

Tracking individual herring within a semi-enclosed coastal marine ecosystem: 3-dimensional dynamics from pre- to post-spawning

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ABSTRACT: Pelagic fish typically swim in shoals, but a full understanding of behaviour, including individual spatiotemporal dynamics and the relationships between individuals and the social unit, can only be achieved through studies of individual fish. We studied horizontal and vertical movement of tagged individual Atlantic herring (*Clupea harengus* L.) inside a semi-enclosed ecosystem throughout the dynamic spawning season. Twenty-four fish were successfully tagged with acoustic transmitters and followed for up to 62 d (average 28 d) using a network of ultrasonic receivers. Herring samples from gillnets provided information about gonadal maturity. During pre-spawning, all individuals remained within the range of a single receiver, but with marked and predictable diel vertical migrations (DVMs). As maturation progressed, the number of herring on the spawning grounds gradually increased, while swimming depth and DVMs gradually decreased. However, the daily vertical distance moved by single individuals increased markedly as spawning approached, and the individual variability in both horizontal and vertical positioning also increased over time. During the period assumed to include spawning, individuals moved more frequently between the receivers, with dives towards the bottom presumed to represent spawning events. The results indicate a development from low variability in individual positioning and strong school coherence before spawning, to high variability during spawning that could reflect individual states of maturation. The study demonstrates that novel acoustic tagging technology opens up the possibility of investigating the dynamic trade-offs between collective behaviour and individualism in schooling pelagic fish.

KEY WORDS: *Clupea harengus* · Individual behaviour · Diel vertical migration · Tagging · Acoustics · Telemetry · Pelagic fish

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INTRODUCTION

An ultimate advantage of aggregation may be energy saving in the broadest sense, i.e. efficiency in foraging, locomotion and protection from predators (Ritz et al. 2011). Pelagic fish typically school during much of their life cycle (Shaw 1978), and behavioural studies therefore typically aim at understanding dynamics at the school level (e.g. Pitcher & Parrish

1993, Pitcher et al. 1996, Mackinson 1999, Gerlotto et al. 2006). A number of studies have attempted to link schooling behaviour to environmental factors (Blaxter & Parrish 1965, Domenici et al. 2002, Gerlotto et al. 2006) or fish state such as degree of gonad maturation or stomach content, as an indicator of internal motivation (Nøttestad et al. 1996, Axelsen et al. 2000, Skaret et al. 2003). However, in order to elucidate individual spatiotemporal dynamics and the relation-

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ship between individuals and the school, we must learn how individuals behave. Several studies have applied theoretical models to address individual behaviour in schools (e.g. Aoki 1982, 1984, Vabø & Nøttestad 1997, Couzin et al. 2005, Viscido et al. 2005, Vabø & Skaret 2008), and tagging of individual fish has been done for mark-recapture experiments (e.g. Fridriksson & Aasen 1950, 1952, ICES 1964, Arnold et al. 2002, Josse et al. 1999), but to the best of our knowledge, no study has looked at the detailed behaviour in time and space of individual pelagic schooling fish *in situ*.

There are several reasons for the lack of field studies of individual behaviour in pelagic species. Controlled field experiments following single individuals are difficult to perform in open ocean systems for pelagic fish, which are dynamic both on the large scale due to extensive migrations, and on small scales due to splits and joins of schools (Pitcher et al. 1996). For acoustic observation methods, which are often employed to study pelagic fish behaviour, sufficient resolution to resolve single individuals in schools is rarely achieved (but see Handegard et al. 2009). Furthermore, tagging methods that are often used for larger fish like salmon, cod and halibut have traditionally been difficult to apply to small pelagic fish, which are typically more sensitive to tag implantation (Harden-Jones 1968, Jacobsen & Hansen 2004). Recently, however, small and lightweight acoustic tags that can be inserted into small pelagic fish have been developed (Arnold et al. 2002, Langård et al. 2012), allowing for behavioural studies of individuals.

This study was carried out in a semi-enclosed sheltered marine basin system off the coast of western Norway, which hosts a resident, thoroughly described population of Atlantic herring (*Clupea harengus* L.) (Lie et al. 1978, Aksland 1983, Johannessen et al. 2009, Langård et al. 2014a,b). This population shows fidelity to a specific pre-spawning location and spawning occurs within the basins, which creates ideal experimental conditions for the controlled use of tags.

The spawning period is particularly interesting for studying individual behaviour in a collective species such as herring. Since the timing of spawning is not fully synchronised among individuals, there may be major discrepancies in interests between individuals and the collective (Skaret 2007, Langård et al. 2014a). Previous studies, for instance, have shown that a minority of individuals that are ready to spawn have followed spent individuals out of the spawning area and missed the spawning opportunity due to the

powerful attraction of the collective unit (Axelsen et al. 2000, Skaret et al. 2003).

Despite being adapted to a life in the pelagic, herring spawn demersally up to 10 to 15 times during their lifetime (Blaxter & Hunter 1982, Slotte 1999). Herring typically spawn in one to several waves (Lambert 1987), and while individual herring may empty their gonads within 2 to 4 h (Holliday 1958), spawning *in situ* at school level has been observed to take 1 to 7 d (Johannessen 1986, Axelsen et al. 2000). Spawn is deposited on the bottom, where the fertilised eggs stick to stones and coarse gravel (Runnström 1941). After spawning, herring immediately resume feeding after a winter starvation period (Slotte 1999). Since herring are subjected to predation from a range of predators, and particularly demersal gadoids, they continuously need to trade-off between predator avoidance, reproductive success and feeding. This influences the selection of pre-spawning and spawning sites, vertical dynamics and time of spawning (Nøttestad et al. 1996, 2004, Axelsen et al. 2000, Slotte & Fiksen 2000, Skaret et al. 2003).

We tagged herring with miniature acoustic transmitters in order to acquire detailed descriptions of the diel horizontal and vertical distribution and movements of individuals. By relating the spatio-temporal positioning from pre- to post-spawning to the change in maturation state, individual state-dependent spatial preferences and variability in the dynamic spawning period could be studied. Based on previous studies at school level, we predicted that the individual variability in spatial positioning should increase as herring at different stages of maturation approached spawning.

