

State-dependent spatial and intra-school dynamics in pre-spawning herring *Clupea harengus* in a semi-enclosed ecosystem

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ABSTRACT: Distribution and aggregation patterns of pelagic fish in marine ecosystems are difficult to predict and understand, particularly since focussed studies are typically limited to single field efforts. Our study targeted coastal pre-spawning herring *Clupea harengus* in a small semi-enclosed coastal marine ecosystem, investigating their spatial and intra-school dynamic characteristics during the pre-spawning period over 6 consecutive years by means of hydro-acoustic surveying. Prior to spawning, the herring were consistently located at a specific site characterised by a deep trench that led to the deepest basin in the system and provided a potential escape route from predators. As the herring approached spawning, they moved in the direction of the spawning grounds, mimicking the long-distance spawning migration of Norwegian spring-spawning herring. There were consistent trends across years in the school characteristics demonstrating state-dependent schooling dynamics. Schools were found closer to the bottom and more densely packed during late than early pre-spawning. Furthermore, a higher diversity in maturity stage between individual herring, assumed to be associated with stronger motivational conflicts, resulted in increased heterogeneity in school packing density. Our repeated investigations from a small site pinpoint some key behavioural traits in herring, trading off survival, energy saving and reproductive success.

KEY WORDS: Herring · Spawning · Spatial dynamics · School dynamics · Gonad maturity state · Hydro-acoustics

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INTRODUCTION

Pelagic schooling fish are abundant and play a key role in most marine ecosystems (Pikitch et al. 2012). Their spatial distributions are determined by a complex set of motivational and environmental factors (Krebs & Davies 1978, Krause & Godin 1995, Weetman et al. 1998, 1999, Domenici et al. 2002) that makes them difficult to predict (Pitcher & Parrish 1993). Since schooling dynamics are the collective output of behavioural decisions, the spatial positioning at any point in time is the result of individuals balancing stimuli from their environment, their neighbouring conspecifics and their internal motivational states,

such as hunger and fear (Pitcher & Parrish 1993, Parrish & Edelstein-Keshet 1999). In spite of the complex nature of schooling, field studies of schooling dynamics are typically limited to single efforts, either recording multiple schools over large areas (Pitcher & Wyche 1983, Nøttestad et al. 1996, Gerlotto et al. 2006) or monitoring single schools over a restricted period of time (Axelsen et al. 2000). Based on such efforts, plausible adaptive explanations for observed aggregation patterns and behaviour may be put forward, but alternative explanations can usually not be properly assessed, and the biological states of the fish are rarely taken into account (but see Nøttestad et al. 1996, Mackinson 1999, Axelsen et al. 2000).

Herring *Clupea harengus* spend most of their life in schools (Blaxter & Hunter 1982, Fuiman 1989), but schooling dynamics change as they go through different seasonal phases. During the spawning period, the morphological and structural features of herring schools change markedly over time (Nøttestad et al. 1996, Axelsen et al. 2000). The suggested explanation is that differences and changes in individual motivational state affect intra-school dynamics. Individual metabolic rate and aerobic scope have been shown to influence the behaviour of individuals within schools (Killen et al. 2012), and feeding and nutritional state affect individual position preferences (e.g. Krause et al. 1992). Axelsen et al. (2000) observed a single spawning herring school split partially into a pelagic and a demersal component and attributed this to motivational conflicts between pelagic pre- and post-spawners avoiding the risky demersal zone and ripe herring searching towards the bottom to spawn. Such state-induced intra-school dynamics in herring were later supported by both field studies (Johnsen & Skaret 2008) and modelling (Vabø & Skaret 2008).

The schooling dynamics of herring in the pre-spawning period have been less studied. Norwegian spring-spawning (NSS) herring populations typically overwinter in immense schools before undertaking long migrations to coastal spawning areas in January or February (Kvamme et al. 2003, Holst et al. 2004). During overwintering, feeding ceases and gonads build up, while predator avoidance and energy conservation are given priority (Huse & Ona 1996, Slotte 1999). In smaller, local, herring populations the dynamics are different, with shorter distances between pre-spawning and spawning areas and fewer individuals to join together for protection (Fernö et al. 1998). How this influences the schooling dynamics is still unknown.

The semi-enclosed fjord system of Lindåspollene in south-western Norway is inhabited by a small herring population, the Lindås herring, whose presence has been documented regularly since 1962 (ICES 1969). Herring in this ecosystem have been observed to aggregate in a single large school before spawning (Lie et al. 1978, Aksland 1983), but whether this is a

consistent feature of the local population over time has not yet been determined. The main objectives of this study were to establish whether the local herring consistently aggregate in this manner during the pre-spawning period and to quantify the school dynamic features in relation to the development and variability of gonad maturity state.

MATERIALS AND METHODS

Study site

Lindåspollene is a small semi-enclosed coastal marine ecosystem near Bergen in south-western Norway (Fig. 1a). A narrow sill (7.5 m wide, 3.5 m deep) connects the adjacent fjord (Lurefjorden) to Lindåspollene, which consists of 3 distinct, 60 to 90 m deep basins. Between the outer basin Straumsosen (maximum depth: 60 m) and the middle and deepest basin Spjeldnesosen (90 m), there is a 5 to 10 m deep sill (Aure 1972). The inner basin Fjellangervågen

