

State-dependent spatial and intra-school dynamics in pre-spawning herring (*Clupea harengus* L.): site fidelity within a semi-enclosed coastal marine ecosystem

Lise Langård^{1,2*}, Ole Andreas Fatnes¹, Arne Johannessen¹, Georg Skaret², Bjørn Erik Axelsen², Leif Nøttestad², Aril Slotte², Knut Helge Jensen¹, Anders Fernö¹

¹Department of Biology, University of Bergen, PO Box 7803, NO-5006 Bergen, Norway,

²Institute of Marine Research, PO Box 1870 Nordnes, NO-5817 Bergen, Norway

*Corresponding author: Lise.Langaard@imr.no

ABSTRACT

Distribution and aggregation patterns of pelagic fish in marine ecosystems are hard to predict and understand, particularly since focused studies are typically limited to single field efforts. Our study targets coastal pre-spawning herring 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

INTRODUCTION

Pelagic schooling fish are abundant and play a key role in most marine ecosystems (Pikitch et al. 2012). Their spatial distribution is determined by a complex set of motivational and environmental factors (Krebs & Davies 1978) that makes it hard 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 compromising stimuli from their environment, their neighbouring conspecifics and their internal motivational states, such as hunger and fear (Pitcher & Parrish 1993, Parrish & Edelman-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 or by monitoring single schools over a restricted period of time. 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 spend most of their life in schools (Blaxter & Hunter 1982, Fuiman 1989), but schooling dynamics change as they go through different life history and seasonal phases. In 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. Axelsen et al. (2000) observed a single spawning herring school split partially into one pelagic and one 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 have later been verified both in field studies (Johnsen & Skaret 2008) and through 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 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 (Anon 1969). The herring in this ecosystem has 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. Two specific questions were addressed: (i) Does gonad maturity influence schooling dynamics? and (ii) Does variability in gonad maturity between individuals affect schooling dynamics?

MATERIALS AND METHODS

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 (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 (pers. comm. R. Bergfjord). A general description of the Lindåspollene ecosystem (topography, hydrography, biota features) can be found in Dahl et al. (1973) and in Dahl & Lie (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 characterized 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 the 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, 6.5 m width, 79 GRT) 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 in daytime. Each survey period started with a 7 hour-long meso-scale survey at 3-5 knots (08:00-18:00 h local time), covering the 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 (2-3 knots), with transect line spacings of 5-15 m. The repeated short and close transect lines involves a certain risk of pseudoreplication, but the studied schooling behaviour may potentially change within seconds, and overall the samples covered different time periods (Fig. 2a) with data from several years.

Data collection

Acoustic recording

Acoustic data were recorded using a Simrad EK60 split-beam echosounder operating at 38 kHz. The transducer was mounted on the hull of RV ‘Hans Brattstrøm’ 1.2 m below the surface. This vessel has 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 (Svelling et al. 2002, Langård et al. 2008) was used in order to monitor diel variations in schooling. A total of 172 school observations were made during the 6 years 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 24-36 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 gillnets were set in 3 series of 3 nets each near the surface (max depth 5 m). 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 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 afternoon (between 17:00 and 19:00) and hauled the next morning (09:00-12:00).

Individual herring were measured for total length (L) to the nearest 0.5 cm below and total body weight (W) to the nearest g below, 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. 2011). Herring stomach fullness was estimated in 2008 to 2011 according to a relative 6-point scale on which 1 corresponded to empty stomach and 6 to full (Mjanger et al. 2011).

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

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

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 1m^{-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

$$TS = 10 \cdot \text{LOG}_{10}(\sigma_{bs}) \quad (3)$$

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 1m^{-1}) and TS is the Target Strength (dB re 1m^2) (MacLennan et al. 2002). The following relationship between TS, L and D was used (Ona 2003):

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

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:

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

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) normalized 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.

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). 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. 2a). 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. 2b. 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 two 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 co-variate 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, 6) Roughness.

In order to assess whether differences in maturity stages within a school affects its dynamics we followed two 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 co-variate 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 predictor. This predictor contained the levels “present” or “absent”. All statistics were performed using R version 2.15.2 (R Development Core Team 2012, <http://www.r-project.org>).

RESULTS

With few exceptions, the hydrographic conditions were well within the ranges normally acceptable for herring (Runnström 1941, Fig. 3). Average temperatures were generally between 5 and 7 °C, but 2010 and 2011 were markedly colder than the preceding years. During early pre-spawning in 2010, temperatures were < 3 °C, which is close to temperatures herring tend to avoid (Østvedt 1965). Salinity was generally between 30 to 32 PSU (Fig. 3), albeit somewhat lower close to the surface, probably due to freshwater run-off. Oxygen levels averaged 7 to 8 mg l⁻¹ but were lower in deep waters early in the study period and were generally lower early in the pre-spawning period in 2009 and 2010 and in the late pre-spawning period of 2007 (Fig. 3). Our data did not permit a formal analysis linking environment and behaviour, but we note that 2009 and 2010 had cold surface waters corresponding with deep school distribution during early pre-spawning (Fig. 3 and Table 1).

In all years our observations suggest that the herring were present in one 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 (Figs. 1 and 4). Most schools were observed in the north-western part of the trench, but the herring generally shifted north-westwards towards the shallower spawning grounds during the pre-spawning periods (Linear Mixed Effect; LME ANOVA $p < 0.001$; Fig. 4).

