

Paper 1



Spawning of herring: day or night, today or tomorrow?

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Abstract

Diel variations in schooling patterns and spatial dynamics during spawning were studied in Norwegian spring-spawning herring (*Clupea harengus*) off south-western Norway by acoustic surveying, diel cycle experiments and school tracking by sonar, and bottom gillnet sampling. Herring formed horizontally extensive, loosely packed demersal layers shortly after darkness. At night, the fish disappeared in the acoustic dead zone, but lifted off the bottom early in the following mornings. At daytime the herring reorganised into dense pelagic schools. The evening descent to the spawning habitat was considered as part of a precautionary strategy towards visual predators, as the bottom is a high-risk zone for archetypal pelagic fish like herring. Large numbers of gadoids, which are potential herring predators, were present in the area. Herring not ready to spawn dominated the bottom samples in 4 out of 5 days, suggesting that pre-spawning herring followed the descent of ripe herring. The herring spawning layers shifted in a south-easterly direction from day to day in diel spawning waves.

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1. Introduction

Herring (*Clupea harengus* L.) have a pelagic lifestyle, but spawn demersally (Runnstrøm, 1941; Stacey and Hourston, 1982; Aneer et al., 1983). They spawn over a relatively short period annually (Blaxter and Hunter, 1982), and up to 10–15 times during a lifespan (Blaxter and Hunter, 1982; Slotte, 1999). The population of Norwegian spring-spawning herring spawns along the coast from Lofoten to Lista (Runnstrøm, 1941; Dragesund et al., 1997) during early spring.

Herring is a schooling species (Blaxter and Hunter, 1982; Pitcher, 1983; Fernö et al., 1998), that forms highly synchronised and polarised groups (Breder, 1976; Pitcher, 1983). Predator protection is the primary function of schooling (Pitcher and Parrish, 1993), and there is evidence that herring trade off predation risk for reproduction, which ultimately affects the size, shape, density and vertical distribution of the schools (Misund, 1993; Nøttestad et al., 1996; Axelsen et al., 2000). Before spawning, herring become risk-averse to maximise the likelihood of completing reproduction. Schools immigrating to the spawning location are large,

densely packed, and swim fast and deep (Nøttestad et al., 1996), hence increasing the efficiency of synchronised escape manoeuvres and decreasing the risk of detection by predators (Pitcher and Parrish, 1993). After spawning, feeding becomes more important, and herring form smaller, more loosely packed schools near the surface (Stacey and Hourston, 1982; Nøttestad et al., 1996).

For a successful reproduction, eggs and milt must be deposited on a suitable bottom substrate (Runnstrøm, 1941; Rajasilta et al., 1997). The spawning is not fully synchronised and herring remain at the spawning site for 3–5 days (Nøttestad et al., 1996; Axelsen et al., 2000). The maturity states of individuals differ amongst and within schools at the same site (Nøttestad et al., 1996; Axelsen et al., 2000), leading to a highly dynamic, and poorly understood schooling behaviour (Nøttestad et al., 1996). Generally, schools of Norwegian spring-spawning herring on the spawning grounds are observed as horizontally elongated demersal layers within a few meters off bottom (Runnstrøm, 1941; Johannessen et al., 1995). However, pelagic schools with high packing densities above demersal layers were observed by Nøttestad et al. (1996), and Axelsen et al. (2000) observed a single spawning school split into a pelagic and a demersal component staying in continuous contact. Herring staying

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pelagically presumably reduce predation risk, as staying near the bottom is associated with high risk due to the reduced number of potential escape directions (Axelsen et al., 2000). Large gadoids feed on herring and herring eggs during the spawning season (Toresen, 1991; Høines et al., 1995; Høines and Bergstad, 1999). Gadoids are visual predators and the predation risk for spawning herring should, therefore, be higher in daylight than in darkness.

Herring is one of the worlds most studied species (Blaxter and Hunter, 1982). Despite this, only a few studies have investigated schooling behaviour right before and during spawning (Nøttestad et al., 1996; Mackinson, 1999; Axelsen et al., 2000), and these studies did not explore possible diel variations. Our main goal was, therefore, to investigate diel variation in school patterns and spatial dynamics during spawning in relation to the maturation state of the fish and external factors like predation.

