an eastern part. c) Sub-area C, n = 23.

D) Comparison of sub-areas



II) Comparison of behavioural categories

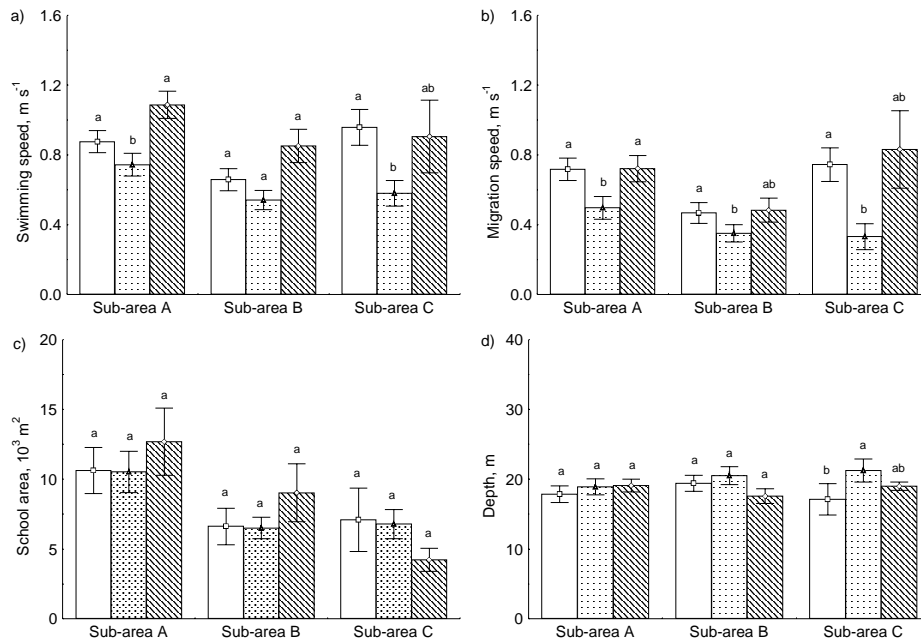


Figure 8. Comparison of the sub-areas within each behavioural category (I) and the school categories within each sub-area (II) for the 1995 survey: a) swimming speed, m s^{-1} , b) migration speed, m s^{-1} , c) school area, 10^3 m^2 , d) school depth, m. White columns: sub-area A / migrating, light grey: sub-area B / stationary, dark grey: sub-area C / avoiding. The whiskers show $\pm 1.96 \times$ standard errors. Different letters³ indicate differences between the sub-areas / behavioural categories with a significance level of 0.05 (Kruskal-Wallis rank tests and *post hoc* tests: Mann-Whitney U tests). Migrating schools: $n_A = 94$ (school area: 89), $n_B = 40$ (37), $n_C = 23$ (21); stationary: $n_A = 145$ (135), $n_B = 113$ (106), $n_C = 47$ (43); avoiding: $n_A = 25$ (24), $n_B = 13$, $n_C = 2$.

³ The highest value gets the letter code a and the next value the letter code b, if this value is significant lower than the highest value and so on. Not significantly different values get the same letter code.

DISCUSSION

Behavioural Categories

Movement patterns were used to classify the schools into migrating, stationary and avoiding schools. The direction of migration of avoiding schools differed from the direction of migrating and stationary schools, supporting that the classification criteria were reasonable. The direction of migration of avoiding schools was similar to the vessel's heading (Misund & Aglen 1992), indicating an influence of the vessel. In the present study the correlation between vessel heading and school bearing was not caused by capture of the school between fields of higher sound intensities to the sides of the vessel, forcing the schools forward, as has been reported by Misund & Aglen (1992). Avoiding schools usually moved at an angle towards the vessel track prior to avoidance, followed by an approximately 90° change in direction and movement away from the vessel track. The direction of migration then became similar to the vessel's heading. The migration direction of migrating and stationary schools implies that for these schools the vessel did not influence this parameter. The differences between the behavioural categories in swimming and migration speeds also suggest that the criteria for the classification were valid.

