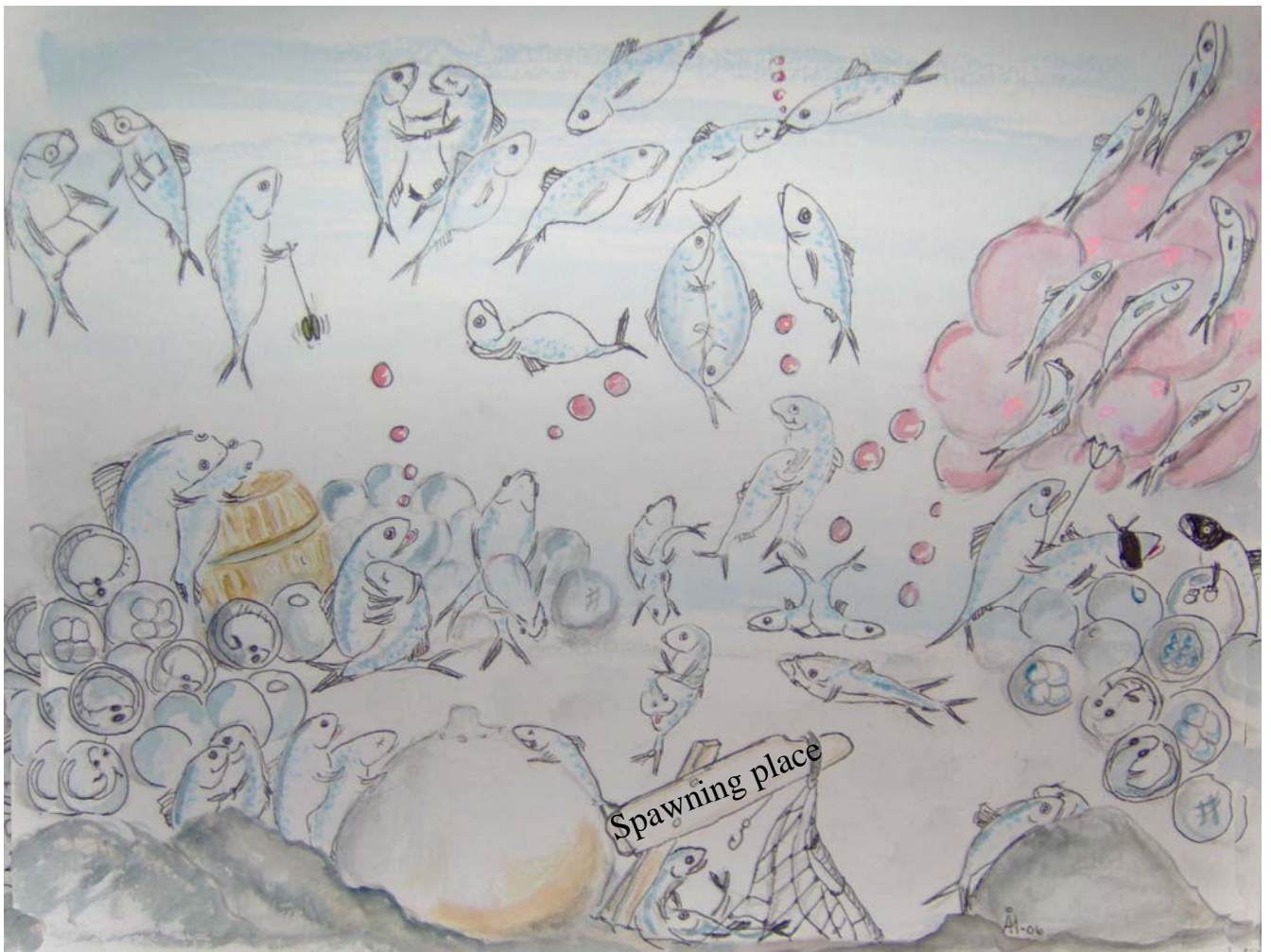


# Paper 5





# Mass formations in giant fish shoals founded in conflicting motivation

Espen Johnsen<sup>1\*</sup> and Georg Skaret<sup>1\*</sup>

<sup>1</sup> Institute of Marine Research, P.O. Box 1870, Nordnes, N-5817 Bergen, Norway