2. Materials and methods

2.1. Study area

The study was carried out off Karmøy (59°15'N, 5°05'E), on the west coast of Norway, from 29 March to 3 April 2000. During the study period, the time of sunrise changed from 05:12 to 05:00 h and the time of sunset from 18:13 to 18:22 h. Two research vessels; the “Håkon Mosby” and the “Hans Brattstrøm” were utilised in the study. A known spawning location extending about 2 nmi² with high densities of herring was selected in order to map the schooling dynamics during the spawning process. The bottom depth ranged from 30 to 40 m. The weather was generally cloudy with light north-westerly winds not exceeding 10 m s⁻¹ during the study period, although the wind speed increased towards the end of the study.

2.2. Experimental design

Two exploratory mini-surveys were conducted in order to map the distribution of the fish in the area. Based on the fish distributions, two survey grids were fixed for the school dynamic study, one designed to cover the horizontal extent of the spawning layer (zigzag) and one to estimate the fish density in the adjacent spawning area (parallel) (Fig. 1a). The two surveys were repeated three and four times, respectively. In order to map the vertical movements of fish over time, two 24 h diel cycle experiments were conducted on 2 and 3 April. During these experiment the ship was positioned immediately above the demersal spawning layers, continuously recording the vertical distribution and fish density using the echosounder. The Dynamic Positioning System (DPS) of “Håkon Mosby” was utilised in order to keep the vessel at a fixed location (within an area of 25 m²) during the experiments. Unfortunately, relatively rough weather conditions caused some formation of air bubbles in the surface layer, effectively reducing the usable materials from the diel cycle experiments to 14 and 8 h for diel cycle 1 and 2, respectively.

2.3. Acoustic recordings

Both research vessels were equipped with Simrad EK 500 echo sounders running 38 kHz transducers, while “Hans Brattstrøm” operated an additional Simrad EQ 55 (49 kHz) echo sounder used for mapping of the spawning layer on the bottom. Acoustic recordings were scrutinized according to catch composition and signal characteristics. The acoustic diel cycle data from the EK 500 were post-processed using Bergen Echo Integrator system (BEI) (Knudsen, 1990), averaging the nautical area scattering coefficient s_A (m² nmi⁻²) (MacLennan et al., 2002) over 10 min intervals. Sonar data Echoview v.2.10 © software was used to analyse the school dynamic parameters, including depth (m) and vertical extent (m), volume density S_V (dB re 1 m²) and s_A (m² nmi⁻²). A total of 246 herring aggregations (schools, layers) were analysed. The range resolution was about 10 cm (500 bins on 50 m operational range). The fish densities of the spawning layers recorded using the EK 500 unit were estimated according to (Foote et al., 1997):

$$TS = 20 \log_{10}(L) - 71.9$$

where L is the mean total fish length in cm obtained from the gill net samples. The total biomass of the spawners was estimated using the horizontal area of the demersal layer. The packing densities of the schools ρ_V were calculated according to:

$$\rho_V = \frac{s_A}{1852^2 \langle \sigma_{sp} \rangle \Delta z}$$

where s_A is the nautical area scattering coefficient of the school, $\langle \sigma_{sp} \rangle$ is the mean spherical scattering cross section (m²) (MacLennan et al., 2002), and Δz is the depth over which the acoustic data were integrated, i.e. the vertical extension of the school EV_{school} (m).

The diel cycle observations were divided in eight 3-h time periods starting at 24 UTC (local time = UTC + 2 h). The vertical school extension EV_{school} (m), the distance from the school midpoint to the bottom BD_{school} (m) and the linear mean volume backscattering (mm²), corresponding to $V \cdot S_V$ in the terminology adopted by MacLennan et al. (2002), were averaged for all time periods.

A Kaijo Denki KCH 1827 multi-beam scanning sonar on the “Hans Brattstrøm” was used to check for pelagic schools migrating in and out of the spawning area (Nøttestad et al., 1996). The horizontal area, and swimming speed and direction of recorded schools were estimated (Axelsen et al., 2000). Subsequent to the tracking, the schools were recorded using the EK 500 unit in order to estimate the vertical extension, depth and acoustic density of the schools.