During late pre-spawning, schools stayed closer to the bottom than during early pre-spawning, and school packing densities were also higher (Tables 1 and 2). No differences in the other parameters were found (Table 2).

The Maturity Diversity Index (MDI) reached its maximum prior to the late pre-spawning periods (Fig. 2b). Schools in the high MDI period had higher packing densities, roughness and

circularity, while they remained closer to the bottom than schools in the low MDI period, and the school vertical extension was lower in the high MDI period (Table 2).

The gillnet samples of potential predators confirmed that cod had been feeding on herring (Table 3). Adult consumers of herring were mostly cod > 50 cm in length, while stomachs with content in cod < 50 cm usually contained herring eggs. The vertical school extension unexpectedly increased when predators were present (General Linear Mixed Model; GLMM ANOVA, $p < 0.05$). Other school parameters were not significantly influenced by predator presence.

The lengths and weights of the herring ranged from 305 to 322 mm and from 217 to 293 g respectively (Table 4). 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.

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

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 over an extended period of time and in consecutive spawning seasons. Early pre-spawning herring in Lindåspollene consistently displayed fidelity to an area with close access to the deepest basin in the system. As maturation progressed the herring aggregated closer to the spawning ground. When approaching spawning, the schools also remained closer to the bottom, while packing densities increased. The diversity of gonad maturity stages was found to affect the heterogeneity of packing density within the school.

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 do normally not feed before spawning, but start shortly afterwards (e.g. Parsons & Hodder 1975, Crawford 1980, Huse & Ona 1996, Slotte 1999) reflecting the change in trade-offs between feeding and reproduction (Nøttestad et al. 1996, Axelsen et al. 2000). It is difficult to quantify the effects of predation pressure on school dynamics from our data, even though it was documented that herring encountered various predators, and in some cases had been preyed upon. Herring that aggregate within the same restricted area season after season should be an easy target for predators, and our gillnet samples suggested that herring was a main prey item for large cod. The abundance as well as consumption and digestion rates of cod in the system could, however, could not be quantified.

Spatial dynamics and site fidelity

Pre-spawning herring aggregated in one major school in a small area in all 6 years of our study, confirming previous anecdotal observations (Lie et al. 1978, Aksland 1983). 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 CTD data showed that the hydrography in the pre-spawning area did not differ markedly from the surrounding areas, with similar ranges in temperature and oxygen levels. On the other hand, the pre-spawning area differs in topography and is characterized 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 (Langård et al. unpublished observations). Compared to NSS herring, the potential migration distances of the local herring in Lindåspollene are very short, and the overwintering, migration and pre-spawning periods appear largely to merge. However, the migration patterns in Lindåspollene bear similarities on a small scale to those of NSS herring. The small meso-

scale shift in the distribution of local herring between the early and late pre-spawning period can 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.

School dynamic patterns as a function of maturation state

Herring approaching spawning aggregated in dense schools close to the bottom. Higher packing densities and shorter distances to the bottom closer to spawning have been observed in several studies (Nøttestad et al. 1996, Mackinson 1999, Skaret 2007). High packing density is usually attributed to anti-predator behaviour (Breder 1951), and herring may seek shelter behind conspecifics for protection (Hamilton 1971, Pitcher & Wyche 1983, Pitcher & Parrish 1993, Axelsen et al. 2001). The maturation process could also be accelerated by close contact with ripening individuals releasing pheromones (e.g. Ware & Tanasichuck 1989, Scott et al. 1994, Winters & Wheeler 1996) in a dense school.

A high Maturity Diversity Index (MDI) should reflect high diversity in motivational states among individual fish within a school, which could lead to more variable depth preferences resulting in increased school extension (Axelsen et al. 2000, Skaret 2007, Johnsen & Skaret 2008, Vabø & Skaret 2008). Our results are, however, not in accordance with this, as 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 al. 2003) and thereby not break out in a vertical split. Still, the high heterogeneity in packing density (roughness) associated with high MDI levels may reflect conflicts between individual fish at different stages of maturation.

Environment and predation

Our study design did not permit detailed analyses of links between environmental factors and herring behaviour. However, any variation in temperature, salinity or oxygen levels did not affect the choice of pre-spawning area that remained the same throughout the study period. Our results suggest that environmental conditions to some extent affected school

characteristics, but there were still consistent patterns in schooling dynamics among years that were strongly related to maturation state. As herring would be expected to aggregate more tightly under predatory threat the increased vertical school extension in the presence of predators is difficult to explain, but may reflect vertical avoidance reactions of herring encountering predators.

CONCLUSIONS

Throughout the 6 years 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 2002, Huse et al. 2010) may well stabilise the choice or 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. Although the changes were generally relatively small, 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 a potential in explaining the dynamics of fish schools.

Detailed long-term studies of herring school dynamics in small-scale ecosystems may reveal general state-dependent schooling patterns that are valid also for coastal and oceanic herring populations. 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 (Langård et al. unpublished data) could pave the way from state-dependent individual behaviour to a better understanding of dynamics at the school level.