\* These authors contributed equally

**Adaptive collective behavioural formations are common in a range of social animals as different as insects, birds and fish<sup>1</sup>. There is theoretical acceptance that the majority of biological pattern formation is founded in the concept of self-organisation with simultaneous local interactions leading to global patterns<sup>2-4</sup>. Model results further suggest that variable individual behavioural motivation constitute an important organising principle in animal collective formations<sup>4</sup>. There is, however, no empirical evidence to support the model theory and establish a link between behavioural motivation and observed natural formations. Among the most extreme pattern formations in nature are those displayed in free-ranging fish shoals<sup>1, 5</sup>. Here, we document significant differences in maturation state between the upper and lower components of vertical hourglass formations in giant shoals of herring (*Clupea harengus* L.). The results imply conflicting individual motivation for spawning as the underlying mechanism of the formations, and provide unequivocal support for individual behavioural motivation as an organising principle in animal groups.**

Fish shoals are archetypal examples of collective systems<sup>3, 6</sup>, and a shoal is *per se* an adaptive formation with protection towards predators recognised to be the main function for most species<sup>7, 8</sup>. *In situ* studies of free-ranging marine shoals are typically descriptive of formation and structure based on hydroacoustics<sup>5, 9, 10</sup> revealing little of individual positioning or underlying mechanisms behind observed formations. A body of works, mainly from lab and freshwater, on the other hand, has revealed that shoals need not be homogenous mixtures of individuals, but segregated according to phenotypical traits like length, body colour and parasite load (See review in<sup>11</sup>). In individual based schooling models such segregation is shown to emerge when simple behavioural rules differ between individuals<sup>12-14</sup>, and it has been suggested that motivation modifying the behaviour may be important in organising collective formations<sup>4</sup>. However, empirical evidence from the lab to support this is lacking, let alone from free-ranging marine aggregations.

The herring is an obligate collective species living in a permanent context of social interactions through all stages of life<sup>15</sup>. Unlike most pelagic fish, herring are bottom spawners dependent on a habitat associated with high density of predators<sup>16</sup> to reproduce. As a consequence, they should minimise the time spent at the bottom without losing group contact. This pressing trade-off between reproduction and survival, with a short time window to complete spawning and a natural variation in maturity state<sup>17</sup>, makes herring spawning a rare example of a natural system where a link between individual motivation and collective behavioural formations has been suggested<sup>17, 18</sup> and can be investigated - a link until now merely established in computer models<sup>4</sup>.

By analysing time series of acoustic data from the herring spawning areas, we identified numerous vertical hourglass formations, previously only anecdotally reported<sup>17</sup>, and we tested the hypothesis that the formations are causally related to

conflicting individual motivation for spawning. To link acoustic and biological data, we selected acoustic recordings with a clear bimodal depth distribution (See Fig. 2) characterising the hourglass formations, and a herring sample taken from either upper or lower component of the formation (Fig. 1).

There was a significantly higher proportion of spawning herring in the lower than the upper shoal components (Rao-Scott,  $p < 0.005$ ) (Fig. 3), indicating differential motivation for spawning as the underlying fundament of the hourglass formation. While spawning individuals totally dominated ( $>90\%$ ) the samples from lower component, the upper samples had a mixture of pre-spawners, spawners and post-spawners with dominance of pre-spawners (Fig. 3). Pre-spawners were totally dominating in two of the five stations taken from the upper component, and one of the five consisted exclusively of post-spawners (Fig. 2). The last two stations from upper component consisted of a mixture of pre-spawners and spawners. The samples from lower component did not have a single occurrence of post-spawners.

Also on the one occasion with subsequent sampling from the upper and lower components done close in time and space (Fig. 1), the proportion of spawners was significantly higher in the bottom component ( $p < 0.001$ ). Although there was a difference in average body length between the components ( $p = 0.034$ ), the marked difference in proportion of spawners supports that there is a difference in motivation.