The threshold for vessel avoidance may be related to noise level, the life stage of herring, feeding conditions and predators (Olsen 1971; Misund 1994; Engås & al. 1995; Misund & al. 1996). Mohr (1969) observed that the herring reacted strongly to vessel and gear during the spawning migration. Migrating schools often react more strongly and are more difficult to catch by pelagic trawl than feeding and spawning schools (Misund 1994, but see Olsen 1971). In our study the low extent of avoidance may reflect a high feeding level. The stationary schools were probably foraging, and therefore frequently changing direction and moving little. Nøttestad & al. (1996) observed a variable swimming direction during feeding and searching in herring.

Acoustic Sampling

The vessel followed a predetermined survey track while recording schools, with the result that the sampling of schools within the survey area was non-random. Within the survey track, however, the schools detected at the sonar screen were sampled relatively randomly. However, some of the smallest schools may have been wrongly interpreted as noise, and consequently not have been tracked. This may have biased the distribution of the school categories in favour of migrating schools, since these schools are often larger than feeding schools (Eggers 1976; Pitcher & Parrish 1993; Nøttestad & al. 1996), and may have led to both excessively low proportions of stationary and avoiding schools and overestimations of the school areas. The low resolution of the sonar SR240 and the imprecise method for measuring and calculating school area (Kvamme 1999) may also have contributed to an overestimation of the school area, explaining the large differences between estimated school areas in 1995 and 1996. For this reason, the estimates of school area were only used as indexes for comparisons between sub-areas or school categories. Since the key issue in this study is the migration pattern, possible bias in school area and number of schools in the different behavioural categories should not influence our main conclusions.

Direction of Migration

All parameters except school area were measured from the centre of the school. At school level, this centre moves stochastically within the school, causing a higher variation in school direction than the real variation. Nevertheless, there is no evidence of any bias in the errors, and when using the direction of migration of each school and requiring a certain duration of

the school registrations, the stochastic nature of the errors should thus cause the bias to largely cancel out. The direction of migration calculated in this study should therefore reflect the real instantaneous direction of migration.

Scale

The sampling method, at a vessel speed of 10-12 knots, led to relatively brief school registrations. The advantage of this method is that a large number of schools could be sampled within a short period of time while following a predetermined survey track, as in abundance surveys. The shortest school registrations (< 21 ping) were omitted to reduce bias. This sampling method results in studies of the movement of individual schools on a small spatial scale and registration of the schools' direction of migration and mean depth, swimming and migration speeds on meso-scale (~100 m, Fernö & al. 1998). By studying the mean values of these parameters within the sub-areas and describing the dominant pattern in each case, the behaviour of the herring could be projected to macro-scale (> 1000 m, Fernö & al. 1998). This study thus covered several spatial scales, making it possible to reveal trends in both the general migration pattern and individual school behaviour of herring.

It has been shown that the scale of measurement and analysis largely influences the results of studies of spatial correlation between predator and prey (Rose & Legget 1990) and distribution of herring schools (Mackinson & al. 1999). In this study, the importance of scale is illustrated by the differences in direction of migration within the sub-areas. Splitting of sub-areas A and B into western and eastern parts reduced the variation, which thus depended on the scale of the measurements and on how the survey area was split up. In studies of migration dynamics, however, the number of sub-areas should be limited in order to reveal possible major trends within larger sub-areas. If the material from July 1995 had been studied as a whole, neither the differences between young and older herring nor the western direction of migration in coastal areas would have been revealed. It is thus vital to evaluate the scale both in sampling and analysing data.