2.4. School categories

The herring aggregations were categorised according to their position in the water column: *Pelagic schools*: >90% of the herring located above the bottom layer (>10 m off the bottom); *Demersal layers*: >90% located within the bottom

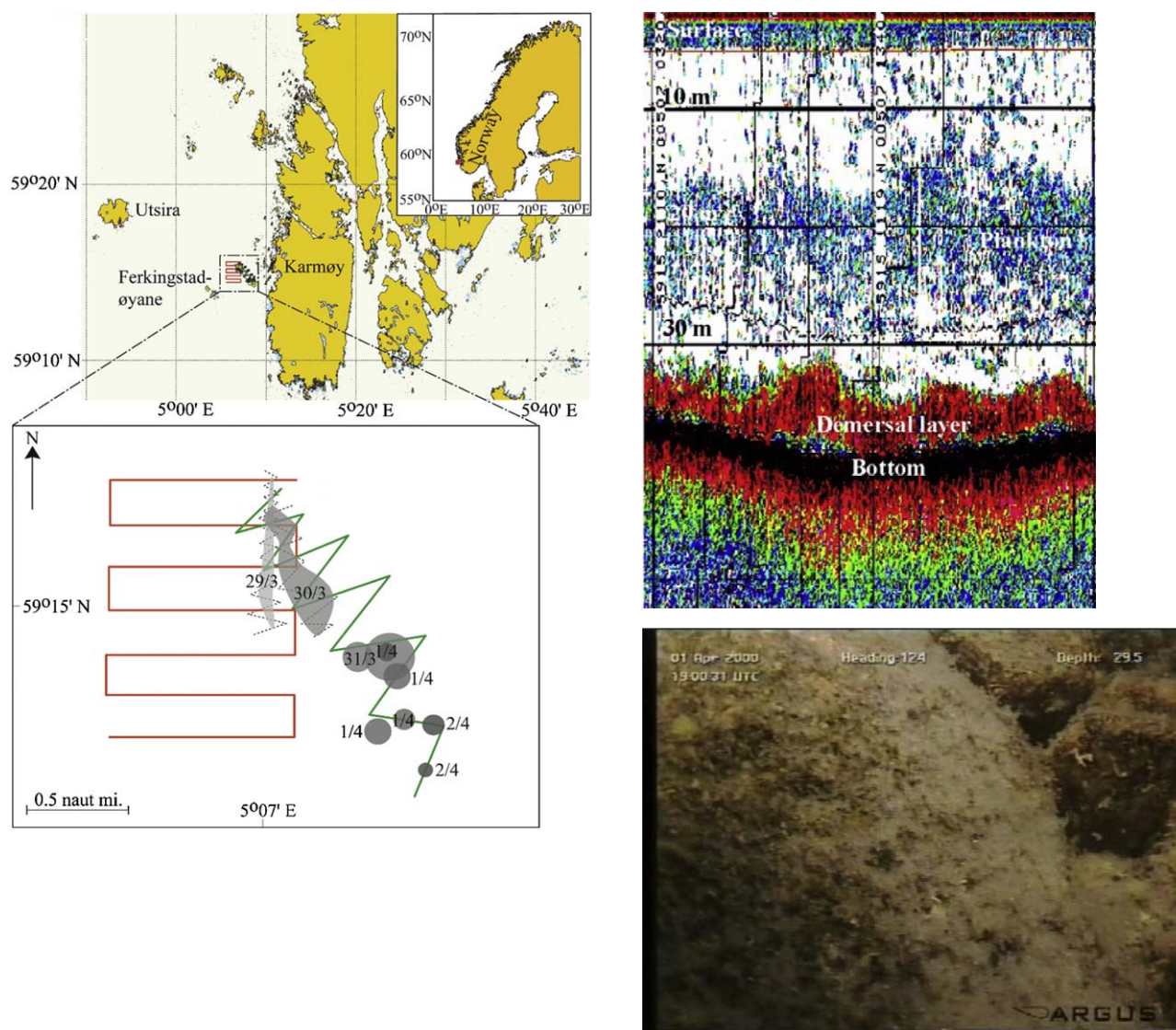


Fig. 1. (a) Distribution of demersal layers based on acoustic recordings with different shadings for each day. The red, parallel track indicates the spawning area survey (repeated four times), the green zig-zag track the distribution survey for demersal layers repeated three times, and the black adaptive localisation and mapping surveys. (b) S_V echogram at 38 kHz of a demersal layer of herring. (c) Eggs deposited on a boulder at the studied spawning site.

layer; and *Transition schools*: 10–90% located within the bottom layer and 10–90% above the bottom layer.

2.5. Biological sampling

Herring samples were obtained daily from 30 March to 3 April using 25 m long by 4 m high gillnets (mesh size: 37 mm when @ 5 kg) set on the seabed overnight. This mesh size is selective towards adult herring above 20 cm total length, but is inefficient towards juveniles. The influence of juvenile fish at the spawning grounds of Norwegian spring-spawning herring is, however, negligible (Johannessen et al., 1995). Total fish length, total wet weight and gonad maturity index GI (1–8) (Anonymous, 1962) were determined for all sampled fish. Two predator samples were obtained using 25 m long by 4 m high gill nets (90 mm meshes), and one sample using a Super Campelen demersal shrimp trawl.