A pressing question when observing collective formations in biological systems is whether they are adaptive behaviours or simply epiphenomenal patterns. Indeed, a formation perceived as a cooperative adaptive tactics may be conflict veiled by the necessity to perceive the collective<sup>1</sup>. However, when motivational conflict is inevitable due to the inherent natural variation in biological systems, natural selection may reward individuals in collectives large enough to persist despite diverging preferences for location. Given a temporally dynamic depth preference with progressing maturity state, the hourglass formation in our case may be maintained over time through a positive feedback loop, classical in self-organising systems<sup>3,4</sup>. Suggesting the structure to be adaptive is thus not implicating altruism, but merely a slightly higher average fitness for individuals in larger shoals during reproduction.

Note that depth preference is not expected to automatically follow from maturation state since pre-spawners have to undergo a process of 24-h ovulation before being *able* to spawn<sup>19</sup>, whereas spawners can wait for days before depositing the spawn<sup>20</sup>. This important distinction may explain the almost absence of pre-spawners in the lower shoal components (Fig. 3), in contrast to the relatively high frequency of spawners from the upper components.

In summary, our study demonstrates that internal motivational conflict is the behavioural basis of collective mass formations in free-ranging shoals of herring. The study provides empirical support to the hypothesis of individual motivation as an important organising principle in animal aggregations and new insight into the underlying mechanisms of fish shoal patterns.

## **METHODS**

**Data collection.** The acoustic data material was acquired along the Norwegian coast in February-March 1994-2006 (except for the years 1996 and 2002) in part as abundance estimate surveys of Norwegian spring spawning herring, in part as distribution mapping and/or behavioural studies within selected herring spawning sites (Fig. 4). The data were collected during 170 days at sea covering roughly 30000 nautical miles (n.mi.) (1 n.mi.=1852 m). Biological data from a total of 260 trawl stations were available from the surveys.

The collection of data is done by experienced personal and follows a standard scheme. Acoustic recording is done with a 38 kHz SIMRAD EK 500 echo sounder and integrator (replaced with EK 60 in 2005) and post-processed using the Bergen Echo Integrator (BEI)<sup>21</sup>. In the herring spawning areas, acoustic signal characteristics combined with trawl catches provide unambiguous evidence in cases of herring presence. Biological sampling is done by use of pelagic trawl. Trawling is carried out upon recordings of herring and not at random or fixed stations. A total of 100 random herring are sampled from each catch. The maturity state is categorised according to a standardised scale (Anon., 1962), where the categories maturing ('4') and mature ('5') in this study are pooled into a common 'pre-spawner' category. The transformation from 'pre-spawner' to 'spawner' ('6') happens through an ovulation (female) or spermiation (male) phase, lasting for approximately 24 hours<sup>19</sup>. Individuals with empty or quasi-empty gonads are categorised post-spawners ('7').

**Data processing.** The acoustic density values originating from herring were stored in the unit of nautical area scattering coefficient (NASC) ( $\text{m}^2 \text{n.mi.}^{-2}$ )<sup>22</sup> in a database with a horizontal resolution of one n.mi. and a vertical resolution of 10 m, referenced to the surface. In the final selection of stations (N=8), the raw data were displayed at maximum resolution in depth bins ranging the equivalent length of the distance between two pings (transmitted sound signals) in the horizontal direction (5.14 m at standard ping rate of  $1 \text{ sec}^{-1}$  and cruise speed of 10 knots) and 1 m in the vertical (see Fig. 1) in the unit of  $S_v$  (dB re  $1 \text{ m}^{-1}$ ).

