MIGRATION BEHAVIOUR OF NORWEGIAN SPRING SPAWNING HERRING WHEN ENTERING THE COLD FRONT IN THE NORWEGIAN SEA

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The distribution of Norwegian spring spawning herring when migrating to the feeding areas in the Norwegian Sea in spring was mapped by acoustic surveys in April 1995 and 1996. The schooling behaviour of the herring was recorded by a high-resolution sonar, and the swimming speed and swimming direction were quantified by tracking individual schools for up to one hour. In early April the herring migrated in the Norwegian Sea from the continental shelf off Norway, between 66° and 68°N, and westward to 2°W. When reaching the cold-water front, at about 0°, the herring turned southward along the front. During daytime the herring migrated in large schools at 300-400 m depth; at night they rose to surface and either dispersed or maintained schooling.

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INTRODUCTION

The large-scale migration behaviour of the herring, *Clupea harengus*, in the Norwegian Sea during its summer feeding migrations, autumn aggregation migrations, and winter spawning migrations is well documented. Information on the migration of this transoceanic herring stock has been gathered from tagging experiments, acoustic recordings and analysis of fisheries data. Experimental tagging by FRIDRIKSSON & AASEN (1950) showed that the herring occurring north of Iceland in the summer months were spawning along the coast of western Norway in winter. Sonar and echo sounders were used to record the herring in the cold-water areas east of Iceland/north of the Faroe Islands in late autumn, and follow the spawning migration across the Norwegian Sea to the Norwegian coast (DEVOLD 1951; 1953).

Another characteristic of the herring in the Norwegian Sea is its substantial seasonal variations in vertical distribution (DEVOLD 1963). During the spawning migrations the herring were found in large schools or extended layers at 300-400 m depth in daytime, and rose to the surface at night. On the spawning grounds, the herring were observed in large midwater or bottom schools and bottom layers in daytime, and scattered in extended layers at night (DEVOLD 1963). In early summer the herring were found in dense schools near the surface or in mid-water at depths up to 300 m (JAKOBSSON 1963; ØSTVEDT 1965).

As evident from fisheries, the herring were mainly feeding in the areas north and north-east of Iceland during the summer months and early autumn (JAKOBSSON 1962). In the sixties there was also a subpopulation that fed in the northern Norwegian Sea south-west of Bear Island (DEVOLD 1968), but this unit migrated to the east coast of Iceland during autumn 1966 and joined the rest of the stock (JAKOBSSON 1968). After the collapse in the late sixties, the stock fed off northern Norway in summer, aggregated and wintered in fjords in western and northern Norway, and spawned at the traditional grounds off western Norway (RØTTINGEN 1992). When the stock recovered during the late eighties and early nineties, the herring made more extended feeding migrations in the Norwegian Sea in summertime, and migrated back to the Ofoten/Tysfjord area of Norway in autumn (RØTTINGEN 1992).

A critical factor influencing the spatial distribution of herring in summertime in the Norwegian Sea is their behaviour along the front between cold Arctic water in

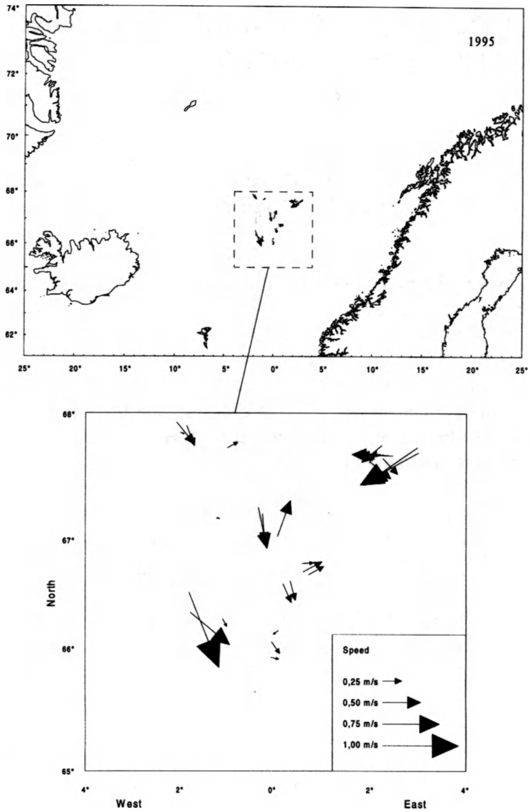

Figure 1. Study area (upper) and migration vectors (lower) of herring schools tracked for 5-65 min in April 1995.