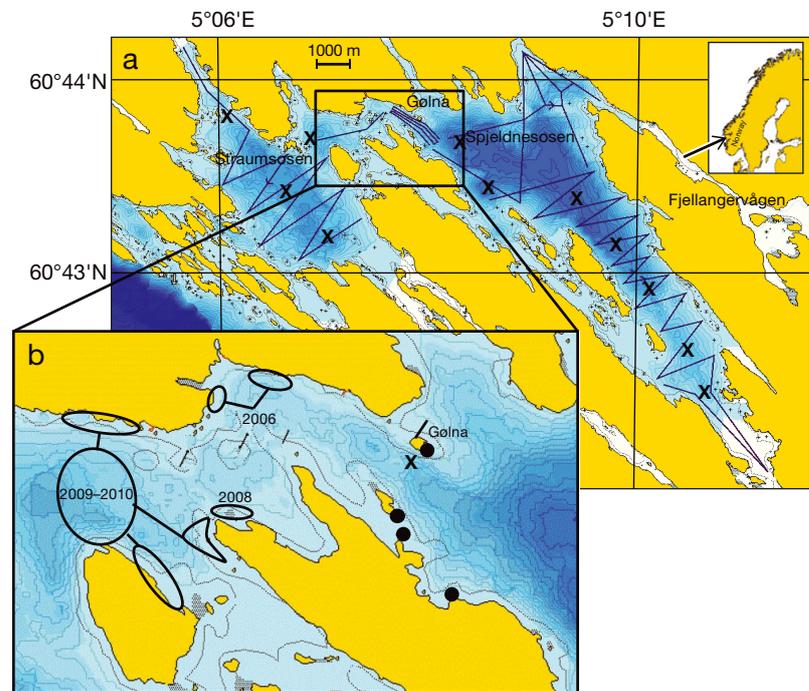


Fig. 1. Lindåspollene, south-western Norway, showing (a) pre-defined transect grid carried out during 2006 to 2011 to investigate the distribution of herring schools, where X denotes positions for CTD stations; (b) main study area, where solid circles denote herring gillnet positions, lines denote predator nets, open ellipses denote documented spawning grounds, and X marks the main CTD station. The underwater platform was placed underneath the herring school at the pre-spawning area (Gølna, between the gillnet and CTD position), and a stationary echosounder was mounted on an aluminium rod attached to the rocks at Gølna in the upper pelagic, pinging horizontally with an angle of 15° towards the surface from 2 m below (see Fatnes 2011)

(75 m) is anoxic from a depth of ~18 m to the bottom (Dahl et al. 1973), and adult herring have rarely been observed there (R. Bergfjord pers. comm.). A general description of the Lindåspollene ecosystem (topography, hydrography, biotic features) can be found in Dahl et al. (1973) and Lie & Dahl (1981). The relatively sheltered Lindåspollene differs from Lurefjorden with regard to environmental conditions, species abundance and food organisms (Dahl et al. 1973, Lie et al. 1978). Lindåspollene is characterised by moderate boat traffic, and only small-scale gillnet and hand line fishing is permitted, making it ideal for small-scale ecosystem studies. During the winter, Lindåspollene is often ice-covered (Wassmann 1983), which puts constraints on fieldwork. The Lindås herring is a key species in this ecosystem (Lie et al. 1978, Langård et al. 2006) and has been described in detail by Lie et al. (1978).

Survey design

In order to locate herring in the pre-spawning period, acoustic surveys (Fig. 1a, modified according to ice cover) were performed by the research vessel RV 'Hans Brattstrøm' (24.3 m LOA [length overall], 6.5 m width, 79 GRT [gross register tonnage]) between February and April from 2006 to 2011. The availability of the vessel placed some constraints on the timing and duration of each monitoring period. All surveys were carried out during daytime. Each survey period started with a 7 h long meso-scale survey at 3 to 5 knots (08:00 to 18:00 h local time), covering most of Lindåspollene, followed by high-density mini-surveys in areas where herring had been observed (Fig. 1a). The mini-surveys were carried out at relatively slow speeds (2 to 3 knots), with transect line spacings of 5 to 15 m. The repeated short and close transect lines involve a certain risk of pseudo-replication, but the studied schooling behaviour may potentially change within seconds, and overall the samples covered different time periods (Fig. 2) with data from several years.

Data collection

Acoustic recording

Acoustic data were recorded using a Simrad 38 kHz split-beam transducer with 12° beam angle. The transducer was mounted on the hull of RV 'Hans Brattstrøm' 1.2 m below the surface. This vessel has

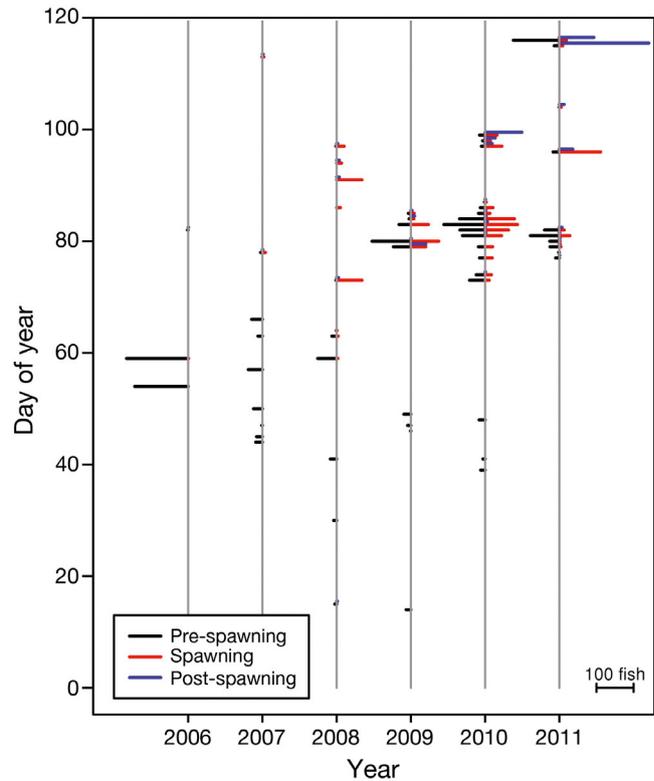


Fig. 2. *Clupea harengus*. Overview of the biological sampling data from 2006 to 2011. Observations of pre-spawning (stages 1–5), spawning (stage 6) and post-spawning (stages 7–8) herring