Acknowledgements. We would like to thank KO Fjeldstad, R Sevrinsen and K Øyjordsbakken of RV “Hans Brattstrøm” for their collaboration and practical assistance. We are very grateful to R Bergfjord for sampling and data collection, and for providing equipment and working/storage room. We are also indebted to J de Lange, J Røttingen, A-L Johnsen, A

Haugsdal, V Lokøy and F Midtøy for biological sampling help. JM Andersen is thanked for help with the GIS figures and S Kolbeinson with editing the figures. The work was funded by the University of Bergen and the Institute of Marine Research.

LITERATURE CITED

- Aasen O (1982) On the correlation between arrival and spawning of the Norwegian winter herring. *J Cons perm int Explor Mer* 27:162-166
- Aksland M (1983) Acoustic abundance estimation of the spawning component of the local herring stock in Lindaaspollene, western Norway. *FiskDir Skr (Ser HavUnder)* 17:297-334
- Anker-Nilssen T, Lorentsen SV (2004) Seabirds in the Norwegian Sea. In: Skjoldal HR, Sætre R, Fernö A, Misund OA, Røttingen I (eds) *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, p 435-446
- Anon (1969) Report of the working group on the establishment of an international herring research scheme. *Int Coun Explor Sea Coop Res Rep Ser A* 11:1-36
- Aure JN (1972) Hydrografien i Lindåspollene. Master thesis, University of Bergen (in Norwegian)
- Axelsen BE, Nøttestad L, Fernö A, Johannessen A, Misund OA (2000) 'Await' in the pelagic: dynamic trade-off between reproduction and survival within a herring school splitting vertically during spawning. *Mar Ecol Prog Ser* 205:259-269
- Axelsen BE, Anker-Nilssen T, Fossum P, Kvamme C, Nøttestad L (2001) Pretty patterns but a simple strategy: predator-prey interactions between juvenile herring and Atlantic puffins observed with multibeam sonar. *Can J Zool* 79:1586-1596
- Baker RR (1978) *The evolutionary ecology of animal migration*. Hodder and Stoughton, London
- Blaxter JHS, Hunter JR (1982) The biology of the clupeoids. *Adv Mar Biol* 20:1-223
- Blaxter JHS (1985) The herring: a successful species? *Can J Fish Aquat Sci* 42:21-31
- Breder CM Jr (1951) Studies on the structure of fish shoals. *Bull Am Mus Nat Hist* 98:1-27
- Corten A (2002) The role of "conservatism" in herring migrations. *Rev Fish Bio Fish* 11:339-361
- Crawford RH (1980) A biological analysis of herring from the Atlantic coast of Nova Scotia and Eastern Northumberland Strait. Department of Fisheries, Halifax, NS (Manu Tech Rep Ser)
- Dahl O, Østvedt OJ, Lie U (1973) An introduction to a study of the marine ecosystem and the local herring stock in Lindåspollene. *FiskDir Skr (Ser HavUnders)* 16:148-158
- Dahl O, Lie U (1981) Lindåspollene – et naturlig forskningsakvarium. *Naturen* nr. 3 (in Norwegian)
- Fernö A, Pitcher TJ, Melle W, Nøttestad L, Mackinson S, Hollingworth C, Misund OA (1998) The challenge of the herring in the Norwegian Sea: Making optimal collective spatial decisions. *Sarsia* 83:149-167
- Fuiman LA (1989) Vulnerability of Atlantic herring larvae to predation by yearling herring. *Mar Ecol Prog Ser* 51:291-299
- Gerlotto F, Soria M, Fréon P (1999) From two dimensions to three: the use of multibeam sonar for a new approach in fisheries acoustics. *Can J Fish Aquat Sci* 56:6-12
- Grémillet D, Wilson RP, Storch S, Gary Y (1999) Three-dimensional space utilization by a marine predator. *Mar Ecol Prog Ser* 183:263-273
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol (Berl)* 91:295-311
- Haug T (1998) *Sjøpattedyr - om hval og sel i norske farvann*. Universitetsforlaget, Oslo
- Holst JC, Røttingen I, Melle W (2004) The herring. In: Skjoldal HR, Sætre R, Fernö A, Misund OA, Røttingen I (eds) *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, p 203-226