MATERIALS AND METHODS

Study area

Lindåspollene is a small semi-enclosed ecosystem in south-western Norway comprising 3 basins (see Lie et al. 1978), connected by a shallow channel (7.5 m wide, 3.5 m deep) to the outside fjord (Fig. 1). Tidal currents are the main driving forces of seawater exchange through the shallow channel, and mean current speed is ca. 0.25 m s⁻¹ and tidal height range is 35 to 50 cm. Due to the relatively low water exchange with the outside fjord, there is a stable deeper stratum in the basins below 20 to 25 m depth, with higher seasonal variability in temperature and salinity above this depth. Deepwater exchange does

not occur annually and oxygen depletion therefore may occur in the deeper layers (Aure 1972). Zooplankton biomass in the basins is low (Aksnes & Magnesen 1983). The bottom substrate is dominated by rocks and boulders in the littoral zone, with gravel and sand in small bays and mainly soft mud in the deeper parts (Lie & Dahl 1981). Only small-scale gillnet and handline fishing is permitted in the basins, and boat traffic is limited, making them ideal for small-scale ecosystem studies.

The resident herring are mainly distributed in 2 of the basins in the system, with maximum bottom depths of 60 and 90 m. Previous studies have shown that the herring have a fidelity to a specific pre-spawning site, and that they spawn at particular sites inside the basins (Lie et al. 1978, Aksland 1983, Langård et al. 2014a). This information was used to decide the locations of the acoustic receivers within the system.

Set-up of acoustic receivers

In February 2010, stationary acoustic receivers (VR2, Vemco) were moored at 5 locations in the basin system (Fig. 1), covering a total range of approximately 2500 m from the innermost to the outermost location. Receiver 1 (R1) was placed close to the previously documented pre-spawning loca-

tion ('Pre-spawning area'), and Receiver 2 (R2) close to what was presumed to be the spawning site ('Spawning area'), Receiver 3 (R3) was placed inside an outlet leading into an adjacent basin connected to the outside fjord ('Secondary fjord outlet'), Receiver 4 (R4) was placed on the inside of the main entrance to the outside fjord ('Primary fjord outlet'), and Receiver 5 (R5) was placed on the outside of the main fjord entrance (Østvedt et al. 1973, Aksland 1983, Johannessen et al. 2009; Fig. 1). The receivers recorded ultrasonic signals down to a depth of 51 m and within a range of 200 to 400 m depending on ambient oceanic and weather conditions and bottom topography (see Skilbrei et al. 2010). The receivers were positioned in such a way as to maximise the total area covered within what was believed to be the migration path and to minimise areas of overlap between receivers. The system was not calibrated with a range-testing tag, but the data analysis showed that there was a theoretical detection overlap between R1 and R2 in a maximum of 0.1% of the recordings, and no overlap between the other receivers. The receivers were moored to weights on the seabed, and kept at a depth of about ~10 m by a float. All the receivers covered areas sloping down from 0 m to deeper waters. At R1, the maximum depth within the detection range was about 65 m, at R2 40 m, R3 50 m, R4 60 m and R5 40 m. The bathymetry at R1 was steeper than at the other loca-

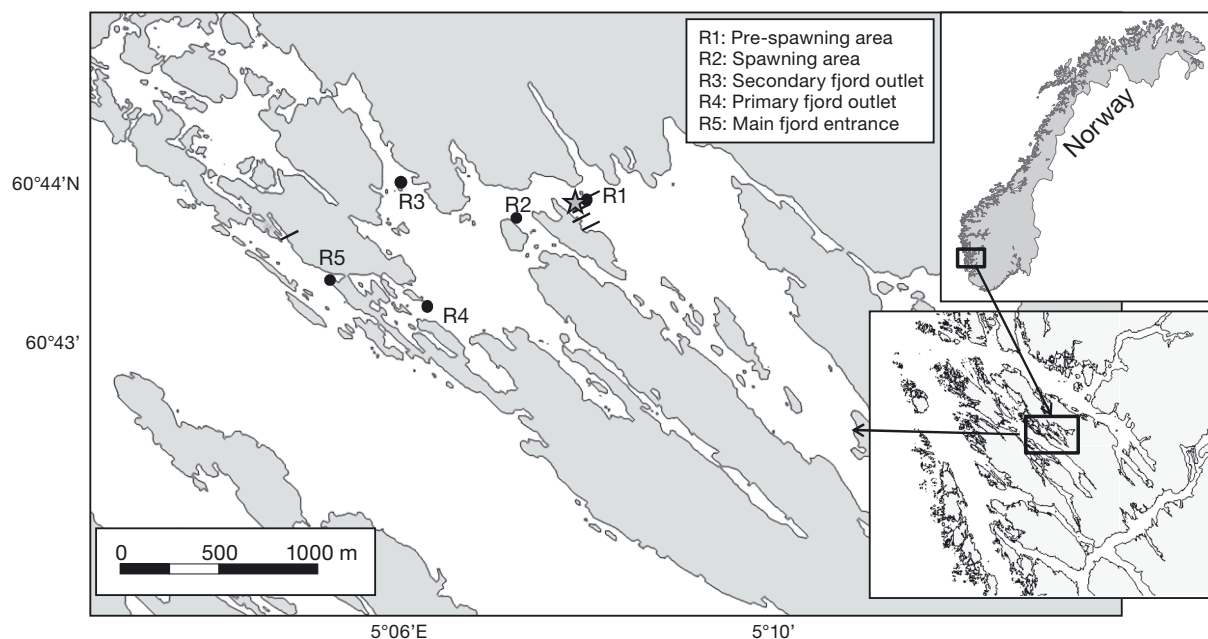


Fig. 1. Study area in Lindåspollene, Norway. Black filled circles: 5 acoustic receivers (R1–R5); black lines: herring gillnet sampling locations; ☆: location of CTD casts

tions. The acoustic receivers were not available for use after 11 April 2010, (day of the year [DOY] 101), so the investigation was then terminated, with receivers having been in the water for 62 d.