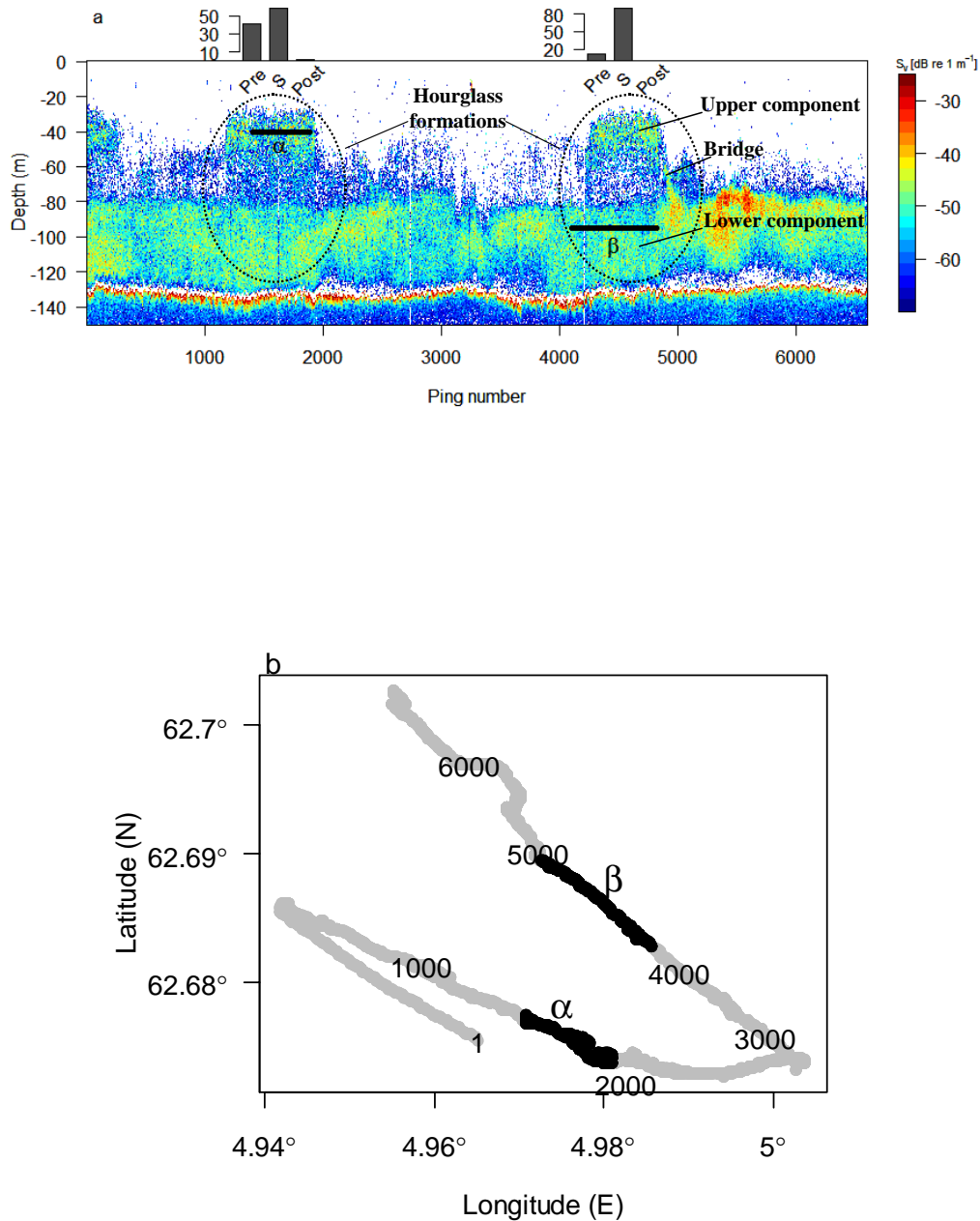
**Analyses.** Only acoustic recordings that could be linked to biological samples from trawl catches were selected for the analyses. In addition, only stations where the acoustic density between the modal peaks did not reach zero, indicating a split between the two shoal components were considered. All trawl stations without a full herring sample (100 fish) were discarded. Two stations were excluded due to mix-in of saithe (*Pollachius virens*) in the catch. Eventually, eight stations were left, five from upper shoal components and three from lower including 100 fish from each station. The stations originated from four different years. Importantly, selection was done prior to looking into the biological data.