previously been shown to have negligible impact on herring behaviour (Axelsen et al. 2000, Skaret et al. 2005). In 2010, the observations were supplemented by data collected in February and March using a small boat (15 ft Pioneer) equipped with a 15 HP engine, running a Simrad EK60 split-beam echosounder operating at 120 kHz. The transducer was mounted at the bow of the boat and submerged to about 0.25 m below the surface during operations. Transmission power of 1000 W was used for both echosounder systems, while pulse durations of 1.024 and 0.256 ms were used for the RV 'Hans Brattstrøm' and the Pioneer, respectively. In 2008, a stationary acoustic underwater platform with a Simrad EK60 120 kHz split-beam echosounder (Langård et al. 2008, see Fig. 1) was used in order to monitor diel variations in schooling. A total of 172 school observations were made during the 6 yr of the study.

Biological sampling

Herring were sampled in January to April every year using monofilament gillnets (25 m long by 4 m

high) with stretched mesh sizes of 24 to 36 mm. These mesh sizes were chosen in order to fish selectively for herring larger than 20 cm total length, while allowing juveniles to pass through. The gill-nets were set in 3 series of 3 nets each near the surface (max depth 5 m, Fig. 1b). We may ask whether the herring sampled in the upper 5 m are representative of the acoustic observations, but the recordings from the stationary acoustic platform showed that the school dissolved into surface layers at dusk, which is typical for herring in this period (Blaxter 1985, Skaret 2007). The gillnets were positioned so as not to interfere with boat traffic but to be as close to the pre-spawning area as possible, and always within a 450 m radius (Fig. 1b). Additional monofilament gillnets and entangling nets (57–79 mm mesh sizes) were set on the bottom in order to catch potential predators on herring and herring eggs such as cod *Gadus morhua*, pollack *Pollachius pollachius* and haddock *Melanogrammus aeglefinus*,

and to monitor the presence of herring eggs in their stomachs, serving as indications of the time of spawning. Nets were set in the early evening (between 17:00 and 19:00 h) and hauled the next morning (09:00–12:00 h).

Individual herring were measured for total length (L) to the nearest lower 0.5 cm and total body weight (W) to the nearest lower 1 g, and scored for gonad maturity stage according to an 8-point scale (1–2: immature; 3–5: maturing; 6: running/spawning; 7: spent; 8: resting stage) based on macroscopic visual inspection (Mjanger et al. 2013; Table 1). Herring stomach fullness was estimated in 2008 to 2011 according to a relative 6-point scale on which 1 corresponds to an empty stomach and 6 to a full one (Mjanger et al. 2013).

Fulton's condition factor K (Ricker 1975) was calculated for all sampled herring as:

$$K = 100 \cdot \frac{W}{L^3} \quad (1)$$

Table 1. *Clupea harengus*. Macroscopic maturity stages (1–8) for herring

Maturity stage	Females	Males
1	Immature (a) Juvenile stage. Gonads thread-like, thin and completely transparent and colourless. Difficult to determine sex.	Immature (a) Juvenile stage. Gonads thread-like, thin and completely transparent and colourless. Difficult to determine sex.
2	Immature (b) Gonads are somewhat larger in volume, sex is easier to determine. The gonads continue to be transparent and colourless with a hint of colour.	Immature (b) Gonads are somewhat larger in volume, sex is easier to determine. The gonads continue to be transparent and colourless with a hint of colour.
3	Maturing (a) Gonads opaque but developed in volume. Distinct veins. Ovaries have yellow/white eggs in lamellae and can occupy half of the body cavity or more.	Maturing (a) Gonads opaque but developed in volume. Distinct veins. Testes white or with white spots. Firm consistency.
4	Maturing (b) Gonads larger in volume. Distinct veins. Ovaries yellowish or white, can occupy 2/3 or more of the body cavity depending on the condition of the fish. Eggs can be seen distinctly and feel grainy. Eggs in the front part of the gonad are beginning to become transparent.	Maturing (b) Gonads larger in volume. Distinct veins. Testes light grey or white, milt thick and slow-flowing.
5	Maturing (c) Ovaries fill the entire body cavity. Most of the eggs are transparent.	Maturing (c) Testes are grey or white. Milt runs easily. Gonads are not yet running. However, light pressure on the abdomen causes the milt to run.
6	Spawning Running gonads. Light pressure on the abdomen causes the eggs to run.	Spawning Running gonads. Light pressure on the abdomen causes the milt to run.
7	Spent Gonads loose, contain remaining eggs.	Spent Gonads loose, contain remaining milt.
8	Resting Gonads are small. Eggs are not visible. Difficult to distinguish from stages 2/3.	Resting Gonads are small. Difficult to distinguish from stages 2/3.

Hydrographical data

Ambient temperature, salinity and oxygen conditions were monitored in the pre-spawning area and at selected sites in Straumsosen and Spjeldnesosen (Fig. 1a) by means of vertical CTD casts using a SAIV model SD204. All CTD casts were deployed from the surface to 5 m above the bottom. Only downcast data were processed.