Acoustic transmitters

Herring were tagged with small acoustic Thelma Biotel transmitters. Two types of transmitters were used. In order to investigate horizontal positioning, individually coded LP-7.3 mm (LP) transmitters provided transmitter ID (7.3 mm refers to the diameter and LP to low power). Vertical positioning was studied by means of ADT-9-SHORT Acoustic Depth Transmitters (ADT) (SHORT refers to length of transmitter). LP transmitters (length 18 mm) and ADT transmitters (length 34 mm) weighed 1.2 and 3.3 g in water, respectively. The transmitters had a random delay of 60 to 180 s between transmissions (average 120 s), in order to minimise signal collisions, allowing a large number of fish to be tracked on the same frequency (69 kHz). The LP transmitters had an expected battery life of ~5–8 mo, and the ADT transmitters of ~4.5–7.5 mo.

Tagging and release

Herring were captured by jigging from 9–12 February 2010 (DOY 40–43). On capture, individuals were measured to the nearest lower 0.5 cm, placed ventral side up in a net fitted with soft plastic material to avoid damaging them, and scales were removed for age determination. To insert the acoustic transmitters, a 10 mm incision was made posterior to the pelvic fin, and a transmitter sterilized in surgical spirit was carefully inserted forward into the peritoneal cavity in the abdomen just behind the pelvic fins. The incision was closed with histoacryl tissue adhesive (0.1 ml). The whole procedure took a maximum of 60 s (see Langård et al. 2012 for further details of the tagging procedure). The fish were then transferred to a lidded tank (500 l) with circulating seawater, where they remained for 3 to 4 h for recovery and continuous observation onboard the vessel, until no visible effects of tagging, such as injury or abnormal swimming were seen. They were then released by lowering the tank into the water in the area of capture. The experiment and tagging procedure were approved by the Norwegian committee for the use of animals in scientific experiments (FDU).

A total of 28 herring were tagged with either ADT ($n = 9$) or LP ($n = 19$) transmitters. The tagged herring were of similar length (mean \pm SD = 32.3 ± 1.4 cm) and age (9.5 ± 1.9 yr).

Biological and hydrographical sampling

In order to investigate the development in herring gonadal maturity during the period of tracking, biological samples of herring were obtained from gillnet catches in the study area (Fig. 1). Herring were sampled from February to April 2010 (see Fig. 2) using monofilament gillnets, 25 m long by 4 m high, with stretched mesh sizes of 24 to 36 mm. A total of 71 gillnet samples were acquired over 16 sampling days during the study period. Individual herring were measured for total length (TL) rounded down to the nearest 0.5 cm. The gonad maturity index (GMI) was set according to an 8-point scale based on macroscopic visual inspection, where GMI 1–2 denotes immature, GMI 3–5 maturing, GMI 6 spawning, GMI 7 spent and GMI 8 resting (for further details about the staging criteria, see Langård et al. 2014a). CTD casts (STD/CTD, model SD204, SAIV) measured temperature, salinity and oxygen in the pre-spawning area (Fig. 1). Each measurement was rounded off to the nearest metre and averaged over the samples during each of the 3 defined periods (see next section). Spawning was documented by underwater video recordings of herring spawn and by the presence of eggs in predator stomachs (inspected visually on board the vessel).

Data analyses

In order to link the individual behaviour inferred from the transmitters to development in maturation and spawning, we allocated the acoustic detections to 3 periods, which were defined according to average gonad maturity state derived from the gillnet samples as follows: Pre-spawning (P1)—the day on which the proportion of individuals with GMI 4 (maturing) was the highest in the sample; Ripe (P2)—first day on which the proportion of GMI 5 (maturing) was the highest; and Spawning (P3)—first day on which the proportion of GMI 6 (spawning) was the highest. In order to take the variable sampling effort into account, we used bootstrapping and defined the periods 1000 times, leaving out 1 random gillnet sample each time. We then used the average value and arrived at the following end days for each period

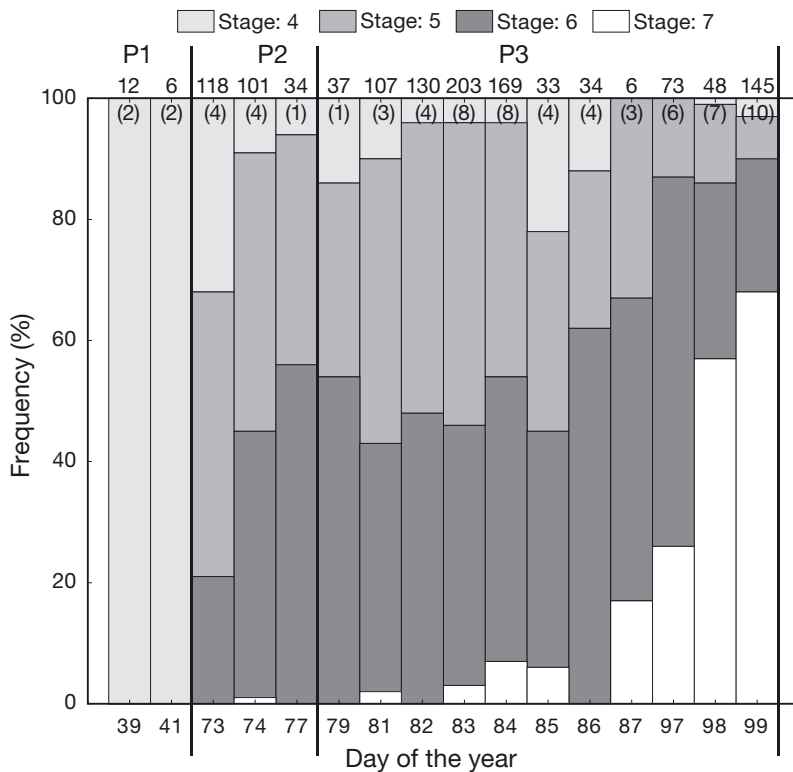


Fig. 2. Development of the gonad maturation index (GMI) for herring throughout the study period. The vertical lines distinguish the 3 defined maturation periods (P1: pre-spawning, P2: ripe, P3: spawning). Number of sampled fish is shown at the top of each bar and number of gillnets in parentheses. Note that the scale on the x-axis is not linear

(DOY \pm SD): 50 ± 5.65 for P1 (19 February), 78 ± 0.50 for P2 (19 March) and 99 ± 0.23 for P3 (9 April, Fig. 2). That spawning had occurred was verified by video observation of eggs in shallow waters (0–15 m) on 27 March (DOY 86) close to the spawning area (Fig. 1).