3. Results

Fig. 1b shows an S_V echogram at 38 kHz of a demersal layer of spawning herring. The spawning substrate was closely examined using the Remotely Operated Vehicle (ROV) “Aglantha” and consisted mostly of boulders, rocks and gravel, with herring eggs deposited in thick layers on the bottom (Fig. 1c). The seawater temperature and salinity, as recorded during daily CTD-profiling, ranged from 5 to 6 °C and from 33 to 34‰, respectively.

3.1. Horizontal dynamics

The demersal layers of spawning herring moved in a south-easterly direction from day to day, with a total horizontal displacement of about 0.8 nmi during the study period (Fig. 1a), with overlapping distributions between the first 2 days and between the third and fourth day, otherwise not.

Table 1

Multi-beam sonar tracking. Linear fish density corresponds to SV (dB re 1 m⁻¹) in the linear domain (* the last school was not successfully integrated)

Time	Track duration (min)	Swimming speed (m s ⁻¹)	Direction	Linear fish density (mm ²)	Biomass (tons)	EV _{school} (m)	A _{school} (m ²)	BD _{school} (m)
12:34	27	0.11	W	430 ± 160	16	19.5 ± 3.7	841 ± 40	14.3 ± 3.4
17:27	96	0.15	SE	600 ± 740	15	14.2 ± 3.0	491 ± 95	9.2 ± 3.4
14:12	78	*	W	*	*	20	1708 ± 142	13

The biomass of the two spawning layers observed on 29 and 30 March was estimated to be 30 and 42 tons, respectively. The herring were too patchy distributed the remaining days to obtain reliable estimates. Altogether three schools were identified and tracked using the multi-beam sonar, and two of these successfully integrated using the EK 500 system (Table 1).

3.2. Vertical dynamics

Demersal spawning layers were usually recorded in the evening. The proportion of demersal layers relative to other school categories, was highest between 18:00 and 24:00 h (>80%). Little herring was recorded between 24:00 and 03:00 h, and only in one of the diel cycle experiments. Pelagic schools and transition schools dominated at daytime (>70%) and the demersal layers recorded were small.

Schools were distributed shallower during the day than at night (General Linear Model (GLM ANOVA, $P < 0.001$)) (Fig. 2a) and were closer to the bottom between 21:00 and 24:00 h than in all time intervals between 06:00 and 18:00 h (Tukey's range test (HSD), $\alpha = 0.05$). Also the vertical school extension changed with time (GLM ANOVA, $P < 0.001$) (Fig. 2b): from 18:00 to 24:00 h the vertical school extension was lower than in all daytime intervals from 09:00 to 18:00 h (HSD, $\alpha = 0.05$).

Little herring was recorded at nighttime during the diel cycle experiments, which is reflected in the low acoustic densities for herring ($s_A < 1000 \text{ m}^2 \text{ nmi}^{-2}$) between 21:00 and 04:00 h (Fig. 3a). The densities increased rapidly around 04:00 in both experiments, as the herring layers lifted off the bottom. Between 21:00 and 04:00 h most of the fish (>80%) were located in the bottom channel, while 40–100% of the herring was pelagic (>10 m over the bottom) between 04:00 and 12:00 h (Fig. 3b).

3.3. Packing densities

The school packing density changed over time (GLM ANOVA, $P = 0.001$) (Fig. 4a), and was higher between 15:00 and 18:00 h than in all other periods (HSD, $\alpha = 0.05$). The packing density also differed between school categories (GLM ANOVA, $P = 0.002$) (Fig. 4b). Transition schools ($3.0 N_{\text{herr}} \text{ m}^{-3}$) and pelagic schools ($1.9 N_{\text{herr}} \text{ m}^{-3}$) were on average more tightly packed than demersal layers ($<0.8 N_{\text{herr}} \text{ m}^{-3}$), but only the difference between transition schools and demersal layers was significant in our test (HSD, $\alpha = 0.05$).