Prey Distribution and Competitors

The availability of prey may have an important influence on the migration and distribution of herring in the summer feeding period (Pavshtiks 1959; Østvedt 1965; Jakobsson & Østvedt 1996; Nøttestad & al. 1999). Feeding conditions can still be good in July (Pavshtiks 1959; Wiborg 1978), and Dalpadado & al. (1996) found a peak in feeding in June-July. Small-sized, foraging herring schools have even been observed in September (Misund 1993b). The herring's stomach samples, with only 16.6% of the stomachs empty (Dalpadado & al. 1996), and the shallow depth distribution, indicate high feeding intensity during the survey period. *Calanus finmarchicus* was the most frequent prey at most stations (Dalpadado & al. 1996). The herring were registered in the upper 60 m, with no diel vertical migration, consistent with other summer observations of herring (Zusser 1958 in Blaxter 1975; Harden Jones 1968; Røttingen 1988).

Feeding conditions varied within the survey area. MOCNESS samples showed that the western part had the highest and the eastern part the lowest zooplankton biomass, with *Calanus finmarchicus* dominating (Dalpadado & al. 1996). Acoustic integration values from the survey also indicated an increase in plankton abundance westwards, especially in sub-area A (figure 14 in Anon. 1996a). Low prey availability on the continental shelf might have been caused by a combination of *Calanus finmarchicus* starting to migrate towards deeper water for overwintering (Østvedt 1955; Pavshtiks 1959; Wiborg 1978; Melle & al. 1993, 1994; Skjoldal & al. 1993) and depletion of prey caused by herring predation. Within sub-area A it

has been observed that the zooplankton were deeper on the continental shelf than near the continental slope (Melle & al. 1994). This may be an indication of an earlier start of the migration to deeper water in coastal areas compared to near the continental slope. Juvenile herring (3-4 years) were probably feeding near the coast the entire summer (Anon 1995, 1996b), and coastward adult migration (Røttingen 1992) probably led to the very high densities in late summer (figure 3 in Anon 1996a). A large herring stock in a relatively small area may partly deplete its zooplankton prey (Manteufel 1941; Melle & al. 1994; Arrhenius 1995; Misund & al. 1998b), and during the survey, the highest concentrations of herring coincided with the lowest density of zooplankton (Dalpadado & al. 1996). Possible spatial differences in the annual migration cycle of *C. finmarchicus* and feeding pressure from herring might therefore explain the differences in prey availability between the eastern and western parts of the survey area.

Interspecific feeding competition with mackerel (*Scomber scombrus*) or blue whiting (*Micromesistius potassou*) may also influence herring migration during the feeding period (Daan 1980; Fernö & al. 1998). Mackerel were mainly registered further west than herring, except in the western part of sub-area A (Anon. 1996a). In sub-area A some blue whiting were also registered, though these were mostly deeper in the water column than herring (Anon. 1996a). During the survey, only young herring (< 8 years) and mackerel had high diet overlap (pers. com., O. Bjelland, Institute of Marine Research, Bergen). It is uncertain to what extent mackerel actually is a food competitor to herring in the feeding period. The combination of sub-optimal feeding conditions and competition may have triggered the western migration observed in coastal areas.

Migration Pattern: Direction of Migration and Speed

Prior to this study it was expected that the herring in July would be concentrated in the area west of Lofoten and that they would migrate to the overwintering area. The results showed that the herring had concentrated near the coast relatively close to the Lofoten area, but the dominant direction of migration was not towards the overwintering area. In **sub-areas A and B** migrating herring schools moved towards the southwest, and young herring from the 1991 and 1992 yearclasses dominated. The observed migration is consistent with acoustic registrations from the beginning of August (figure 4.6-7 in Anon. 1995), which show that the herring distribution was more westerly than in July. The westward movement was probably induced by sub-optimal feeding conditions near the coast. By migrating westwards the herring could improve the feeding conditions and extend the feeding period. Stomach samples from August show that herring stomachs were fuller, and the proportion of empty stomachs lower, in Atlantic than in coastal waters (Dalpadado & al. 1996), supporting that the herring increased the feeding level by migrating westwards in July.