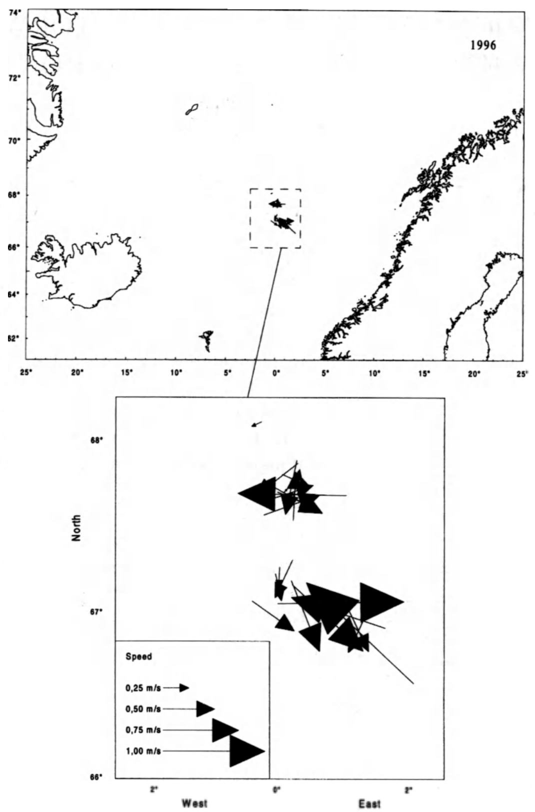

Figure 2. Study area (upper) and migration vectors (lower) of herring schools tracked for 4.2-121.8 min in April 1996.

the East Iceland Current and the warmer Atlantic water in the central Norwegian Sea. In the sixties, the herring were found feeding along the cold front east of Iceland in sea temperatures above 2 °C in early May, but passed through the front and entered the feeding areas north of Iceland in early June (Østvedt 1965).

To investigate the migration behaviour of the herring in relation to environmental features when entering the cold front in the Norwegian Sea, we conducted a series of exploratory cruises in the Norwegian Sea in April 1995 and 1996. The distribution and migration behaviour of the herring were recorded by echo integration and sonar, and the hydrographic conditions along the migration route measured.

SURVEYS

The first exploratory survey was conducted in April 1995 in the area 66°-68°N, 2°W- 2°E (Fig. 1). The purpose of the survey was to map the distribution of herring, and track selected schools for quantification of migration behaviour and school dynamics. A second survey was conducted in April 1996 in an area from about 67°-68°30'N and about 5°E-2°W (Fig. 2). The area was first investigated by an exploratory survey to map the distribution of herring. Tracking of schools for quantification of migration behaviour and school dynamics was then conducted along a southward transect along 0°, starting at about 68°N, and along a westward transect along about 67°N from about 0°-1°20'W.

METHODS

The surveys were conducted by R/V *G.O. Sars* (70 m LOA, 1663 GRT). Continuous acoustic recordings of fish and plankton were made by a calibrated echo integration unit consisting of a 38 kHz Simrad EK500 (Bodholdt & al., 1989) working at a range of 0-500 m. A 95 kHz Simrad SA950 sonar (Misund & al. 1995) connected to a computer with real-time school detection software was used to record and track selected schools (Misund & al. 1994).