In order to remove any false detections, a minimum of 2 signals received per day from a given ID transmitter by a single or 2 adjacent receivers was set as a requirement for inclusion in the analysis. In addition, recordings from 4 ID transmitters were excluded from the analyses, because 2 ID transmitters were consistently transmitting signals from the maximum recording depth (51 m) at one specific receiver, and the 2 other ID transmitters were scattered for long periods of time, and ended up as signals from the maximum recording depth at one particular receiver.

All statistical analyses were performed using R v. 3.0.0 (R Development Core Team 2013). In order to analyse the horizontal distribution over the study period, the number of fish detected per day at each receiver as a function of DOY was investigated using Poisson regression (generalized linear models; GLM). In addition, the horizontal movements of the fish

were studied using the number of changes of receiver for each fish within each period (P1, P2 and P3) as response variable and period as categorical predictor. We used a mixed model with autocorrelation to take the repeated measurements on individual herring into account. The response variable represents count data with a Poisson distribution, and we used a generalized mixed effects model (GLMM). The `glmmPQL` function from the MASS library of R was used for this purpose (Venables & Ripley 2002).

To analyse the vertical distributions based on information from the depth transmitters, we compared records over 24 h among the 3 periods (P1, P2 and P3) using a generalized additive model (GAM) from the `mgcv` library in R (Wood 2006) with splines smoothing. The model was set up using the depth (m) of each individual as the response variable, time of day (24 h system) as a continuous predictor and the 3 defined maturity periods as categorical predictors. Fish ID was included as a random effect factor. Due to variance increasing with the mean, we used quasi Poisson distributions for the

error terms in the model. To investigate how mean depth in general and the difference in mean depth between day and night changed in the course of the season, we also studied the vertical distribution throughout the observation period. We used both GAM and linear mixed effect models (LME) for this purpose. For the GAM, we used the same type of model as described above but with DOY as a continuous predictor and daytime/nighttime as a categorical predictor. In this analysis, samples taken at civil twilight (when the sun is between 0° and 6° below the horizon) were excluded from the data set. This was done in this model because we wished to exclude data from the time at which fish typically move up and down as a response to changes in light conditions. In addition to the GAM, we used the LME to determine whether the difference between day and night samples changed between the pre-spawning and spawning periods. The variables are the same as described for the previous models, but included P1 and P3 in order to make model interpretation as simple as possible. For the fish with the depth transmitters we also compared the total verti-

cal distance moved within each of the 3 spawning periods by using the same type of LME as described above, but using the cumulative vertical distance moved within each period for each fish as the response variable and only the 3 periods as categorical predictors in the model.

RESULTS

Horizontal distribution

A total of 24 fish met the criteria for inclusion in the analysis. The results of the Poisson regressions (Fig. 3) for each of the receivers showed that there was (1) a significant reduction in number of fish with DOY at R1 (pre-spawning area) (GLM; $F_{1,59} = 90.40$, $p < 0.01$), (2) a maximum number of fish at R2 (spawning area) on 18 March (DOY 77) (GLM with second-order polynomial: $F_{2,58} = 38.03$, $p < 0.01$; significance of second-order term: $F_{1,58} = 56.30$, $p < 0.01$), (3) a significant increase over time at R4 (primary fjord outlet) (GLM; $F_{1,59} = 174.11$, $p < 0.01$) and (4) no significant change over time at R3 (secondary outlet) ($F_{1,59} = 0.65$, $p = 0.42$). No recordings were made at R5. The recordings made between 10 February and 1 March (DOY 41 and 60) and during a short period around 12 March (DOY 71) were almost exclusively made at R1. Around 2 March (DOY 61), there was a significant drop in the number of individuals at R1, and a subsequent sharp increase in recordings at R2 (Fig. 3). The short period with a high number of individuals (10 to 13) recorded at R2 was immediately followed by a 5 d period with low numbers (5 to 7). During this period, some individuals occurred at R3, but 8 fish were not detected by any receiver.

There was a significantly lower number of shifts between the receivers in P1 compared to P2 and P3 (GLMM; $t_8 = 3.88$, $p < 0.01$, and $t_8 = 4.93$, $p < 0.01$, respectively, Fig. 4), whereas P2 and P3 were not significantly different (GLMM; $t_8 = 0.51$, $p = 0.63$, Fig. 4). Note also the markedly lower spread in P1 than in P2 and P3.

Vertical distribution

Herring performed diel vertical migrations (DVMs) throughout the tracking, remaining significantly deeper during the daytime than at night (parametric coefficient from the GAM; $t_{43829.43} = 242.50$, $p < 0.01$; Fig. 5). However, there was a significant non-linear decrease in depth distribution over the study period