A more detailed study of the direction of migration within sub-areas A and B revealed a relationship between direction and the distance from the coast. Near the coast the schools migrated west- or southwards in both sub-areas. In the western part of sub-area B no dominant direction of migration was found (as in sub-area C). The differences between the eastern and western part of sub-area B suggest that the herring migrated westwards until satisfactory feeding conditions had been obtained. An eastern migration direction dominated in the western part of sub-area A. There are at least two plausible explanations for the migration pattern in sub area A: **1)** Herring generally migrated towards the coast. In the eastern parts the feeding conditions were sub-optimal, and the herring therefore migrated westwards or southwards to find areas with satisfying feeding conditions. **2)** In the western part mackerel, which had a high diet overlap with young herring (pers. com., O. Bjelland,

Institute of Marine Research, Bergen), were also registered (Anon. 1996a). If the mackerel actually is a food competitor, the herring may have migrated eastwards to reduce interspecific competition. These two explanations are not mutually exclusive.

In the open sea of **sub-area C**, herring schools were registered in the eastern part, and the high variation in the direction of migration here may indicate good feeding conditions. The 1990, 1983, 1991, 1989 and 1992 year classes dominated in this order. The oldest herring (≥ 5 years) covered large areas of the Norwegian Sea during their feeding migration before returning to the area west of Lofoten in July (Anon. 1995). The age distribution of herring in sub-area C is similar to that of long-distance migrating herring, except in the contribution from the 1991 and 1992 year classes (figure 4; Anon. 1995). Parts of the 1991 year class were feeding in central areas of the Norwegian Sea at the end of April, but seemed to return to the coast as early as May or June (figure 4.2-4 in Anon. 1995). The main parts of the 1991 and 1992 year classes probably stayed close to the coast for the entire feeding period (Anon. 1995, 1996b).

The oldest herring may have migrated into sub-area C in at least two ways: **1)** They migrated towards the coastal areas near Lofoten in June-July, and stopped near the frontal area between Atlantic and coastal waters, where feeding conditions probably were better than over the continental shelf (Melle & al. 1993, 1994; Skjoldal & al. 1993), although the distance to the overwintering area was relatively short. The herring may have experienced sub-optimal feeding conditions at the continental shelf in previous years, and may consequently have stopped off to feed in the frontal area instead. A possible parallel to this is observed in migrating birds. During the autumn migration, many birds make a feeding break shortly before crossing ocean areas (Alerstam 1978, 1990). In coastal areas, the prey density may be low, forcing them to move further away from the coast to feed. A domination of juvenile birds among birds exhibiting reverse migration near the coast may be due to more experienced birds making a feeding break before reaching the coastal areas, possibly as a result of their previous experience of sub-optimal feeding conditions in the coastal areas (Alerstam 1978, 1990). **2)** Another possibility is that the oldest herring migrated into coastal areas in June-July, but low prey availability made them return westwards to areas with more food. The prey density threshold for leaving an area may be lower for large herring than small (Nøttestad & al. 1999), which may explain why older herring were found further west than young conspecifics. The absence of herring more than six years old in sub-area A and B (figure 4) supports the first explanation. The feeding conditions probably varied within the coastal areas, and if the oldest herring had visited the continental shelf in June-July, some of them would probably have experienced satisfactory feeding conditions and would have remained there.

The westerly migration in the school subsets from the 1996 survey suggests that a westerly migration is a general way of responding to sub-optimal feeding conditions in coastal areas.