3.4. Fish size and maturity state

A total of 423 individuals were sampled. The total fish lengths ranged from 16 to 38 cm (mean $33.2 \pm 1.9 \text{ cm}$ [S.D.]), and total wet weights from 27 to 500 g ($301.3 \pm 54.7 \text{ g}$), varying little between samples. The catches were dominated by 8-years-olds (67.5%). The majority of the herring (92.1%) had empty stomachs, and only one individual was caught with a full stomach. The stomach contents consisted of calanoid copepods and copepodites, or of herring eggs (Skaret et al., 2002). An increase in the prevalence of running and spent individuals and a decrease of pre-spawning individuals

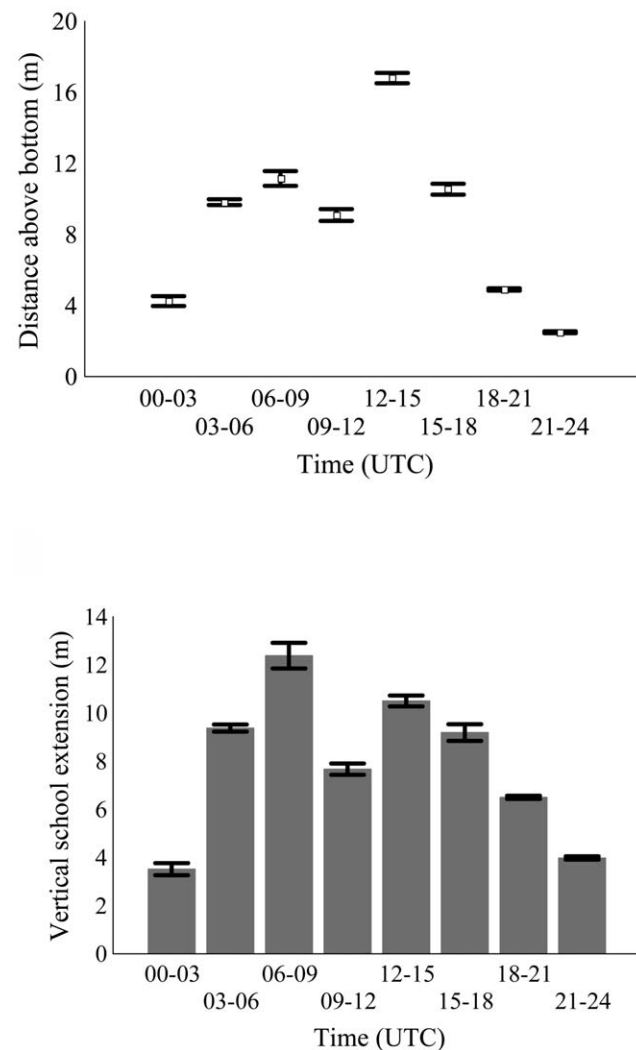


Fig. 2. (a) Mean school distance above bottom ($BD_{\text{school}} \pm 2 \text{ S.E.}$) (m), measured from the vertical midpoint of the school. (b) Mean vertical school extension ($EV_{\text{school}} \pm 2 \text{ S.E.}$) (m).

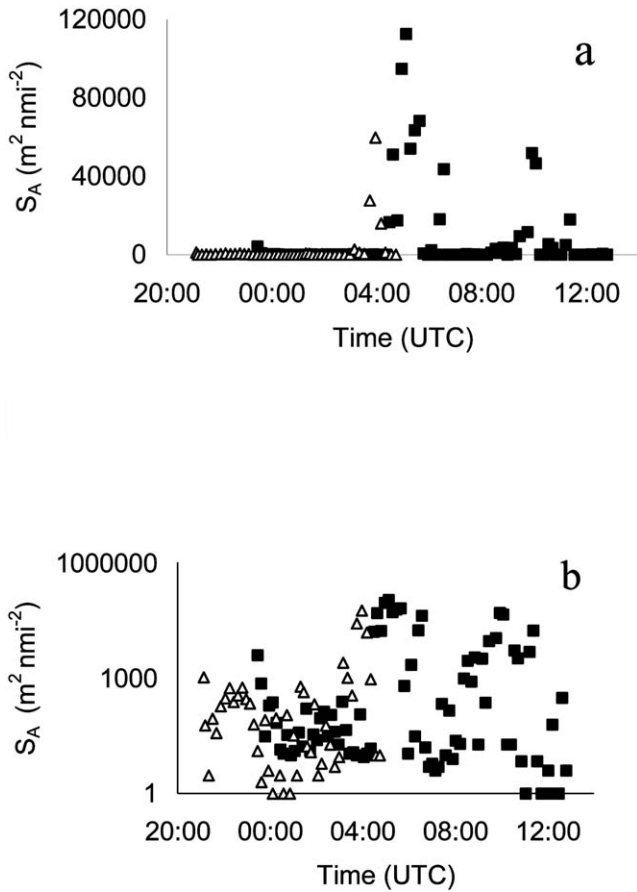


Fig. 3. (a) Mean area backscattering coefficients (s_A , $\text{m}^2 \text{nmi}^{-2}$) of herring integrated over 10 min intervals during the diel cycle stations 1 (■) and 2 (Δ) on linear (a) and \log_{10} (b) scales. Sunrise was at ~05.00.

were observed from the first to the final observation day (Fig. 5). The samples from the middle of the period (1 and 2 April) contained more pre-spawning fish than the first two samples (30 and 31 March), but the sample sizes in the former two were small and may not be representative for the population.