To record migration behaviour and school dynamics, selected schools were tracked for up to about one hour, in one case for about two hours. The schools were then continuously recorded by the sonar system, and the vessel manoeuvred carefully to keep the school within a distance of 100-300 m. This manoeuvering ensured a rather constant, low-frequency noise

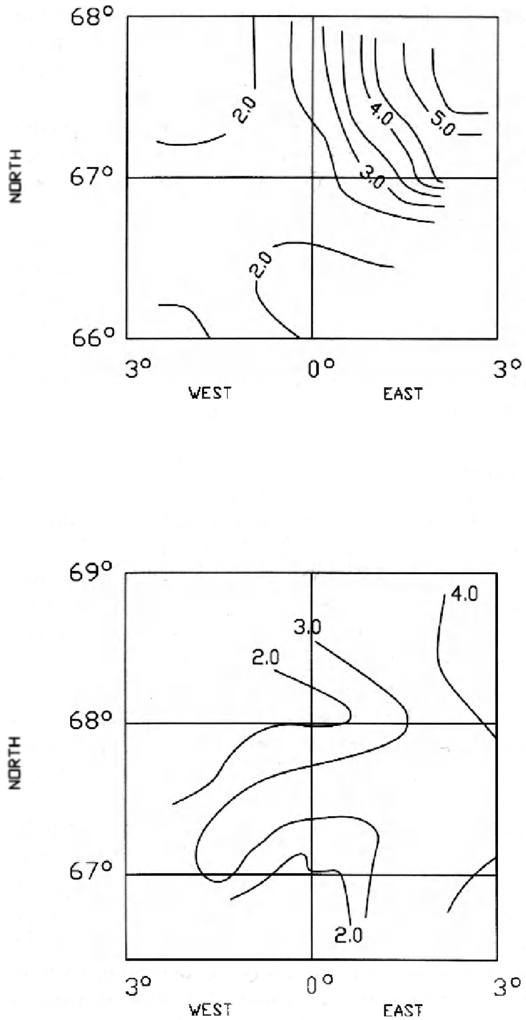

Figure 3. Temperature distribution at 300 m depth in the study areas in April 1995 (upper) and April 1996 (lower). Contours are in °C.

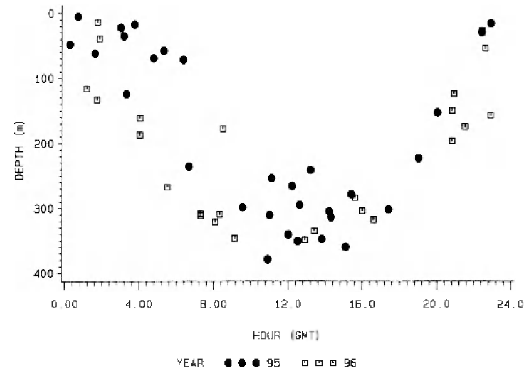

Figure 4. Vertical distribution of herring schools tracked in April 1995 and 1996 related to time of day. Each symbol represents a different school.

from the vessel, and thus limited the risk of vessel avoidance reactions, which usually are elicited by a rapid increase in noise level of vessels (ENGÅS & al. 1995; SCHWARZ & GREER 1984). In April 1996, accurate position of the vessel was obtained from a Starfix differential global positioning system. The migration speed and direction of the schools were calculated by procedures written in the SAS software (MISUND & al. 1997). The dynamics of the schools were noted continuously by a rapporteur in cooperation with a sonar operator, both watching the sonar display. These observations will be reported elsewhere.

Acoustic recordings of fish were identified by use of the Åkra-trawl (VALDEMARSEN & MISUND 1994), which has a vertical opening of about 30 m. By ordinary rigging, the trawl can be used to catch deep recordings, but the trawl can also be rerigged to catch recordings near the surface.

Temperature and salinity were monitored by a CTD sonde up to 500 m depth. In addition, temperature and salinity were monitored continuously from an inlet at 5 m depth in the hull of the vessel.