Mean swimming and migration speeds for migrating schools were 0.89 m s^{-1} (3.4 bl s^{-1}) and 0.60 m s^{-1} (2.3 bl s^{-1}), respectively. This is in accordance with the previously observed swimming speed for herring, both in the field (Misund & Aglen 1992; Hafsteinsson & Misund 1995; Misund & al. 1996, 1997, 1998a; Nøttestad & al. 1996) and in laboratory studies (He & Wardle 1988). In our study, swimming speed was measured relative to the earth's surface, and thus did not reflect the movement of the herring in relation to the water mass. Varying current conditions may have contributed to the large variation in recorded swimming and migration speed. Factors such as fish length (He 1993), speed and direction of currents (Trump & Legget 1980; Nøttestad & al. 1999), temperature (He 1993; Videler &

Wardle 1991; Videler 1993) and other environmental conditions (Jakobsson 1969; Jakobsson & Østvedt 1996) may influence swimming speed in herring. Neither temperature (figure 15-16 in Anon. 1996a) nor the length of herring could explain the differences between the sub-areas, with higher speeds in sub-areas A and C than sub-area B. In previous studies herring have been observed to avoid areas with unfavourable conditions, such as low temperature and sub-optimal feeding conditions, on their feeding migration, by rapidly returning from such areas (Jakobsson 1969; Jakobsson & Østvedt 1996). Acoustic plankton densities (figure 14 in Anon. 1996a) indicate that the prey density was lower near the coast in sub-area A than in sub-areas B and C, and lower prey density may explain the faster migration in sub area A. The high swimming and migration speed in sub-area C may be explained by the larger size of herring compared to sub-areas A and B.

The longest distances in a straight line from a school observation to the inner parts of the overwintering area were about 930 and 560 km in the middle and end of July, respectively. Norwegian spring-spawning herring has a high migratory capacity (Nøttestad & al. 1999), and should be able to reach the overwintering areas in Vestfjorden despite a westward migration in July. Mean migration speed for migrating schools was 0.60 m s^{-1} , or about 52 km a day. The herring were thus capable of covering a distance of 930 km in 18 days. The migration from the feeding area near Spitsbergen and Bjørnøya to the overwintering area east of Iceland in 1968 started in the beginning of September, and after 20 days the distance Bjørnøya-Jan Mayen, about 740 km, had been covered (Jakobsson 1969). Røttingen & Røttingen (1991) estimated that herring moved up to 830 km in two to three weeks during the spawning migration. Usually, the herring do not enter the overwintering area in Vestfjorden before September - October (Røttingen 1988, 1992; Dommasnes & al. 1994; Røttingen & al. 1994; Huse & Ona 1996). In July there are still about two months left, and from an energetic point of view the herring should continue feeding as long as this activity is more profitable than overwintering. The gain may depend on factors such as the herring's length and condition, prey availability and the costs (energy, time) of a possible migration (Nøttestad & al. 1999). The herring scarcely feeds in the overwintering area (Dommasnes & al. 1994; Huse & Ona 1996; Slotte 1999), and it should therefore be advantageous to feed as long as there are suitable prey relatively close to the overwintering area. With a migration speed of 0.60 m s^{-1} , the herring can feed at a distance of up to 1000 km from the overwintering area throughout August, and still reach the overwintering area in September-October.

The Feeding Strategy of Herring

The schools in sub-area A, which had the highest proportion of migrating schools, migrated faster and were larger than the schools in the other sub-areas. Near the coast, westerly or southerly migration dominated, and the fast migration out of these areas was probably triggered by sub-optimal feeding conditions. In sub-area B, the swimming speed was lower and the schools smaller than in sub-area A and the proportion of stationary schools high. This probably reflects a higher proportion of feeding schools in this area. Near the coast the schools migrated westwards, whereas the direction of migration in the western part varied. Feeding conditions were probably better in sub-area B than in A, as the entire sub-area B is situated near the continental slope and thereby the front. The westward migration of schools near the coast may be due to increasing plankton abundances westwards. In sub-area C there was no trend in the direction of migration, the speed was similar to sub-area A and the school size was about the same as in sub-area B. The best feeding conditions were found in this sub-area, and most of the herring was probably feeding. By migrating out of sub-optimal coastal areas the herring could thus improve their feeding conditions and extend the feeding period.