3.5. Predators

Potential fish predators caught in gillnet and bottom trawl samples are shown in Table 2. Both of the saithe from the gillnet sample had stomachs that were filled with herring eggs. Only one pollock from the bottom trawl sample had been feeding on herring eggs, but a large proportion (73–78%) of the cod, haddock and saithe had consumed herring eggs. No predators with remnants of herring were caught.

4. Discussion

4.1. Distribution and individual state of the herring

Demersal layers of herring were located at shallow depths (30–40 m) on gravel and stone bottom in bank water with salinities between 33 and 34 and temperatures of 5–6 °C

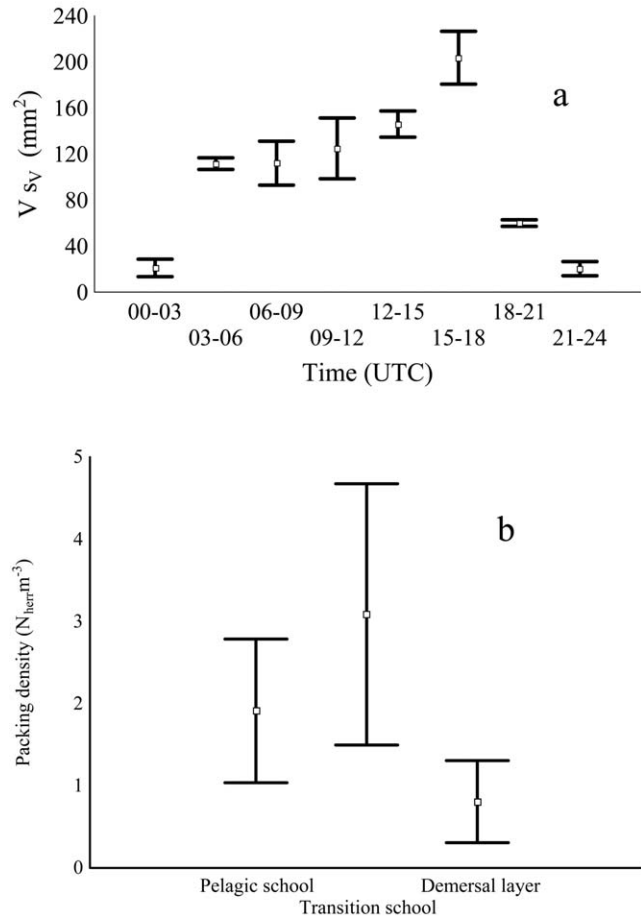


Fig. 4. (a) Linear fish density (mm^2), or S_V ($\text{dB re } 1 \text{ m}^{-1}$) in the linear domain (MacLennan et al., 2002) of herring ± 2 S.E. during the diel cycle. (b) Mean packing density (N_{herr} m^{-3}) of herring ± 2 S.E. for the different school categories.

(Runnstrøm, 1941). There were several indications that most of the herring schools remained at the study site throughout the study period. No immigrating schools, characterized by large size, high packing density and fast and deep swimming

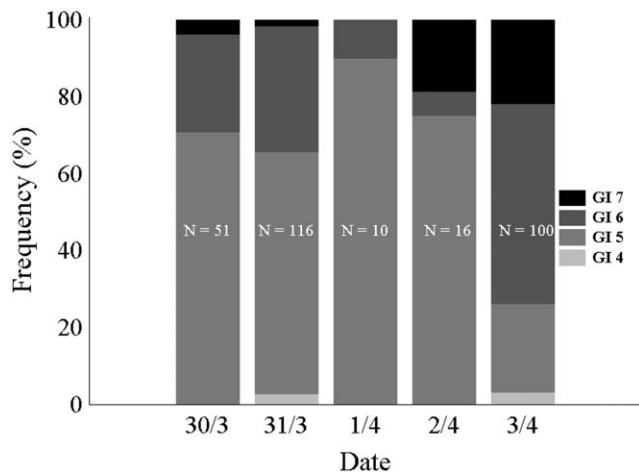


Fig. 5. Distribution of gonad maturity indexes (GI) from day to day in the gillnet samples (N : number of herring sampled; GI 4,5: pre-spawning; GI 6: running; GI 7: spent) (Anonymous, 1962).