- Huse I, Ona E (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES J Mar Sci* 53:863-873
- Huse G, Fernö A, Holst JC (2010) Establishment of new wintering areas in herring co-occurs with peaks in the 'first time/repeat spawner' ratio. *Mar Ecol Prog Ser* 409:189-198
- Johnsen E, Skaret G (2008) Adaptive mass formations in fish shoals founded in conflicting motivation. *Mar Ecol Prog Ser* 358:295-300
- Kaartvedt S, Røstad A, Klevjer T (2009) Sprat *Sprattus sprattus* can exploit low-oxygen waters for overwintering. *Mar Ecol Prog Ser* 390:237-249
- Kjørsvik E, Lurås IJ, Hopkins CCE, Nilssen EM (1990) On the intertidal spawning of Balsfjord herring (*Clupea harengus*). *ICES Comm Meet Pelagic Fish Comm* 1990/H:30
- Krebs JR, Davies NB (1978) An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford
- Kvamme C, Nøttestad L, Fernö A, Misund OA, Axelsen BE, Dalpadado P, Melle W (2003) Migration patterns in Norwegian spring-spawning herring: why young fish swim away from the wintering area in late summer. *Mar Ecol Prog Ser* 247:197-210
- Langård L, Nøttestad L, Johannessen A, Fernö A, Øvredal JT, Vabø R, Skaret G, Nilsson G (2006) How and why acoustic detectability and catchability of herring change with individual motivation and physiological state in a variable environment: a multi-scale study on a local herring population in southwestern Norway. *ICES CM*. 2006/O:09
- Langård L, Øvredal JT, Johannessen A, Nøttestad L, Skaret G, Fernö A, Wahlberg M (2008) Sound production in pre-spawning herring, cod and haddock in a naturally enclosed ecosystem. *Bioacoustics* 17:38-40
- Lie U, Dahl O, Østvedt OJ (1978) Aspects of the life history of the local herring stock in Lindåspollene, western Norway. *FiskDir Skr (Ser HavUnders)* 16:369-404
- Mackinson S (1999) Variation in sturcture and distribution of pre-spawning Pacific herring shoals in two regions of British Columbia. *J Fish Bio* 55:972-989
- MacLennan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in fisheries acoustics. *ICES J Mar Sci* 59:365-369
- Mjanger H, Hestenes K, Svendsen BV, de Lange Wenneck T (2011) Håndbok for prøvetaking av fisk og krepsdyr (prosedyre for håndbok for prøvetaking av fisk og krepsdyr). V. 3.16
- Nero W, Magnuson JJ (1989) Characterization of patches along transects using high-resolution 70-kHz integrated acoustic data. *Can J Fish Aquat Sci* 46:2056-2064
- Nøttestad L (1994) Stimdynamiske studier på norsk vårgytende sild (*Clupea harengus* L.) under gyteperioden ved Karmøy. Master thesis, Univeristy of Bergen (in Norwegian)
- Nøttestad L, Akstrand M, Beltestad A, Fernö A, Johannessen A, Misund OA (1996) Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus*) in a coastal spawning area. *Sarsia* 80:277-284
- Nøttestad L, Fernö A, Mackinson S, Pitcher T, Misund OA (2002) How whales influence herring school dynamics in a cold-front area of the Norwegian Sea. *ICES J Mar Sci* 59:393-400
- Nøttestad L, Fernö A, Misund OA, Vabø R (2004) Understanding herring behaviour: Linking individual decisions, school patterns and population distribution. In: Skjoldal HR, Sætre R, Fernö A, Misund OA, Røttingen I (eds) *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, p 227-262
- Ona E, Zhao X, Svellingen I, Fosseidengen JE (2001) Seasonal Variation in Herring Target Strength. *Herring: Expectations for a New Millennium*. Alaska Sea Grant College Program

- Ona E (2003) An expanded target-strength relationship for herring. *ICES J Mar Sci* 60: 493-499
- Parrish JK, Edelman-Keshet L (1999) Complexity, Pattern, and Evolutionary Trade-offs in Animal Aggregation. *Science* 294:99-101
- Parsons LS, Hodder VM (1975) Biological characteristics of southwest Newfoundland herring, 1965-71. International Commission for the Northwest Atlantic Fisheries, Dartmouth, NS p 145-160 (Resources Bulletin No 11)
- Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, O'Conover D, Cury P, Heppell SS, Houdes ED, Mangel M, Plaga'nyi E, Sainsbury K, Steneck RS, Geers TM, Gownaris N, Munch SB (2012) The global contribution of forage fish to marine fisheries and ecosystems. *Fish Fish* (Early view, online version of record published before inclusion in an issue. DOI: 10.1111/faf.12004)
- Pitcher TJ, Wyche CJ (1983) Predator avoidance behaviour of sand-eel schools: why school seldom split. In: Noakes DLG, Linquist BG, Helfman GS, Ward JA, Junk A (eds). *Predators and prey in fishes*. Junk, The Hague, p 193-204
- Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. second ed. In: Pitcher TJ (ed) *The Behaviour of Teleost Fishes*. Chapman & Hall, London, p 364-439
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1-382
- Runde A (2005) Overlapping mellom sild (*Clupea harengus*) og sei (*Pollachius virens*) i tid og rom - Interaksjoner og effekter på stimadferd. Master thesis, University of Bergen (in Norwegian)
- Runnström S (1941) Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway. *FiskDir Skr (Ser HavUnders)* 6(8):5-71
- Scott AP, Lilley NR, Vermeirssen ELM (1994) Urine of reproductively mature female rainbow trout, *Oncorhynchus mykiss* (Walbaum), contains a priming pheromone which enhances plasma-levels of sex steroids and gonadotropin II in males. *J Fish Biol* 44:131-147
- Shannon CE (1948) A mathematical theory of communication. *The Bell System Technical Journal* 27:379-423, 623-656
- Simpson EH (1949) Measurement of diversity. *Nature* 163:688
- Skaret G, Nøttestad L, Fernö A, Johannessen A, Axelsen BE (2003) Spawning of herring: day or night, today or tomorrow? *Aquat Living Resour* 16:299-306
- Skaret G, Axelsen BE, Nøttestad L, Fernö A, Johannessen A (2005) The behaviour of spawning herring in relation to a survey vessel. *ICES J Mar Sci* 62:1061-1064
- Skaret G (2007) Collective behaviour of herring around the spawning peak. PhD dissertation, University of Bergen, Norway
- Slotte A (1999) Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *J Fish Biol* 54:338-355
- Steven GA (1933) The food consumed by shags and cormorants around the shores of Cornwall (England). *J Mar Biol Assoc of UK* 14:277-291
- Svellingen I, Totland B, Øvredal JT (2002) A remote-controlled instrument platform for fish behaviour studies and sound monitoring. *Bioacoustics* 12:335-336
- Vabø R, Skaret G (2008) Emerging school structures and collective dynamics in spawning herring: A simulation study. *Ecol Model* 214:125-140
- Ware DM, Tanasichuk RW (1989) Biological bias of maturation and spawning waves in Pacific herring (*Clupea harengus pallasii*). *Can J Fish Aquat Sci* 46:1776-1784