This study has shown that July may be an important part of the herring's feeding period. The differences in migration patterns between sub-areas suggest a possible feeding strategy in July. Herring cannot predict feeding conditions in different areas. Prey availability in coastal areas was probably high early in the feeding period, and in years with a small herring stock feeding conditions may be good throughout the feeding period. In such years it would be advantageous to stay near the coast all summer. Young herring made less extensive feeding migrations than older herring (Anon. 1995, 1996b), probably because they have higher migration costs (Nøttestad & al. 1999). The best strategy for young herring may thus be to stay in coastal areas while feeding conditions are satisfactory and to move westwards *if* the conditions worsen. The westerly migration observed in July 1996 suggests that this may be a regular annual migration pattern when food is scarce in coastal areas. The strategy of older herring may be to swim towards the coast in June-July for a feeding break in frontal areas before entering the overwintering area.

Why herring are not found in the most optimal habitat is a question of how its migration pattern (direction and speed) is controlled by predictive (genetic, learning) and reactive mechanisms (Fernö & al. 1998). The genetic part may work on a large spatial (1000 km) and temporal (100 years) scale, learning on an intermediate scale (10-100 km, years) and reactive mechanisms on small scale (1-100 m, days). The temporal and spatial trends in prey availability, temperature and currents, for example, are probably so regular on a large scale that the high selective pressure has led to evolution of large-scale orientation mechanisms. Medium-scale environmental variance in the Norwegian Sea, like changes in the North Atlantic oscillation (Alheit & Hagen 1997), results in a need for flexible knowledge, provided by learning of orientation mechanisms that may vary from generation to generation. A possible example of variation in migration pattern caused by learning is the changes observed in herring's migration pattern in the 1960s (Dragesund & al. 1980; 1997). The environment also varies spatially and temporally on a small scale, for example in terms of prey depletion. On this scale, a reactive strategy tuning the predictive orientation mechanisms (genetic and learning) to the unpredictable local variation becomes crucial. The combination of these three mechanisms makes the fish capable of orientation in an environment that is both partly predictable and stochastically varying (Fernö & al. 1998). From genetics and learning the individual obtains "advice" concerning movement, and then fine-tunes its migration to the most recent knowledge, near-field information, by reactive orientation mechanisms. In this way an organism in a sub-optimal habitat will be capable of finding, if not the best, at least a better, more suitable habitat. Fernö & al. (1998) have suggested that sub-optimal feeding conditions may trigger a large-scale western migration after spawning, on the basis of a prediction of high concentrations of food. This may also happen near the coast in July. In the present study, the herring probably followed a westward track (predictive orientation mechanism) adjusting the migration direction to local environmental conditions (i.e. food, temperature and currents) by reactive orientation mechanisms. A combination of predictive and reactive orientation mechanisms may explain both the dominance of a westerly migration direction and the variation.

Concluding Remarks

To the best of the authors' knowledge, this is the first time the July migration pattern of Norwegian spring-spawning herring has been described. The study has shown that the herring migrated westwards during a time of year when it had previously been assumed to be migrating eastwards, probably in order to improve feeding conditions and maximise energy reserves before overwintering. Knowledge of the migration pattern of a stock is crucial for abundance estimation, concerning both survey design and *ad-hoc* corrections of the

abundance indices (MacLennan & Simmonds 1992; Gunderson 1993; Hafsteinsson & Misund 1995; Axelsen & Misund 1997). Changes in stock distribution during an abundance survey may bias abundance estimates, and to correct for this we need information about the speed and direction of the migration. The present study show that it is possible to obtain information about these parameters during a routine survey with a predetermined survey track. Certain stock models also require input about the migration pattern (Dommasnes & Hauge 1994; Bogstad & al. 1997). The present study also expands our basic knowledge of the factors that influence the migration pattern of herring in the feeding period. In order to increase our knowledge yet further, factors that may influence fish behaviour (i.e. age, weight and length of herring, prey density, temperature, competition, predation risk, currents, light) should be sampled on the same spatial and temporal scale as sonar observations of the behaviour of herring schools. Future studies of swimming speed should also incorporate current speed and direction.

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