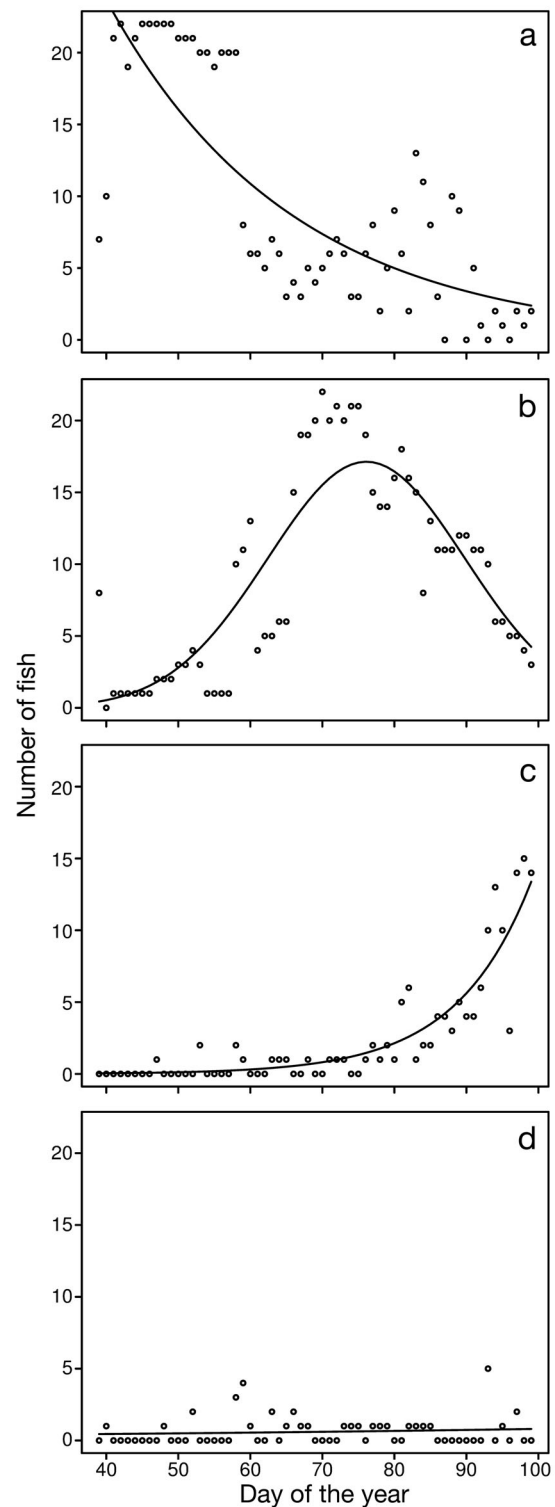


Fig. 3. Numbers of herring observed at 4 of the 5 receivers throughout the study period: (a) pre-spawning area, R1; (b) spawning area, R2; (c) primary fjord outlet, R4; and (d) secondary fjord outlet, R3 (see Fig. 1). The numbers are derived as daily sums of unique fish IDs at a given receiver. The lines are predicted model lines from poisson regression models (GLMs)

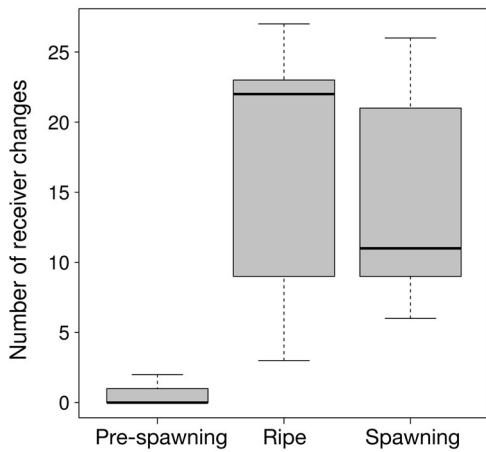


Fig. 4. Number of times a tagged herring was recorded to have moved between receivers during the pre-spawning (P1), ripe (P2) and spawning (P3) periods. Thick horizontal line: median; boxes: 1st and 3rd quartiles; whiskers: maximum and minimum values

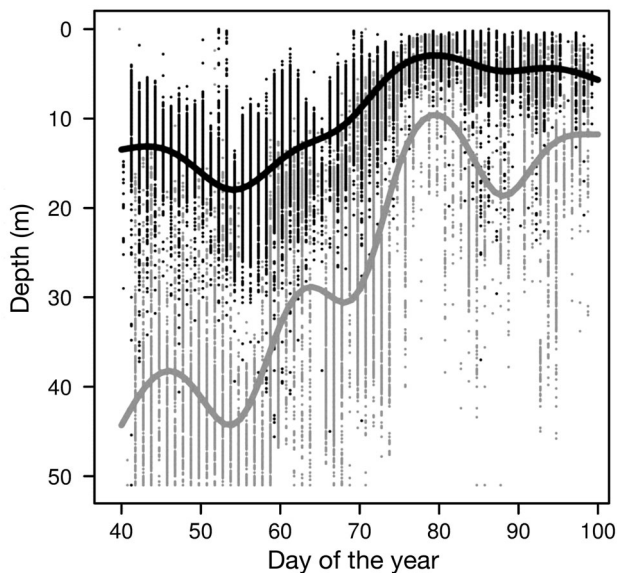


Fig. 5. Detected vertical position of tagged herring as a function of day of the year based on all tag recordings. Dots: recordings. Solid lines: predicted values from the GAM. Grey: daytime; black: nighttime. This model explained 74.3% of the deviance. Note that the maximum detection depth was 51 m, so actual depth of the fish may have exceeded this depth

(smooth terms $s(\text{DOY})$ from the GAM: $F_{43829.43, 8.988} = 873.23$, $p < 0.01$). A decrease in depth distribution was confirmed when we compared different time periods (Fig. 6). Herring were detected significantly deeper during P1 than either P2 or P3 (parametric coefficients from the GAM: $t_{47277.27} = 20.19$, $p < 0.01$, and $t_{47277.27} = 99.78$, $p < 0.01$, respectively). Detection depths of herring between P2 and P3 were also sig-