Analyses of acoustic data

Volume backscattering strength (S_v ; dB re 1 m^{-1}) measurements from the acoustics were analysed using the Sonardata Echoview v.5.1[©] software. Herring schools were readily identified and distinguished from other acoustic backscatter using a minimum S_v threshold of -70 db. Measurements of mean school vertical extension (m), mean school depth (D ; m) and distance from the bottom to the deepest extent of the school (m) were recorded. The herring packing density ρ (m^{-3}) was estimated according to:

$$\rho = 10^{\left(\frac{S_v - TS}{10}\right)} \quad (2)$$

and

$$TS = 10 \cdot \log_{10}(\sigma_{bs}) \quad (3)$$

where σ_{bs} is the backscattering cross section (m^2) of the acoustic target, S_v is the mean school volume backscattering strength (dB re 1 m^{-1}), and TS is the target strength (dB re 1 m^2) (MacLennan et al. 2002). The following relationship between TS , L and D was used (Ona 2003):

$$TS = 20 \cdot \log_{10}(L + 0.25) - 2.3 \cdot \log_{10}\left(\frac{1+D}{10}\right) - b_{20} \quad (4)$$

where b_{20} for herring in February corresponds to -66.1 dB and -68.3 dB for 38 kHz and 120 kHz, respectively (Ona et al. 2001). Note the addition of 0.25 cm to the total length in order to compensate for the practice of rounding down the recorded total length.

The circularity of the school (C) was calculated as:

$$C = \left(\frac{(5 \times 10^5) \cdot \left(P \sqrt{\frac{A}{\pi}} \right)}{A} \right)^{-1} \quad (5)$$

where P and A are the estimated vertical cross section perimeter and area of the school, respectively. The heterogeneity in packing density within a school vertical cross section, or the school roughness R_{sc} (Nero & Magnuson 1989, Gerlotto et al. 1999) nor-

malized to ρ was calculated as:

$$R_{sc} = \frac{\sqrt{R_h \cdot R_v}}{\rho} \quad (6)$$

where the roughness in the horizontal (R_h) and vertical (R_v) directions were calculated according to:

$$R_h = \sum \frac{(E_{ij} - E_{i,j+1})^2}{N-1} \quad (7)$$

$$R_v = \sum \frac{(E_{ij} - E_{i+1,j})^2}{N-1} \quad (8)$$

and where E denotes a single sample bin within the school, i is the row (depth) index, j is the column ('ping') index, and N is the total number of sample pairs. Different volumes of single sample bins with depth due to the widening of the sound beam were not corrected for.

In order to assess the possible influence of nearby predators on the recorded school parameters, all single targets in the vicinity of schools were manually identified and classified as potential predators based on echogram appearance. For each school recording, the presence or absence of predators was noted.

Location of the spawning grounds

The location and timing of spawning events were documented whenever possible. In 2006 and in 2008 to 2010, the spawning locations were identified on the basis of video observations of herring spawn and visual observations of large aggregations of common eider ducks *Somateria mollissima*, which are frequent foragers on herring eggs (Kjørsvik et al. 1990). The silicon intensifier target (high resolution, wide angle) underwater camera was primarily used for confirming egg deposition on the bottom after spawning and only occasionally used for underwater filming of herring schools, other fish species and bottom substrate. In these years, the spawning grounds were located in the north-western part of Spjeldnesosen, near the shallow threshold separating Straumsosen and Spjeldnesosen (Fig. 1b). The bottom topography at these spawning sites was mostly flat, with a substrate consisting mainly of rocks and boulders. In 2007 and 2011, the locations of the spawning grounds could not be identified.

Data analysis

Maturation model

The biological dataset for 2006 to 2011 varied with regard to sampling effort between years, depending

on vessel availability (Fig. 2). Statistical modelling was used to calculate the probability of occurrence of herring maturity stages 4 to 7 by day of the year in order to interpolate the progression of gonad maturity in periods without gillnet samples. The sampling locations are shown in Fig. 1. We used generalized linear mixed-effects models (GLMMs) with a binomial error term for the calculation of probabilities. The response variable was binary and describes whether a fish was within the given maturation stage or not. A continuous variable that defined the day of the year was the only predictor. In order to allow for a changing slope depending on day of the year, a second-order polynomial was included in the model. If non-significant, it was removed from the model. Since samples were acquired over several years, the model took account of random variability due to year.

In order to evaluate whether the individual maturity state of the herring affects schooling dynamics, we defined 2 categories of maturation: 'early pre-spawning' (probability of Stage 6 < 0.5) and 'late pre-spawning' (probability of Stage 6 \geq 0.5). A GLMM with a quasi-Poisson error term was used to test for differences between the categories. We used Poisson regression since the variance in the different measures of school dynamics tended to increase with the mean. Depth in the area where each school was recorded was used as a covariate in the model. The 6 school characteristics (response variables) that were tested in separate models were (1) packing density, (2) vertical extension, (3) mean depth, (4) distance from bottom, (5) circularity and (6) roughness.

In order to assess whether differences in maturity stages within a school affect its dynamics, we followed 2 main steps. First, we used the probability curves to calculate a maturity diversity index (MDI) that describes the expected diversity of herring maturity within the school depending on day of the year. The MDI values were calculated by using the Shannon index (Shannon 1948, Simpson 1949) on stage probabilities derived from the maturity stage models. The final MDI measures were rescaled to range only between 0 and 1 (MDI/max MDI). Secondly, the effects of MDI on school dynamics were evaluated through the same type of GLMM as described above for the comparisons between early and late pre-spawning periods. In these models, the MDI values were divided into low and high MDI levels, where the low and high levels are <0.5 and \geq 0.5, respectively. The depth in the area where each school was sampled was used as a covariate in the models.