- Wassmann P (1983) Sedimentation of organic and inorganic particulate material in Lindåspollene, a stratified, land-locked fjord in western Norway. *Mar Ecol Prog Ser* 13:237-248
- Winter GH, Wheeler JP (1996) Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. *ICES J Mar Sci* 53:73-88
- Østvedt OJ (1965) The migration of Norwegian herring to Icelandic waters and the environmental conditions in May-June, 1961-1964. *FiskDir Skr (Ser HavUnder)* 13(8):29-47

Tables

Table 1. *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 text for details). * School roughness x 10³.

Parameter	Period	Year	Mean	N	SD	Min.	Max.
Packing density (ind/m³)	Early	2006	0.95	17	0.94	0.03	2.96
	Early	2007	1.61	39	1.35	0.19	5.87
	Early	2008	0.17	7	0.08	0.08	0.30
	Early	2009	0.88	38	0.96	0.06	4.81
	Early	2010	0.69	12	0.93	0.02	3.37
	Early	2011	0.36	19	0.21	0.01	0.73
	Late	2006	0.35	1	–	0.35	0.35
	Late	2009	2.81	14	4.07	0.11	13.26
	Late	2010	1.63	7	1.22	0.44	4.05
	Late	2011	0.47	18	0.58	0.02	2.55
Vertical extent (m)	Early	2006	6.74	17	2.12	4.32	11.15
	Early	2007	5.35	39	1.65	2.50	10.44
	Early	2008	4.35	7	0.90	2.99	5.48
	Early	2009	8.03	38	3.00	3.18	13.70
	Early	2010	6.28	12	2.80	3.61	12.98
	Early	2011	4.92	19	1.66	2.09	7.89
	Late	2006	8.20	1	–	8.20	8.20
	Late	2009	5.40	14	1.23	3.68	7.56
	Late	2010	5.30	7	1.22	3.41	6.76
	Late	2011	5.04	18	2.02	1.83	8.84
Mean depth (m)	Early	2006	16.59	17	2.16	13.28	21.68
	Early	2007	16.08	39	1.92	10.82	21.16
	Early	2008	15.52	7	2.01	12.95	18.64
	Early	2009	23.37	38	5.13	16.55	36.87
	Early	2010	29.49	12	12.25	16.14	64.20
	Early	2011	18.47	19	3.87	14.35	28.50
	Late	2006	25.45	1	–	25.45	25.45
	Late	2009	21.53	14	4.31	15.83	28.89
	Late	2010	22.47	7	7.07	16.23	33.49
	Late	2011	17.12	18	3.53	5.64	21.13

Distance from bottom (m)	Early	2006	6.78	17	4.44	1.54	16.68
	Early	2007	7.52	39	4.55	0.00	16.09
	Early	2008	8.05	7	2.89	4.16	12.10
	Early	2009	10.73	38	9.69	0.00	39.14
	Early	2010	3.54	12	5.34	0.00	15.30
	Early	2011	9.45	19	4.23	3.28	16.36
	Late	2006	0.64	1	-	0.64	0.64
	Late	2009	2.48	14	3.51	0.00	9.22
	Late	2010	0.00	7	0.00	0.00	0.00
	Late	2011	6.47	18	4.62	2.01	17.66
Circularity (%)	Early	2006	43.96	9	9.29	29.31	54.15
	Early	2007	37.52	39	10.82	18.94	75.59
	Early	2008	12.31	1	-	12.31	12.31
	Early	2009	40.09	8	14.38	27.00	60.61
	Early	2010	38.03	7	9.75	26.99	49.42
	Early	2011	47.83	14	9.89	33.72	71.43
	Late	2006	49.98	1	-	49.98	49.98
	Late	2009	40.48	13	9.89	26.29	52.11
	Late	2010	33.18	4	3.92	28.97	37.48
	Late	2011	42.70	17	8.42	29.57	54.74
Roughness (dB re 1 m²/m³)*	Early	2006	1.88	9	0.85	0.70	3.27
	Early	2007	0.92	39	0.36	0.46	1.75
	Early	2008	0.77	7	0.22	0.56	1.19
	Early	2009	0.87	38	0.53	0.37	2.63
	Early	2010	3.10	12	6.48	0.29	23.52
	Early	2011	1.91	18	1.15	0.69	5.05
	Late	2006	1.49	1	-	1.49	1.49
	Late	2009	0.92	14	0.71	0.46	2.75
	Late	2010	4.45	7	2.09	2.13	7.82
	Late	2011	1.59	18	0.85	0.50	3.52

Table 2. Summary of results from the generalized linear mixed effects models (GLMM) 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 difference between early and late pre-spawning period, and low and high Maturity Diversity Index (MDI), respectively. The effect of depth in the area of sampling is the covariate in the models. Note that the parameter estimates are on the scale of the link function. Year-days > 100 are not included for the two models.