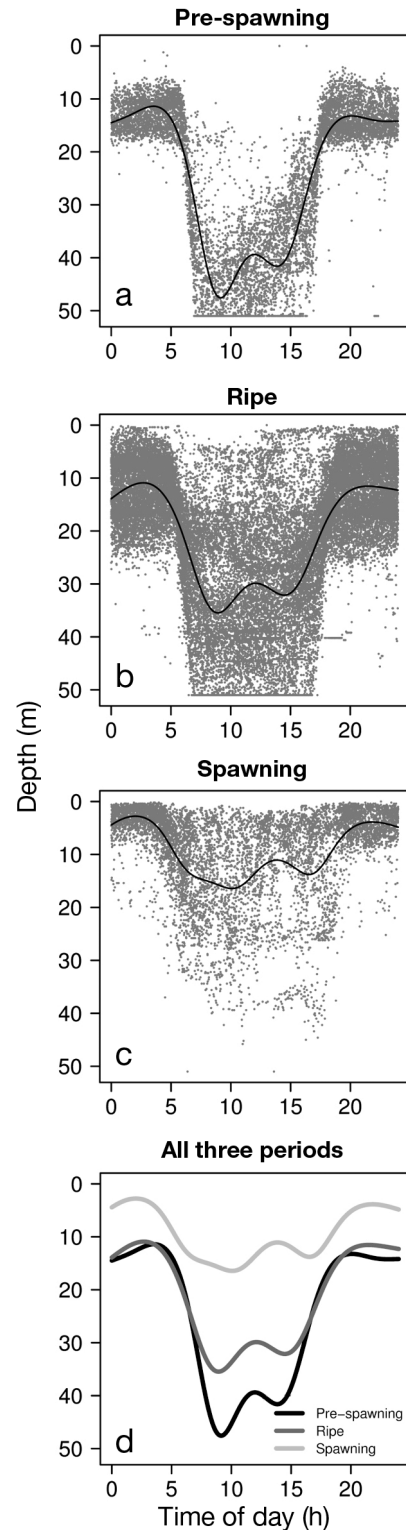


Fig. 6. Detected vertical position of tagged herring as a function of time of day based on all tag recordings. The separate panels contain detections for the 3 periods: (a) pre-spawning (P1), (b) ripe (P2), (c) spawning (P3) and (d) all 3 periods combined. Solid lines: predicted values from the GAM, which explained 59.4% of the deviance. Note that maximum detection depth is 51 m

nificantly different from each other (parametric coefficients from GAM: $t_{47277.27} = 96.54$, $p < 0.01$). The LME confirmed that the differences in depth distribution between day and night were larger during the pre-spawning period than the spawning period (interaction between Period and Light, $F_{1,15609} = 716.13$, $p < 0.01$). The smallest differences in depth distribution between night and day were observed between 12 and 22 March (DOY 71 and 81) (Fig. 6), which coincided with the time when the fish aggregated in the spawning area (Fig. 4).

The cumulative vertical distance that each fish moved was significantly higher in P2 than P1 or P3 (LME; $t_8 = 6.41$, $p < 0.01$, and $t_8 = 5.83$, $p < 0.01$, respectively, while no difference between P1 and P3

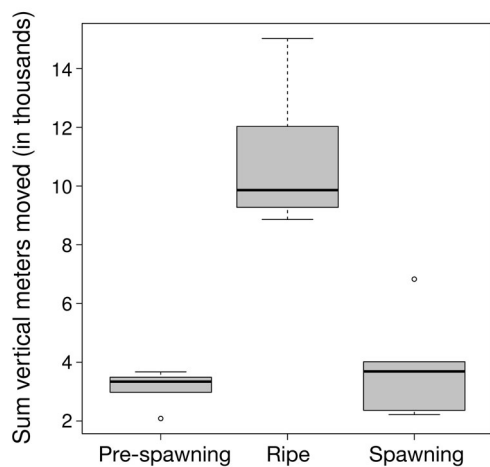


Fig. 7. The cumulative vertical distance moved for tagged herring during the 3 periods: pre-spawning (P1), ripe (P2) and spawning (P3). Thick horizontal line: median; boxes: 1st and 3rd quartiles; whiskers: maximum and minimum values; circles: outliers (any observation that lies 1.5 times the length of the box or further from the box)

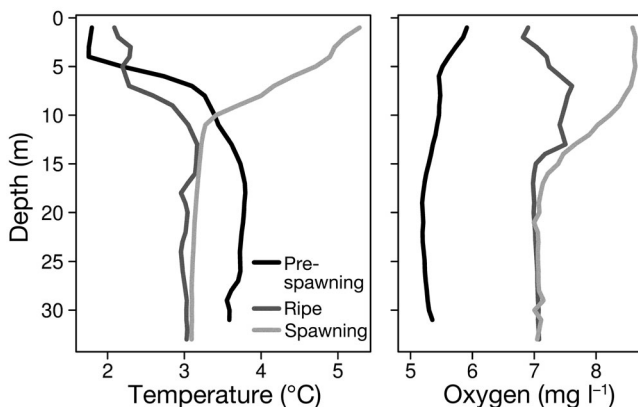


Fig. 8. Temperature ($^{\circ}\text{C}$) and oxygen (mg l^{-1}) profiles from CTD casts from the pre-spawning area for the 3 periods: pre-spawning (P1), ripe (P2) and spawning (P3)

was observed (LME; $t_8 = 0.61$, $p = 0.56$, Fig. 7). Note also the low spread in P1 in spite of the fact that this period had the most extensive DVM. The temperature in the upper 10 m rose by about 3°C from P2 to P3 (Fig. 8), implying a shift from the water being colder above the thermocline than below, to it being warmer above the thermocline than below. Oxygen levels ranged from 5 to 9 mg l^{-1} and increased markedly in the whole water column from P1 to P2 and increased further above 15 m from P2 to P3.

Vertical and horizontal distribution viewed in combination

Fig. 9 displays individual and day-to-day variability in vertical and horizontal distribution combined during the 3 periods for 5 fish. During P1 when there was little horizontal movement, most of the daytime recordings were from depths of 25 to 50 m. In P2, when horizontal movements increased, swimming depth during both night and day gradually decreased. This resulted in a generally shallower distribution and a diminished vertical range. Around 2 March (DOY 61), when a horizontal migration to the spawning area occurred, a behavioural change to shallower distribution was observed in all individuals. At the end of P2, some herring were for the first time equally high in the water column during the day and at night. During P3, herring were frequently found at shallow depths during both the daytime and nighttime, but there were occasional deep daytime dives down to around 40 m, some of which were of long duration (5 to 8 h), and the timing differed between individuals. Notably, the deep dives were followed by a horizontal shift to R4 (primary fjord outlet) (Fig. 9).