RESULTS

Temperature distribution

In April 1995 there were clear horizontal and vertical gradients in the sea temperature within the study area. At surface the temperature was about 6.4 °C around 2°E, dropping to about 5 °C around 0°, and further to about 3 °C around 2°W. At 300 m depth the temperature generally ranged about 0.5- 3 °C lower than at the surface, and was about 5.7 °C around 2°E, and about 2.0 °C at 0°-2°W (Fig. 3).

In April 1996 there was a similar decline horizontally in the surface temperature from east to west, and also vertically from surface to 300 m depth. At 300 m depth there was a south-west 'tongue' of warmer water intruding into the cooler Arctic water (Fig. 3).

Herring distribution and migration

In April 1995, herring schools were recorded throughout the study area between 66°and 68°N, 2°W-2°E (Fig. 1). The herring were 21-38.5 cm in length, and 4-12 years old. During daytime the herring occurred in large schools at 300-400 m depth, and at night they were found in distinct schools or dense shoals from the surface to about 100 m depth (Fig. 4). A total of 28 schools in different positions within the April 1995 study area (Fig. 1) were tracked from about 5 to 65 min, and the horizontal speed varied from 0.51 to 1.52 m s^{-1}

(average 0.82 m s^{-1}, SD = 0.26 m s^{-1}). Schools swam faster the higher the prevailing sea temperature in the range 1.0 °C to 6.3 °C ($r = 0.57, p < 0.05$). Some schools were swimming in rather straight tracks, others changed heading frequently, and a few were circling around. Most schools (6 out of 10) around 2°E showed a western migration, while most schools (12 out of 18) west of 1°E showed a south-eastern migration (Fig. 1). The average migration direction for the schools tracked was 174°, and the average migration speed in that direction was 0.15 m s^{-1}. The eastward migration component of the schools were negatively correlated to the prevailing sea temperature in the range 1.0-6.3 °C ($r = -0.67$, $p < 0.05$), but there was no correlation between the northward migration component and the temperature in the same interval ($r = 0.14$, $p > 0.05$).

In April 1996, herring were recorded throughout the same study area as the previous year (Fig. 2). The herring were 21-39.5 cm in length, and 3-13 years old. As in the previous year, the herring were schooling at 300-400 m depth during daytime, and at night the herring rose to the surface and occurred both in distinct schools or dense shoals (Fig. 4). A total of 25 schools in different positions within the April 1996 study area (Fig. 2) were tracked for 4.2-121.8 min; 16 of the schools were tracked for more than one hour. The horizontal speed of the schools varied from 0.45 m s^{-1} to 1.51 m s^{-1} (average 0.94 m s^{-1}, SD = 0.28 m s^{-1}). In contrast to the previous year, the horizontal speed of the schools was not correlated to the prevailing sea temperature in the range 1.0-5.7 °C ($r = 0.27$, $p > 0.05$). The swimming pattern varied from rather straight tracks, to frequent sideways turns, and even circling around. North of 67°70' N, most schools were heading east (7 out of 13), but south of 67°70' N, most schools were heading south (7 out of 12). The average migration direction for the schools tracked was 165°, and the average migration speed of the schools in that direction was 0.10 m s^{-1}. There was no significant correlation between either the northern or the eastern migration component of the schools and the prevailing sea temperature in the range 1.0-5.7 °C ($r = 0.36$ and 0.06, respectively, $p > 0.05$).

Altogether, the migration behaviour of the herring schools tracked in April 1995 and 1996 was rather similar. The horizontal swimming speed for the tracked schools was not significantly different between the two years (Wilcoxon 2-sample test, $p > 0.05$). This was also the case for the heading (Wilcoxon 2-sample test, $p > 0.05$) and swimming depth of the schools (Wilcoxon 2-sample test, $p > 0.05$). We therefore pooled the recordings for the two years to test for diurnal differences in swimming speed and direction. This analysis revealed that the swimming speed was significantly faster (Wilcoxon 2-sample test, $p < 0.05$) for the schools tracked during the night (average speed = 1.00 m s^{-1}, SD = 0.21 m s^{-1} , n = 27) compared with the schools tracked during the day (average speed = 0.78 m s^{-1}, SD = 0. 28 m s^{-1}, n = 28). There was no significant difference (Wilcoxon 2-sample test, $p > 0.05$) in swimming direction for schools tracked during the day or at night.