Predation pressure

The effect of predation presence on school dynamics were analysed using the same GLMMs as described above, but with predation as the predictor. This predictor contained the levels 'present' or 'absent'. All statistics were performed using R version 2.15.2 (www.r-project.org).

RESULTS

With few exceptions, the hydrographic conditions were well within the ranges normally acceptable for herring (Runnström 1941). The average temperatures at the pre-spawning area were generally between 5 and 7°C, but 2010 and 2011 were more than 2°C colder than the preceding years. Salinity was generally 30 to 32 PSU, and somewhat lower close to the surface. The water column was generally well oxygenated throughout the study period (>3 mg l⁻¹ at depths shallower than 30 m; see also Fatnes 2011). Oxygen levels averaged 7 to 8 mg l⁻¹ but were lower in deep waters early in the study period. The hydrographical conditions at 30 m depth (school depth) were generally similar in the pre-spawning area and other localities in the system (Fig. 1a). Temperature and salinity were lower than in most other coastal and fjord areas (Bagøien et al. 2001).

In all years, our observations suggest that the herring were present in 1 school. The herring displayed a high degree of fidelity to a small pre-spawning area around Gølna Island. The topography of this area is characterised by a trench that gradually becomes shallower towards the north-west (Fig. 1). Early in the pre-spawning period, the school was usually observed in the north-western part of the trench, but at the end of the pre-spawning period, the herring generally shifted north-westward in the direction of the shallower spawning grounds (linear mixed effect, LME, ANOVA $p < 0.001$).

During late pre-spawning, the school stayed closer to the bottom than during early pre-spawning, and school packing density was also higher (Tables 2 & 3). No differences in the other characteristics were found (Table 3).

The MDI reached its maximum prior to the late pre-spawning period (Fig. 3). The school in the high MDI period had higher packing density, roughness and circularity, while remaining closer to the bottom than the school in the low MDI period, and the school vertical extension was lower in the high MDI period (Table 3).

Table 2. *Clupea harengus*. Summary of school descriptor values based on acoustic recordings from 2006 to 2011. 'Early' and 'Late' refer to early and late pre-spawning periods (see 'Materials and methods' for details)

Parameter	Period	Year	Mean	N	SD	Min.	Max.	Parameter	Period	Year	Mean	N	SD	Min.	Max.		
Packing density ρ (ind. m ⁻³)	Early	2006	0.95	17	0.94	0.03	2.96	Distance from bottom (m)	Early	2006	6.78	17	4.44	1.54	16.68		
		2007	1.61	39	1.35	0.19	5.87			2007	7.52	39	4.55	0.00	16.09		
		2008	0.17	7	0.08	0.08	0.30			2008	8.05	7	2.89	4.16	12.10		
		2009	0.88	38	0.96	0.06	4.81			2009	10.73	38	9.69	0.00	39.14		
		2010	0.69	12	0.93	0.02	3.37			2010	3.54	12	5.34	0.00	15.30		
		2011	0.36	19	0.21	0.01	0.73			2011	9.45	19	4.23	3.28	16.36		
	Late	2006	0.35	1	–	0.35	0.35		Late	2006	0.64	1	–	0.64	0.64		
		2009	2.81	14	4.07	0.11	13.26			2009	2.48	14	3.51	0.00	9.22		
		2010	1.63	7	1.22	0.44	4.05			2010	0.00	7	0.00	0.00	0.00		
		2011	0.47	18	0.58	0.02	2.55			2011	6.47	18	4.62	2.01	17.66		
	Vertical extent (m)	Early	2006	6.74	17	2.12	4.32		11.15	Circularity (%)	Early	2006	43.96	9	9.29	29.31	54.15
			2007	5.35	39	1.65	2.50		10.44			2007	37.52	39	10.82	18.94	75.59
			2008	4.35	7	0.90	2.99		5.48			2008	12.31	1	–	12.31	12.31
2009			8.03	38	3.00	3.18	13.70	2009	40.09			8	14.38	27.00	60.61		
2010			6.28	12	2.80	3.61	12.98	2010	38.03			7	9.75	26.99	49.42		
2011			4.92	19	1.66	2.09	7.89	2011	47.83			14	9.89	33.72	71.43		
Late		2006	8.20	1	–	8.20	8.20	Late	2006		49.98	1	–	49.98	49.98		
		2009	5.40	14	1.23	3.68	7.56		2009		40.48	13	9.89	26.29	52.11		
		2010	5.30	7	1.22	3.41	6.76		2010		33.18	4	3.92	28.97	37.48		
		2011	5.04	18	2.02	1.83	8.84		2011		42.70	17	8.42	29.57	54.74		
Mean depth (m)		Early	2006	16.59	17	2.16	13.28	21.68	Roughness (dB re 1 m ² m ⁻³) × 10 ³		Early	2006	1.88	9	0.85	0.70	3.27
			2007	16.08	39	1.92	10.82	21.16				2007	0.92	39	0.36	0.46	1.75
			2008	15.52	7	2.01	12.95	18.64				2008	0.77	7	0.22	0.56	1.19
	2009		23.37	38	5.13	16.55	36.87	2009		0.87		38	0.53	0.37	2.63		
	2010		29.49	12	12.25	16.14	64.20	2010		3.10		12	6.48	0.29	23.52		
	2011		18.47	19	3.87	14.35	28.50	2011		1.91		18	1.15	0.69	5.05		
	Late	2006	25.45	1	–	25.45	25.45	Late		2006	1.49	1	–	1.49	1.49		
		2009	21.53	14	4.31	15.83	28.89			2009	0.92	14	0.71	0.46	2.75		
		2010	22.47	7	7.07	16.23	33.49			2010	4.45	7	2.09	2.13	7.82		
		2011	17.12	18	3.53	5.64	21.13			2011	1.59	18	0.85	0.50	3.52		