DISCUSSION

This study shows that both horizontal and diel vertical spatial preferences of herring change with gonadal maturity state, but also that individual spatial preference is variable. The fish gradually moved horizontally away from the pre-spawning location towards the presumptive spawning site, followed by movement towards the outer basin close to the outlet of the fjord. Pre-spawning fish showed marked DVMs, staying deeper during the day. DVMs gradually decreased over time, while the total vertical distance moved by single individuals increased. As predicted, both the frequency of receiver shifts and the day-to-day variability in horizontal positioning in-

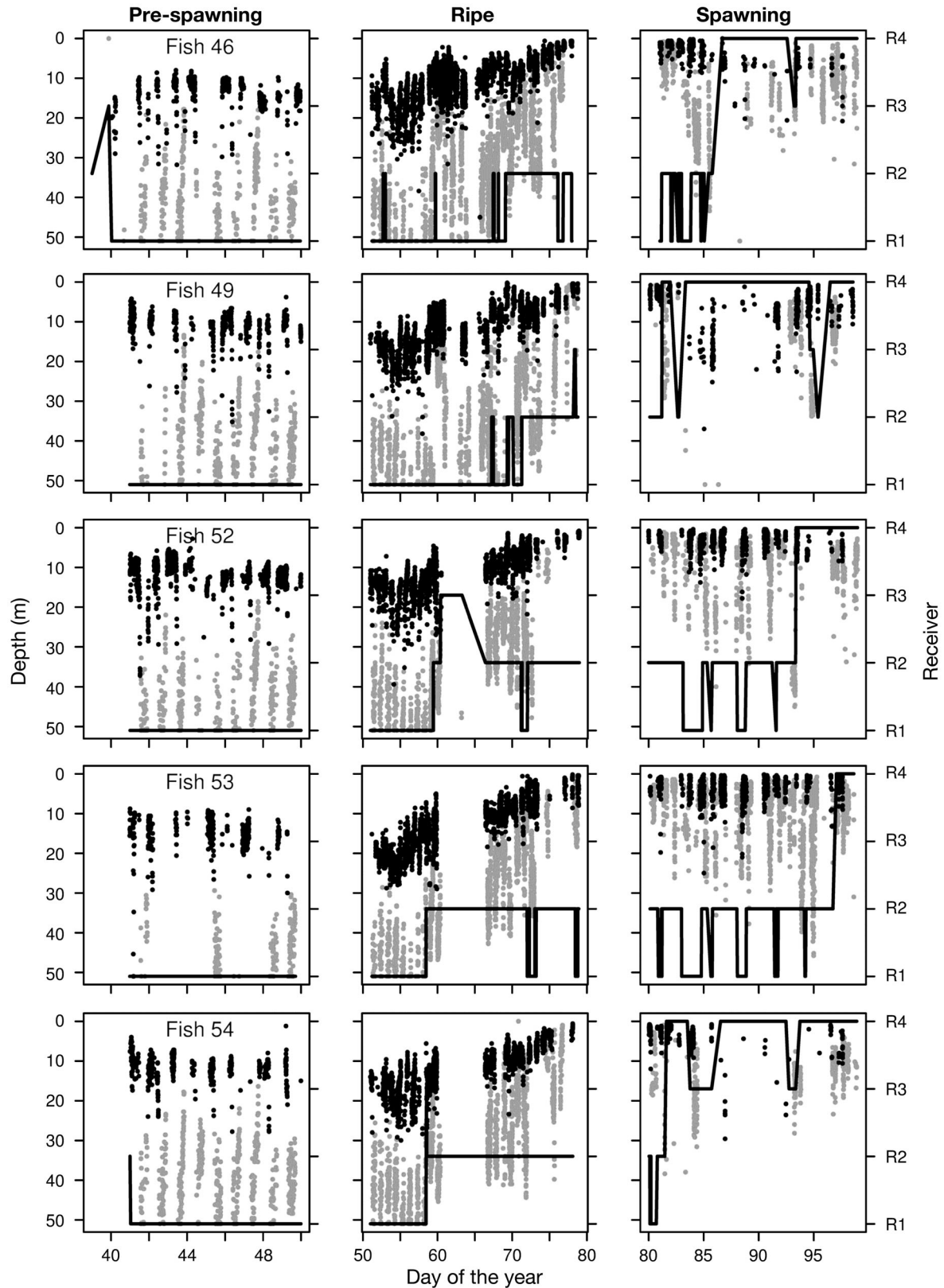


Fig. 9. Detected vertical position of tagged herring as a function of day of the year during daytime (grey) and nighttime (black) for the different periods (pre-spawning [P1], ripe [P2] and spawning [P3]), based on tag recordings for 5 individual fish (IDs indicated in left panels). The solid line marks the position of individual herring in relation to the different receivers (R1–R4)

creased between the pre-spawning and spawning periods, indicating a shift from strong school coherence to a higher degree of individualism.

The study demonstrates that tagging herring for behavioural studies can be effective; only 4 of the 28 tagged fish were discarded from the analyses of the 620 d observation period. Novel acoustic tagging technology thus opens up the possibility of studying individual behaviour in pelagic fish *in situ*. Tracking of individually tagged fish using a network of ultrasonic receivers could provide crucial information that traditional acoustic methods such as echosounders and sonar do not offer. First, the fish can be tracked for long periods without a monitoring vessel. Second, individual fish behaviour within a social unit (like a school) can be studied. Thirdly, fish that leave the school as individuals or in small groups can be observed. Finally, the behaviour of the individual fish may be related to anatomical and physiological characteristics such as size, age, and stage of gonadal maturity.