Table 2
Numbers and size ranges of potential fish predators caught in the trawl and gillnet samples

Predator species	Sample gear	Size-range (cm)	<i>n</i>
Pollack <i>Pollachius pollachius</i>	Trawl	33–62	98
Cod <i>Gadus morhua</i>	Trawl	29–53	42
Haddock <i>Melanogrammus aeglefinus</i>	Trawl	17–49	23
Saithe <i>Pollachius virens</i>	Trawl	37–59	4
	Gillnet	33–35	2

(Nøttestad et al., 1996) were recorded, and only one school emigrating from the spawning ground was observed. This is consistent with the similar estimated biomasses of the demersal layers during the first two study days, the similar length and age distributions of the samples, and the increase in the proportion of running and spent individuals in the demersal layers from the first (<30%) to the last (>70%) day of the study, suggesting progressive spawning (Axelsen et al., 2000). Herring may have different motivations to remain at the spawning ground. Spent herring may stay at the spawning ground to feed on zooplankton (Nøttestad et al., 1996; Axelsen et al., 2000) and herring eggs (Skaret et al., 2002), or await for other herring to complete spawning and reduce predation risk by leaving the area in larger groups (Pitcher and Parrish, 1993; Axelsen et al., 2000). According to the maturation index, most sampled herring were, however, pre-spawners, assumingly remaining at the spawning ground to complete spawning.

4.2. Diel schooling pattern

The observed schooling behaviour throughout the 24-h cycle from the acoustic records is schematically illustrated in Fig. 6. After dark (18:00–24:00 h) herring concentrated close to the bottom in horizontally extended demersal layers, with few herring observed outside layers. At nighttime (24:00–03:00 h), only a few small patches of herring were observed close to the bottom. Fish may have avoided the vessel, but no avoidance manoeuvres were observed, and herring have high reaction thresholds during spawning

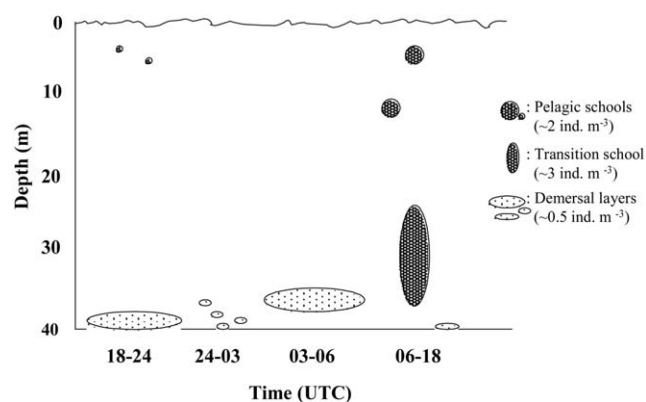


Fig. 6. Generalised schematic illustration of the observed diel pattern in vertical distribution, school shape and packing density of the spawning herring.

(Mohr, 1971; Misund, 1990). Fish schools may disaggregate in darkness (Shaw, 1961; Welsby et al., 1964), but very low light intensities are required for herring to school and spawn (Craig and Priestley, 1960; Kjørsvik et al., 1990; Johannessen et al., 1995). The low recordings at night are thus assumed to be herring staying close to the bottom, where fish echoes and bottom echoes cannot be distinguished (Ona and Mitson, 1996). Spawning herring staying within the acoustic dead zone have been reported before (Johannessen et al., 1995). Our diel cycle observations also showed that nearly all herring recorded at night were located within 10 m from the bottom, and that demersal layers seemed to lift from the bottom around dawn.

During daytime (06:00–18:00 h) pelagic schools, transition schools and small demersal layers were observed indicating a reorganisation of schools. Some transition schools may represent a transition between demersal layers and pelagic schools, whereas others are presumably searching schools. The two “transition” schools being tracked swam deep and had low net swimming speed, characteristic for searching schools (Nøttestad et al., 1996). Slow-swimming transition schools may have visible contact with the bottom to search for suitable spawning substrate, while maintaining group integrity in the pelagic zone for predator avoidance (Axelsen et al., 2000, 2001).