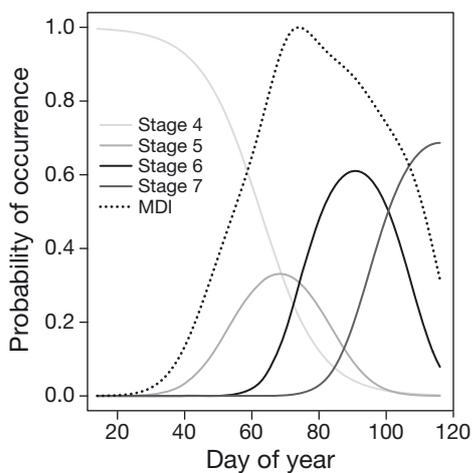


Fig. 3. *Clupea harengus*. Probabilities of finding a given maturation stage of herring depending on time of the year, where Day 0 represents day of year 1 (1 January). The dotted line shows the maturity diversity index (MDI) describing the potential diversity in maturation stages within a school (see 'Materials and methods' for further explanations)

The sampling effort for potential predators on herring varied between years, but the gillnet samples showed that large cod were the most important predator (Table 4), with 60% of cod >50 cm in length with herring in their stomachs, while over 80% of cod <50 cm had fed on herring eggs. The vertical school extension unexpectedly increased when predators were present (GLMM ANOVA, $p < 0.05$). Other school characteristics were not significantly influenced by predator presence.

Anecdotal recordings of predatory seabirds were made. Great cormorants *Phalacrocorax carbo* were frequently observed in all years. These opportunistic foragers (Steven 1933) can dive to depths of 32 m (Grémillet et al. 1999) but feed largely on smaller gadoids (Anker-Nilssen & Lorentsen 2004). Harbour seals *Phoca vitulina*, which are known predators of herring (Haug 1998), were occasionally observed in 2009 and 2010.

Table 3. Summary of results from the generalized linear mixed-effects models (GLMMs) investigating the effect of maturity state and diversity in maturation stages on school descriptors. Parameter estimates and associated test statistics and p-values are presented for the differences between early and late pre-spawning period, and between low and high maturity diversity index (MDI). The effect of depth in the area of sampling is the covariate in both models. Note that the parameter estimates are on the scale of the link function. Days of year > 100 are not included

Response variable	Predictor	df	Level	Parameter estimate	<i>t</i>	p	
Packing density ρ (ind. m^{-3})	Maturity	163	Early	1.053	2.018	0.045	
			Late	1.521			
	Covariate (depth)	163	MDI	Low	-0.046	3.071	0.003
				High	0.030		
			High	0.947		<0.001	
	Covariate (depth)	163		-0.029	2.159	0.032	
Vertical extension (m)	Maturity	163	Early	1.655	1.905	0.059	
			Late	1.507			
	Covariate (depth)	163	MDI	Low	0.004	1.395	0.165
				High	1.958		
			High	1.632		<0.001	
	Covariate (depth)	163		<0.001	0.173	0.863	
Mean depth (m)	Maturity	163	Early	2.468	1.775	0.078	
			Late	2.535			
	Covariate (depth)	163	MDI	Low	0.015	10.369	<0.001
				High	2.394		
			High	2.493		0.007	
	Covariate (depth)	163		0.016	10.718	<0.001	
Distance from bottom (m)	Maturity	163	Early	0.164	2.703	0.008	
			Late	-0.252			
	Covariate (depth)	163	MDI	Low	0.053	12.885	<0.001
				High	0.292		
			High	-0.039		0.017	
	Covariate (depth)	163		0.053	12.293	<0.001	
Circularity (%)	Maturity	104	Early	3.588	0.420	0.675	
			Late	3.561			
	Covariate (depth)	104	MDI	Low	0.004	0.888	0.377
				High	3.398		
			High	3.567		0.012	
	Covariate (depth)	104		0.006	1.445	0.151	
Roughness (dB re 1 $m^2 m^{-3}$)	Maturity	154	Early	-5.774	0.355	0.723	
			Late	-5.835			
	Covariate (depth)	154	MDI	Low	-0.025	2.423	0.017
				High	-6.800		
			High	-6.110		<0.001	
	Covariate (depth)	154		-0.006	0.646	0.519	

The lengths of the herring ranged from 305 to 322 mm and weights from 217 to 293 g (Table 5). The condition factor (K) ranged from 0.75 to 0.88 and was significantly different between years (linear model, LM, ANOVA, $p < 0.001$). Herring generally had empty stomachs, with only about 3% (stomach fullness 2, $n = 102$; 3, $n = 3$; 4, $n = 2$) of the fish in the early pre-spawning period and around 11% (stomach fullness 2, $n = 1$; 3, $n = 2$) in the late pre-spawning period having any contents.