Response variable	Predictor	df	Level	Parameter			
				estimate	t-value	p-value	
Packing density (ind/m³)	Maturity		Early	1.053			
		163	Late	1.521	2.018	0.045	
	Covariate (depth)	163		-0.046	3.071	0.003	
	MDI		Low	0.030			
		163	High	0.947	4.473	< 0.001	
	Covariate (depth)	163		-0.029	2.159	0.032	
	Vertical extension (m)	Maturity		Early	1.655		
			163	Late	1.507	1.905	0.059
Covariate (depth)		163		0.004	1.395	0.165	
MDI			Low	1.958			
		163	High	1.632	4.674	< 0.001	
Covariate (depth)		163		< 0.001	0.173	0.863	
Mean depth (m)		Maturity		Early	2.468		
			163	Late	2.535	1.775	0.078
	Covariate (depth)	163		0.015	10.369	< 0.001	
	MDI		Low	2.394			
		163	High	2.493	2.748	0.007	
	Covariate (depth)	163		0.016	10.718	< 0.001	
	Distance from bottom (m)	Maturity		Early	0.164		
			163	Late	-0.252	2.703	0.008
Covariate (depth)		163		0.053	12.885	< 0.001	
MDI			Low	0.292			

		163	High	-0.039	2.4200	0.017
	Covariate (depth)	163		0.053	12.293	< 0.001
Circularity (%)	Maturity		Early	3.588		
		104	Late	3.561	0.420	0.675
	Covariate (depth)	104		0.004	0.888	0.377
	MDI		Low	3.398		
		104	High	3.567	2.559	0.012
	Covariate (depth)	104		0.006	1.445	0.151
Roughness (dB re 1m²/m³)	Maturity		Early	-5.774		
		154	Late	-5.835	0.355	0.723
	Covariate (depth)	154		-0.025	2.423	0.017
	MDI		Low	-6.800		
		154	High	-6.110	3.695	< 0.001
	Covariate (depth)	154		-0.006	0.646	0.519

Table 3. Summary of cod stomach content from gillnet samples during early and late pre-spawning period from 2006 to 2011 for cod length > 50 cm and < 50 cm. ‘n settings’ denotes number of gillnet settings. No data are available for 2010. ‘Early’ and ‘Late’ refer to early and late pre-spawning periods (see text for details). *In 2007 1 pollack had 1 herring in its stomach. Mean±SD.

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

Table 4. *Clupea harengus*. Summary of herring biological parameters from gillnet samples. Mean±SD.