In both years, most tracked schools were relatively large. Estimation of school size was not attempted because the schools at great depth were tracked by operating the sonar with a tilt angle > -45°, and reliable measurement of school area was thus not possible (Misund & al. 1995). The vertical extent of most schools was more than 50 m.

DISCUSSION

Herring migrated towards and along the cold front in the Norwegian Sea in large, dense schools at 300-400 m depth during daytime, and rose to the surface and scattered or remained in dense aggregations at night. The migration was faster at night than during the day. This is probably because the herring encountered prevailing sea temperatures that ranged from 0.5-3.0 °C lower than at the surface when swimming at great depth during the day. Both the large school size and the great swimming depth in daytime may indicate that the herring try to minimize predation risk (Fernö & al. 1996). At such great depths the herring are probably out of the effective feeding depth of fin whales, which were frequently observed in the study area. In addition, the formation of large schools enhances the precision of migration (Larkin & Walton 1969), and there is possibly a hydrodynamic advantage from swimming close to other individuals in a school (Abrahams & Colgan 1985). MOCNESS-samples of plankton in the actual areas show that the prey organisms most important to herring peaked in abundance at 200-400 m depth (Dalpadado & al. 1996). By swimming at great depth, the herring thereby also increase the probability of encountering prey patches. In fact, stomach samples indicate that the herring were feeding at the migration depths of 300-400 m.

The horizontal speed of the tracked schools indicated that herring were swimming at a speed of about 3 body lengths s^{-1}, which is within the limit of the sustained swimming speed for herring (Videler & Wardle 1991). The average speed in the direction of migration was about 0.10-0.15 m s^{-1} because the schools were not swimming in straight tracks, but made frequent side-to-side movements and even turns. This may indicate that the herring migration is influenced by environmental cues such as food availability, sea temperature and current, and that the sideways movements can be explained by search for directional gradients in such cues. The change of swimming direction may occur through synchrokinesis, in which the individuals at the perimeter of the school first become aware of unfavourable conditions and increase the speed and turn slightly until the whole school has changed to a more favourable heading (KILS 1986).

When entering the frontal areas, the herring were exposed to clear east-west gradients in the prevailing sea temperature of about 2 °C in the different depth layers. Similarly, during the diurnal vertical migrations in these areas, the herring faced temperature gradients in the range of 0.5-3 °C. Having arrived in the western, colder part of the frontal areas, most schools migrated southwards along the front. This indicates that the low sea temperatures in these areas initiated a shift in the migration from a westward to a southward heading. No schools were recorded in areas with prevailing sea temperature lower than 1 °C. This suggests that a temperature barrier exists, which the herring do not cross in the present situation at this time of the year. However, the temperature tolerance of the herring probably changes with the season and other internal and external factors, as herring were recorded in the sixties in areas with prevailing sea temperature down to about 0 °C when crossing the cold front on the migrations to the feeding areas north of Iceland (ØSTVEDT 1965).

In 1995 there were clear correlations between the horizontal speed, the eastwards migration component, and the prevailing sea temperature. These correlations were not present in the 1996 recordings, but that year the front structure in the area studied was complicated by the intrusion of a warmer 'tongue' into the western colder part of the front. Our recordings therefore indicate that the prevailing sea temperature in the cold front in the Norwegian Sea influences the migration behaviour of the herring, and that the herring seem to avoid prevailing sea temperatures lower than 1 °C in early April. However, the inconsistency in the correlations between prevailing sea temperature and the recorded swimming behaviour between the two years indicates that other cues such as food availability and current may influence the herring migration in the cold-front areas in the Norwegian Sea.

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