DISCUSSION

To the best of our knowledge, this is the first *in situ* study of the dynamics of spatial distribution and schooling behaviour of herring throughout the spawning season. The study was repeated over 6 consecutive years. Early pre-spawning herring in the semi-enclosed ecosystem were aggregated in one school that consistently displayed fidelity to an area with close access to the deepest basin in the

Table 4. *Gadus morhua*. Summary of cod stomach content from gillnet samples during early and late pre-spawning periods from 2006 to 2011 for cod length >50 cm and <50 cm. 'n sets' denotes number of gillnet sets. No data were available for 2010. 'Early' and 'Late' refer to early and late pre-spawning periods (see 'Materials and methods' for details). Values are mean \pm SD

Year	Period	n sets	Cod size >50 cm			Cod size <50 cm		
			Mean n cod in catch	n herring in stomachs	n empty stomachs	Mean n cod in catch	n herring in stomachs	n empty stomachs
2006	Early	2	1.50 \pm 0.71	2	1	2.00 \pm 1.41	0	2
2006	Late	3	3.67 \pm 2.89	2	2	1.63 \pm 2.89	0	0
2007 ^a	Early	6	2.00 \pm 1.34	2	2	3.00 \pm 3.52	0	3
2008	Early	2	3.00 \pm 1.41	2	2	0.50 \pm 1.00	0	2
2008	Late	6	4.33 \pm 2.80	17	6	4.33 \pm 5.51	0	0
2009	Late	1	1.00	0	1	2.00	0	0
2011	Early	2	1.50 \pm 0.71	5	1	6.50 \pm 2.12	4	5

^aIn 2007, 1 pollock was also caught and had 1 herring in its stomach

Table 5. *Clupea harengus*. Summary of herring biological parameters from gillnet samples. Values are mean \pm SD. K: Fulton's condition factor

Year	n	Length (mm)	Weight (g)	K
2006	301	313 \pm 15	271 \pm 30	0.88 \pm 0.08
2007	179	306 \pm 18	253 \pm 49	0.87 \pm 0.10
2008	307	312 \pm 20	251 \pm 54	0.81 \pm 0.09
2009	464	322 \pm 18	293 \pm 54	0.87 \pm 0.12
2010	612	319 \pm 18	260 \pm 45	0.80 \pm 0.08
2011	911	305 \pm 29	217 \pm 63	0.75 \pm 0.10

system. As maturation progressed, the herring aggregated closer to the spawning ground. When approaching spawning, the school also remained closer to the bottom, while packing densities increased. Increased diversity of gonad maturity stages between individuals within the school was found to increase the heterogeneity of the school packing density.

The behaviour of herring during the spawning period can be explained in terms of multiple trade-offs between predation, feeding and spawning (Nøttestad et al. 2004). The herring displayed low feeding activity. Herring normally do not feed before spawning, but start shortly afterwards (e.g. Huse & Ona 1996, Slotte 1999), reflecting the change in trade-offs between feeding and reproduction (Nøttestad et al. 1996, Axelsen et al. 2000). The presence of predators presumably influenced the school dynamics. The abundance and consumption and digestion rates of cod could not be quantified, but our gillnet samples suggested that herring was a main prey for large cod. Herring that aggregate within the same restricted area season after season should be an easy target for predators.

Spatial dynamics and site fidelity

Pre-spawning herring aggregated in one major school at the same location in all 6 years of our study, confirming previous anecdotal observations (Lie et al. 1978, Aksland 1983). Swimming in a school may reduce the hydrodynamic cost of swimming (e.g. Herskin & Steffensen 1998, Svendsen et al. 2003, Killen et al. 2012). Staying within a limited area could be an energy-saving strategy (see Mackinson 1999), and video observations showed that maturing herring swam slowly around in a circle with extended pectoral and pelvic fins, permitting energy-efficient gliding behaviour while avoiding sinking (see also Huse & Ona 1996, Kaartvedt et al. 2009). The hydrography in the pre-spawning area did not differ markedly from the surrounding areas within Lindåspollene, with similar ranges in temperature and oxygen levels (see also Fatnes 2011, Langård 2013). On the other hand, the pre-spawning location differs in topography and is characterised by a trench that leads directly to the deepest basin (Spjeldnesosen, ~90 m). The trench could function as an 'emergency exit' for herring under predatory attack. Herring have been reported to hide in deep trenches close to spawning grounds during the day in order to avoid predation (Runde 2005, Skaret 2007), and massive aggregations of overwintering herring in northern Norway stay deep to avoid killer whale attacks (Nøttestad et al. 2002). Herring are specialists in vertical escape (Blaxter 1985), and the fish in Lindåspollene appear to have adopted a precautionary approach by staying in a place that provides an escape route to deeper waters. As spawning approached, the herring tended to shift their distribution closer to the spawning grounds. Tracking of individual fish in 2010 confirmed this meso-scale movement pattern (L. Langård et al. unpubl.).

School dynamic patterns as a function of maturation state

Herring aggregated in one dense school close to the bottom when approaching spawning. In a study of individually tagged herring (L. Langård et al. unpubl.), individuals were observed to move in different directions resulting in school split-up when approaching spawning, likely demonstrating individual priorities of spatial positioning during a phase of potentially conflicting interests. In the present study, individual herring could not be tracked.

Higher packing densities and shorter distances to the bottom closer to spawning were also observed in earlier studies elsewhere (Nøttestad et al. 1996, Mackinson 1999, Skaret 2007). High packing density is usually attributed to anti-predator behaviour (Bredner 1951), and herring may seek shelter behind conspecifics for protection (e.g. Hamilton 1971, Pitcher & Wyche 1983). Close contact with ripening individuals releasing pheromones could also accelerate the maturation process (Ware & Tanasichuk 1989, Scott et al. 1994, Winters & Wheeler 1996).