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

Figures

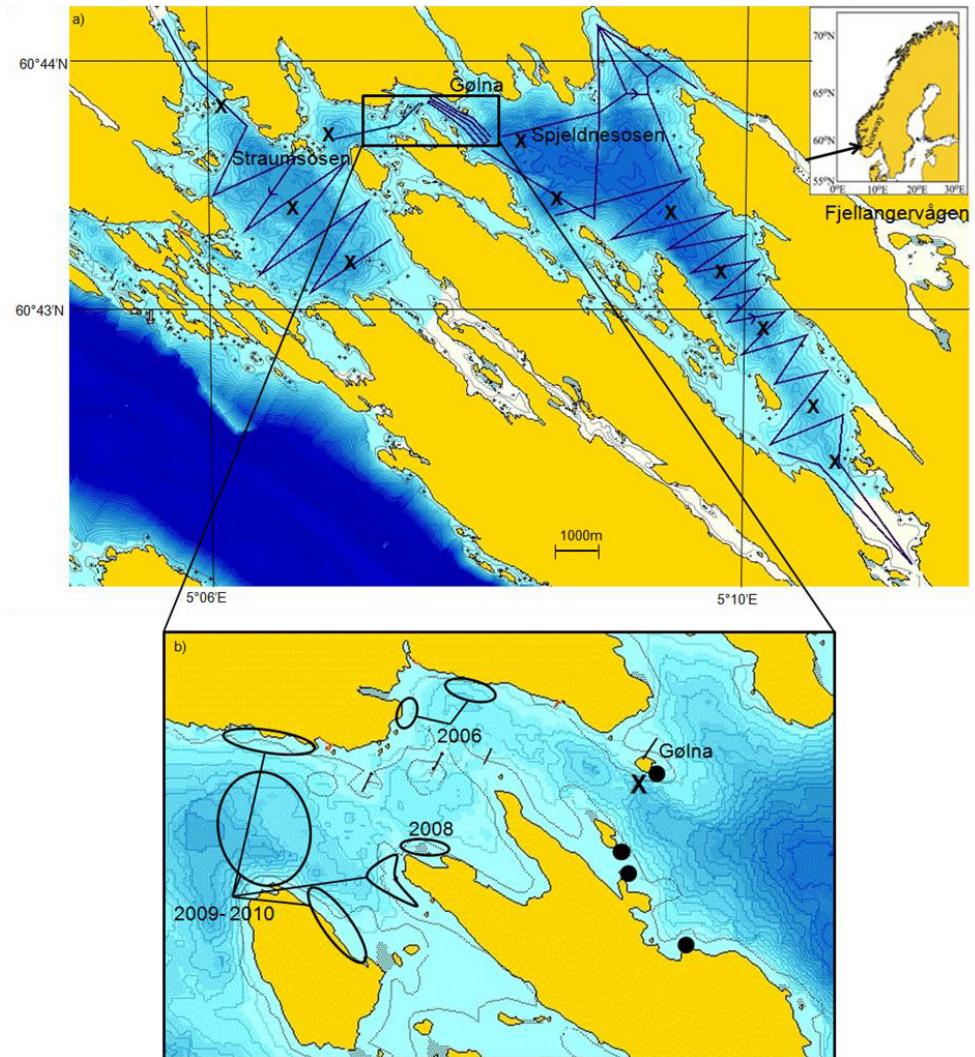


Figure 1. Map of Lindåspollene, south-western Norway showing; a) pre-defined transect grid carried out during 2006 to 2011 to investigate the distribution of herring schools. X denotes positions for CTD stations, b) the main study area; with solid circles denoting herring gillnet positions, and lines denoting predator nets. Open ellipses denote documented spawning grounds and X marks the main CTD station.

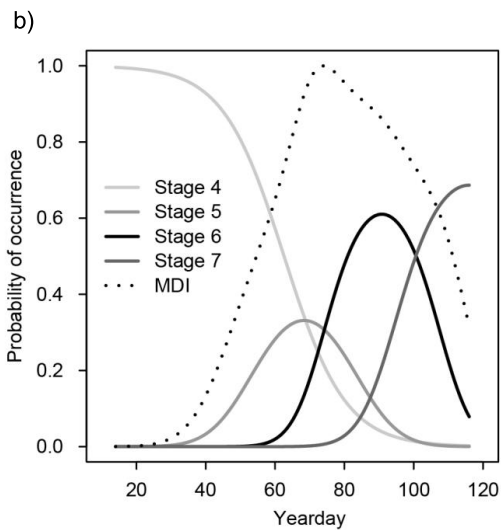
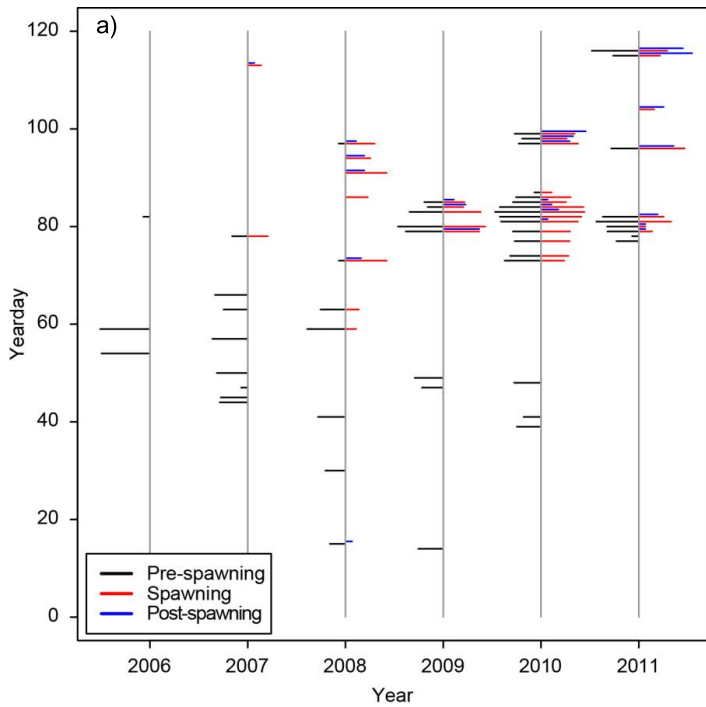


Figure 2. a) Overview of the biological sampling data from 2006 to 2011. Observations of pre-spawning (stage 1-5), spawning (stage 6) and post-spawning (stage 7-8) herring, b) The solid lines show the probabilities of finding a given maturation stage of herring depending on

time of the year, where day 0 represents yearday 1 (January 1st). The dotted line shows the MDI describing the potential diversity in maturation stages within a school (see text for further explanations).