Horizontal distribution and movements in relation to maturation state

The horizontal distribution changed with the state of maturation. The optimal location for energy saving and risk reduction during pre-spawning is likely to be different than the optimal location for egg deposition or feeding. The stable horizontal distribution during pre-spawning corresponds to the overwintering of Norwegian Spring Spawning (NSS) herring that has been suggested to reflect a maximisation of energy conservation and minimisation of predation risk (Huse & Korneliussen 2000). A stable pre-spawning location has been reported in Lindåspollene before (Langård et al. 2014a), but here we show that in addition to little individual horizontal movement with few receiver changes (see Fig. 4), the vertical distance moved by individuals during this phase is also low, and with low variance (see Fig. 7). This indicates a large degree of synchrony and group cohesion that might be advantageous both for energy saving and for maintaining the internal school organisation (Ritz et al. 2011, Rieucau et al. 2014).

As maturation progressed, the herring gradually moved towards the presumptive spawning grounds. Spawning is triggered by an increase in the surface temperature rather than the ambient temperature *per se* (Langård et al. 2014b), and this was supported by the present study, where the transition from P2 to P3 based on maturation state corresponded to a sub-

stantial increase in surface temperature (Fig. 8). The small meso-scale shift between the early and late pre-spawning periods may reflect the long-distance migration of NSS herring between overwintering areas and spawning grounds (Varpe et al. 2005, see also Langård 2014a). The observed gradual movement to the spawning area presumably reflects a shift from the pre-spawning situation with the herring forming a single cohesive school to a situation with movements as individuals or in small groups. By the end of the study period, the number of herring in the outer part of the basin near the primary outlet was gradually increasing. This area may have offered improved feeding opportunities on zooplankton entering from the more productive outside fjord (Lie & Dahl 1981, Aksnes & Magnesen 1983, Salvanes et al. 1995).

Vertical distribution and movements in relation to maturity state and time of day

The swimming depth of the herring changed in the course of the spawning period and with the diel cycle. Pre-spawning herring performed pronounced DVMS, staying deeper during the day than at night. Such behaviour has previously been observed during pre-spawning (Runnström 1941, Skaret 2007) and is consistent with the general DVMS observed in herring (Blaxter & Parrish 1965, Cardinale et al. 2003, Nilsson et al. 2003). Pre-spawning and spawning herring generally do not feed (e.g. Parsons & Hodder 1975, Crawford 1980, Huse & Ona 1996, Slotte 1999), as is also the case in Lindåspollene (Langård et al. 2014a). This lack of replenishment of energy resources makes it even more essential to save energy during the long overwintering and pre-spawning periods by minimising swimming and basic metabolism (Huse & Ona 1996). As a pelagic and physostomous species (Brawn 1962), herring must swim to avoid sinking to the bottom (Huse & Ona 1996, Kaartvedt et al. 2009). Since the negative buoyancy and hence the energy spent to compensate for sinking increases with depth, there should be a significant advantage for herring to stay close to the surface (Nero et al. 2004). Staying in shallow water also reduces gas diffusion through the wall of the swim bladder (Fässler et al. 2009). The descent towards darker waters at daytime should reduce vulnerability to visual predators (Levy 1987, 1990, Clark & Levy 1988, Rosland & Giske 1994, Cardinale et al. 2003). A combination of energy conservation and minimising gas diffusion in shallow water, and avoidance of

the risky surface waters during the day, may thus largely explain the observed vertical dynamics. Herring may also need to trade off additional factors. During their pre-spawning stage, the fish remained within a narrow vertical range below the thermocline at night. The surface temperature was then below 3°C (Fig. 8), which herring cannot tolerate for long periods (Østvedt 1965). Pelagic fish generally avoid hypoxic conditions (Stramma et al. 2011), but the oxygen levels where the herring were observed were generally well above the minimum threshold for herring (30% Oxygen saturation; Domenici et al. 2002).

The swimming depth range of the herring became gradually shallower over the study period, and the DVM pattern also changed. During the spawning period (P3), the fish were frequently found at shallow depths both day and night. There could be several reasons for staying close to the surface when spawning approaches. The higher temperatures close to the surface than below the thermocline in P3 may speed up the maturation process (Gillet 1991, Lovell 1998, Husebø et al. 2009, Óskarsson & Taggart 2009). The shallow distribution could also be linked to inspection of the spawning site or the spawning activity itself, and video observations showed that at least some spawning occurred in shallow waters. It was not possible to extract the bottom depth from the data, since the depth varied considerably within the detection range of acoustic Receiver 2 at the spawning site. Evidence of spawning could not be explored at deep waters, but the single deep dives lasting for several hours followed by migrations to the outer part of the basin may have represented spawning events.

Individual variability

As the herring approached spawning, the individual and day-to-day variability in horizontal and vertical positioning increased, indicating greater differences in individual trade-offs and priorities. Although a relatively low number of herring was recorded, this strongly suggests that the horizontal and vertical positioning, and the relationship between the individual and the group, gradually change throughout the pre-spawning and spawning periods. During pre-spawning, the herring were horizontally relatively stationary, and although they were vertically dynamic they followed a rhythmic and predictable pattern in spite of individual variation in gonad maturation. The coherence in the large group is then likely to be strong and the individuals would be expected to prioritise staying in contact with the

group, while avoiding predator attacks (Hamilton 1971, Nøttestad et al. 2004). Starting around 2 March (DOY 61) in the ripe phase, individual differences in positioning increased and movement patterns became less predictable. Individual fish were now observed at different receivers and the frequency of receiver shifts was much higher than during pre-spawning. Interestingly, the cumulative vertical movements made by individual fish were also much higher than during pre-spawning even though the vertical range was lower. These results likely reflect different state-dependent trade-offs in the individual fish as spawning approached (see Ritz et al. 2011), and the increased movement and individual heterogeneity in behaviour indicated that the fish to a greater degree behaved as individuals.

CONCLUSIONS

This study demonstrates that acoustic tracking is an efficient means of studying the individual behaviour of small pelagic fish such as herring *in situ*. The fish in the semi-enclosed basin system passed through different behavioural phases, linked to their maturation state. Our results indicate that the balance between individualism and group affinity shifts towards individualism when spawning approaches. Future studies could use triangular positioning systems with real-time tracking of a larger number of fish to obtain even more detailed information on state-specific social behaviour in schooling species, including subgroup formation and associations among individuals.

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