The high heterogeneity in packing density (roughness) associated with a high MDI presumably reflects conflicts between individuals in different motivational states and different stages of maturation. There were 2 unexpected findings with regard to vertical school extension. A high MDI should be expected to lead to more variable individual depth preferences resulting in increased school extension (Axelsen et al. 2000, Skaret 2007, Johnsen & Skaret 2008, Vabø & Skaret 2008), but the vertical extension tended to be low when MDI was high. In the prevailing situation with a relatively small school keeping together for a long time period, herring not ready to spawn may stay close to the bottom together with herring approaching spawning in connection with the collective behaviour of herring (Skaret et al. 2003). Another observation was that the vertical school extension increased in the presence of predators, contrary to the expectations that herring would aggregate more tightly under predatory threat. This result might be due to vertical avoidance reactions to predator attacks. Abrahams & Colgan (1985) also suggested that shoals exposed to a predatory threat should increase vertical extension to decrease visual obstruction.

Comparisons with oceanic stocks like NSS herring

The spawning strategy of the local herring in Lindåspollene seems to be shaped primarily by the

small population size, confinement to the restricted area and the collective processes that are crucial to successful survival and reproduction. Some aspects of the behaviour are common to other herring populations, whereas others are specific and some behaviours 'mimic' the behaviour of oceanic populations. The environment in Lindåspollene differs in several respects from the outside marine environment (Dahl et al. 1973, Lie et al. 1978). However, the herring do not feed before spawning and their only concern should be to build up the gonads, save energy and avoid being eaten. Temperature and deepwater oxygen levels are generally lower in Lindåspollene than in the adjacent fjords (Eiane et al. 1999, Bagøien et al. 2001), but herring can also periodically experience hypoxia in Norwegian fjords (Dommasnes et al. 1994, Hognestad 1994), as well as in the Baltic and the Kattegat (Domenici et al. 2002). In addition, the observed interannual variations in hydrographic conditions in Lindåspollene were not associated with marked changes in the spatial and schooling dynamics. The risk of predation in Lindåspollene compared to the variable predation pressure outside (Høines & Bergstad 1999, Runde 2005) is not known.

The most pronounced difference between the herring in Lindåspollene and oceanic NSS herring was the short migration distances. The overwintering, migration and pre-spawning periods appear largely to merge. Yet, the migration patterns in Lindåspollene bear similarities on a small scale to those of NSS herring. The small meso-scale shift observed in the distribution of the Lindås herring between the early and late pre-spawning period may be seen as a weak reflection of the long-distance migration of NSS herring from their overwintering areas to the spawning grounds. NSS herring have been observed to aggregate close to the spawning area some time before moving on to the spawning grounds (Baker 1978, Aasen 1982, Nøttestad 1994), which could correspond to the observed meso-scale distributional shift in local herring.

Some NSS herring are also present in Lindåspollene during the spawning period (Johannessen et al. 2009, unpubl. obs.), but the herring in our study nevertheless remained in one was found school for the duration of the study period. In oceanic NSS herring, the school size to decrease markedly between immigrating schools and schools at the spawning grounds, indicating that the school split into smaller units (Nøttestad et al. 1996). Individual state differences of herring in Lindåspollene could be expected to increase the tendency to split, and individual herring have been observed to split from and rejoin with the

main school (L. Langård et al. unpubl.). However, the number of herring in the system is restricted, and splitting may mean that group size drops below a critical size (Fernö et al. 1998, Krause & Ruxton 2002). A small school of NSS herring has also been observed to remain joined for a duration of 5 d during spawning, but close to spawning the school segregated vertically into a pelagic and a demersal component, indicating conflicts between individuals of different states (Axelsen et al. 2000). Likewise, persistent vertical hourglass formations were observed in huge herring shoals in the main spawning fields in the Møre region in central Norway, with the proportion of spawners to pre- and post-spawners higher in the lower than in the upper component (Johnsen & Skaret 2008). Other school characteristics in oceanic NSS herring also changed throughout the spawning season (Nøttestad et al. 1996). As in our study, the school density was observed to increase when approaching spawning, but unlike in our study, the maturation stage could not be recorded. Studies in small systems may allow a better resolution of the dynamics compared to open-ocean studies involving complicated interactions between the spatial and temporal dynamics.

CONCLUSIONS

This detailed long-term study of herring school dynamics in a small-scale ecosystem has revealed state-dependent schooling patterns that are also relevant for larger oceanic herring populations. Throughout the 6 yr of our study, the herring aggregated within a small area for a long period before spawning, confirming that the pattern observed in the 1970s (Lie et al. 1978, Aksland 1983) is consistent. This location may be understood as a 'base camp' close to the spawning grounds adjacent to the deepest basin in the system, permitting vertical escape. The preferred conservative strategy of herring (Fernö et al. 1998, Corten 2001, Huse et al. 2010) may well stabilise the choice of pre-spawning area. The meso-scale distributional shift closer to spawning may be analogous to the long-distance migration of NSS herring to the spawning grounds.

The state of maturation influenced several aspects of behaviour. This demonstrates the need to consider physiological and behavioural states if we wish to understand the dynamics of fish schools. The diversity in maturation states influenced the roughness and vertical extent of the school. Similar indices of variability in maturation state and satiation state

(stomach fullness and condition factor) could have potential in explaining the dynamics of fish schools. Since school dynamics are the output of behavioural decisions in individuals, it is essential to learn more about the behaviour of single fish. Studies of individually tagged herring (L. Langård et al. unpubl.) could pave the way from state-dependent individual behaviour to a better understanding of dynamics at the school level.

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