4.3. Timing of spawning

Blaxter and Hunter (1982) suggested that herring depend on light to spawn, but spawning has been reported to take place in darkness (Kjørsvik et al., 1990; Johannessen et al., 1995). Herring may thus adjust spawning time in order to optimise survival and reproduction. As herring adopt low-risk behavioural strategies (Vabø and Nøttestad, 1997; Fernö et al., 1998; Axelsen et al., 2000, 2001), the formation of demersal layers in the evening could be a precautionary behaviour towards predators. The predation pressure at Karmøy is high during the spawning season (Torensen, 1991; Høines et al., 1995, Høines and Bergstad, 1999), and even though none of the sampled gadoids in this study had herring in their stomachs, their size makes them potential predators (Høines et al., 1995). An archetypal pelagic fish like herring is vulnerable when staying on the bottom due to the reduced number of escape directions (Pitcher and Parrish, 1993; Axelsen et al., 2000, 2001). Staying on the bottom should, therefore, be less risky in darkness, since visual predators are less active at low light levels (Løkkeborg and Fernö, 1999).

Earlier studies have shown that the timing of spawning may differ from the one observed here (Johannessen et al., 1995; Nøttestad et al., 1996; Slotte, 1998). This is to be expected taking into account the dynamic trade-off between survival and reproduction changing with prevailing conditions (Magurran, 1993). The present study was conducted at the end of the spawning season (Johannessen et al., 1995; Skaret et al., 2001), with low herring densities compared to the peak of spawning (Johannessen et al., 1995; Slotte and

Dommasnes, 2000). Predation risk decreases with increasing school size due to the dilution effect (Magurran et al., 1985; Milinski, 1993; Axelsen et al., 2001), and the reaction to predators should hence be stronger at the end of the spawning season than at the peak of spawning. Intra-specific competition for a successful deposition of spawn may also influence spawning behaviour (Rajasilta et al., 1997). High competition at the spawning peak may compel herring to spawn during the day even though predation risk is high.

4.4. Spatial dynamics and spawning time of individual herring

The school packing density was high during the day, and mean school packing densities of $\sim 3.0 N_{\text{herr}} \text{ m}^{-3}$ for transition schools is high compared to packing densities for herring schools at different times and areas along the Norwegian coast (1.3–1.9 $N_{\text{herr}} \text{ m}^{-3}$) (Misund, 1993). High packing densities of pre-spawning herring at the spawning location have been reported before (Misund, 1993; Nøttestad et al., 1996; Tremorrow and Claytor, 1998; Axelsen et al., 2000), and herring in the pre-spawning phase may reduce the distance to school neighbours as a precautionary behaviour towards predators. Aggregation prior to spawning should also facilitate the exchange of olfactory stimuli. The low packing density ($0.8 N_{\text{herr}} \text{ m}^{-3}$) of demersal layers could be connected to the low predation risk at night.

Directional spawning has earlier been reported in North Sea herring (Stratoudakis et al., 1998) and the movement direction has been related to current patterns (Lacoste et al., 2001). The occurrence of directional spawning could be connected to the thickness of the egg mats as thick layers may induce high egg mortalities (Runnstrøm, 1941; Taylor, 1971). The shift of spawning site from day to day demonstrates that the search for suitable spawning substrate continues throughout the spawning period.

Interestingly, pre-spawning herring dominated over ripe herring at the bottom in four of five gillnet samples, indicating that herring are present in the demersal layers irrespective of their maturation state, and that they repeat the diel schooling pattern at least once before spawning. It might be argued that pre-spawning fish could have spawned during the night if they had not been caught. However, our biological data indicate that the same herring stayed at the spawning ground for several days and no herring with partly emptied gonads were found, suggesting that spawning took place in one batch.

Why do herring then stay in a high-risk zone if they are not ready to spawn? The determined behaviour of ripe individuals heading for the bottom may influence pre-spawning individuals to follow in connection with the collective behaviour of schools (Fernö et al., 1998; Axelsen et al., 2000; Huse et al., 2002). The ripening process of pre-spawning herring could also be accelerated by staying in close contact with ripening individuals near the bottom in a low-risk period during the night. The release of olfactory stimuli triggers the deposition of milt in males (Ware and Tanasichuk, 1989),

which is needed to induce spawning in both sexes (Stacey and Hourston, 1982; Sherwood et al., 1991).

In conclusion, the horizontal shift of spawning site from day to day demonstrates that the search for suitable spawning substrate continues throughout the spawning period. The pronounced vertical migration is presumably a functional response to predation combined with the fact that herring have to spawn at the bottom. The absence of herring outside the demersal layers at night and the domination of pre-spawning individuals on the bottom indicate that herring performed spawning waves moving in a south-easterly direction from day to day.

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