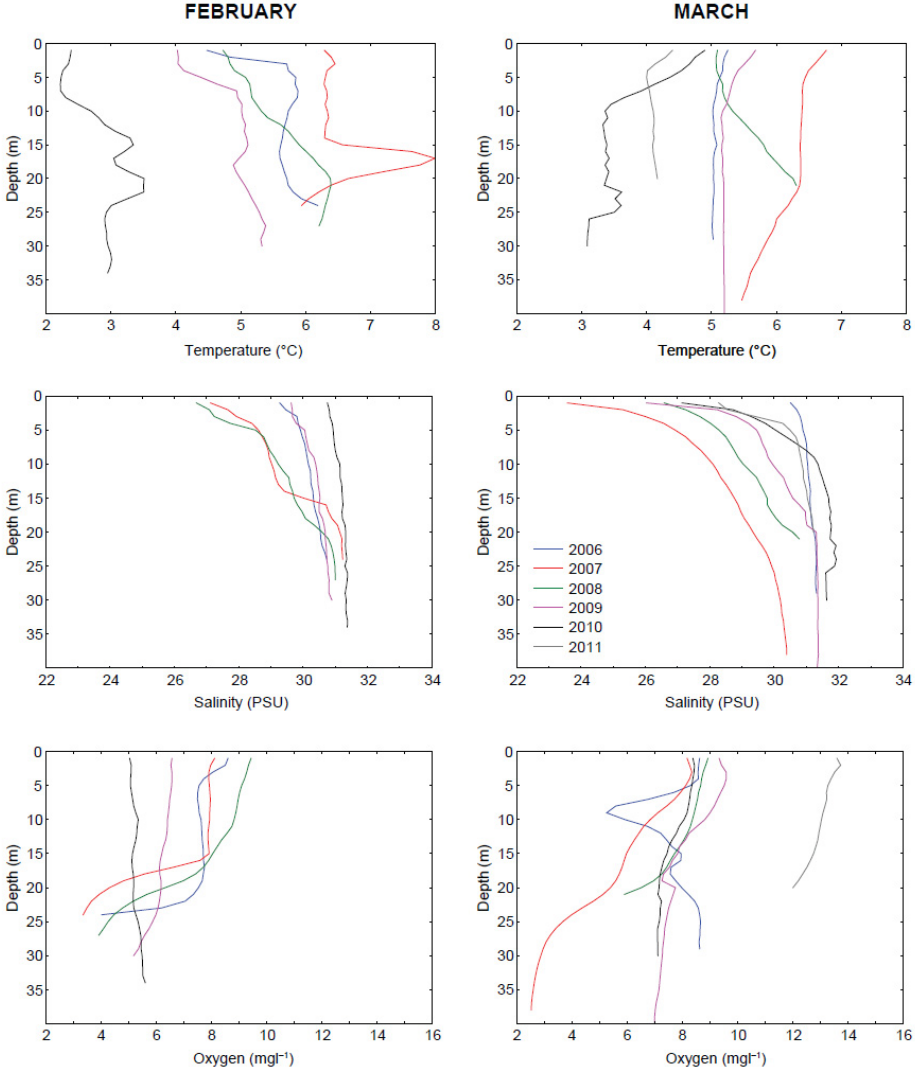


Figure 3. CTD profile taken between yearday 41-53 from 2006 to 2010 (February), and for all years between yearday 72-89 (March).

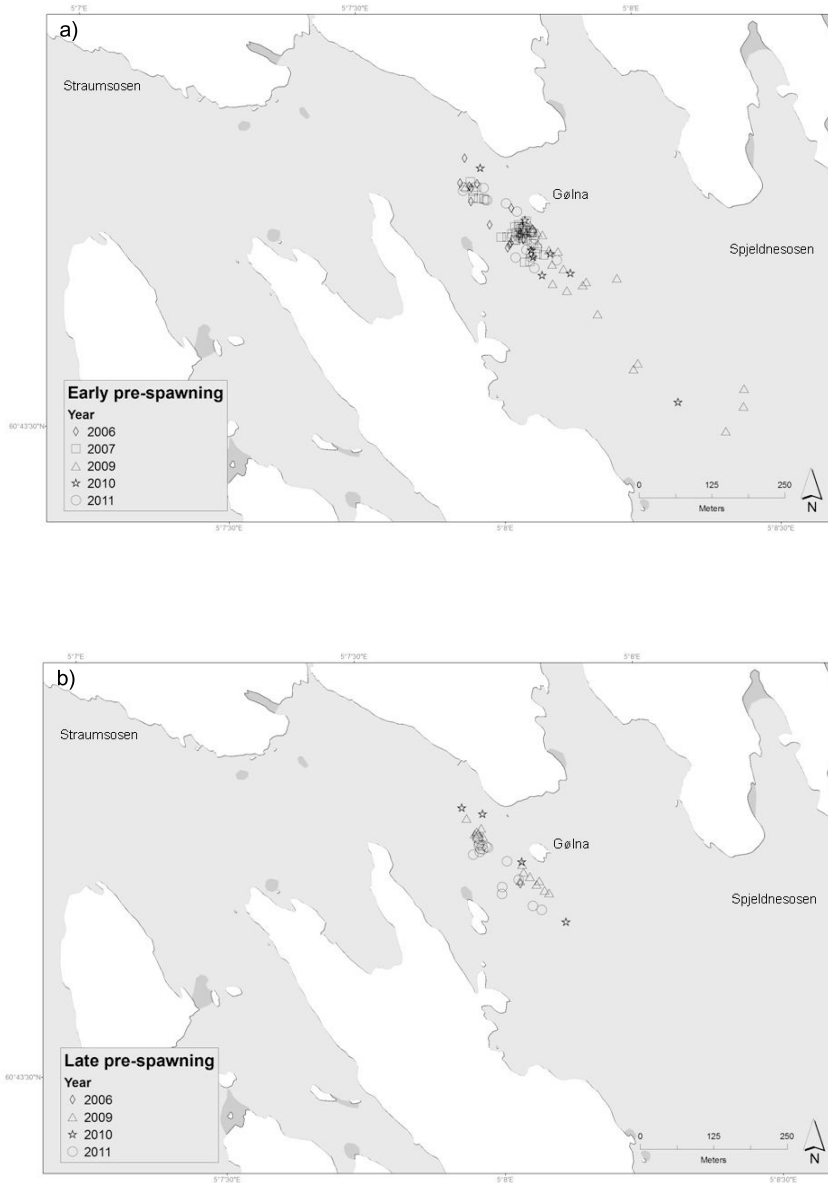


Figure 4. Distribution of school observations from 2006 to 2011 a) early pre-spawning period, b) late pre-spawning period. Note that 30 school observations from the early/late pre-spawning period in 2008 to 2011 are not included due to lack of position data.