**Statistics.** A two-way Rao-Scott likelihood ratio chi-square test design-adjusted to stratified cluster sampling<sup>23</sup> was applied to test the effect of shoal component on proportion of spawners. Each trawl sample is here treated as a cluster (N=8) and the two shoal components (upper and lower) as strata. For the separate comparison between the two adjacent samples displayed in Fig. 1 each sampled fish was assumed to be independent, and a Fisher-Irwin exact test was used to investigate differences between the shoal components regarding proportion of spawners. A regular Student's t-test was used to test for differences in average length between the components.

1. Parrish, J. K. & Edelstein-Keshet, L. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284, 99-101 (1999).
2. Parrish, J. K. & Hamner, W. M. *Animal groups in three dimensions* (ed. Parrish, J. K.) (Cambridge University Press, Cambridge, 1997).
3. Camazine, S. et al. *Self-organization in biological systems* (Princeton University Press, Princeton, NJ, 2001).
4. Couzin, I. D. & Krause, J. Self-organization and collective behavior in vertebrates. *Adv. Stud. Behav.* 32, 1-75 (2003).
5. Makris, N. C. et al. Fish population and behavior revealed by instantaneous continental shelf-scale imaging. *Science* 311, 660-663 (2006).

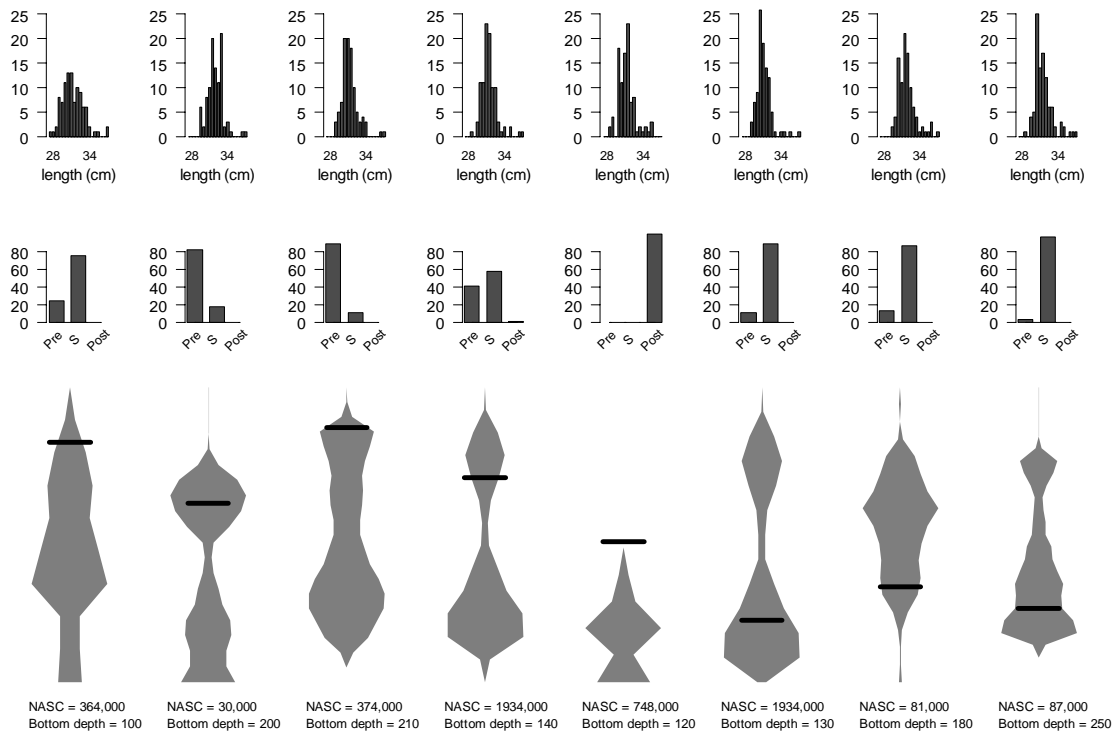
6. Radakov, D. V. Schooling in the ecology of fish (John Wiley & Sons, New York, 1973).
7. Godin, J. G. J. Risk of predation and foraging behavior in shoaling banded killifish (*Fundulus Diaphanus*). *Can. J. Zool.* 64, 1675-1678 (1986).
8. Pitcher, T. J. & Parrish, J. K. in *The behaviour of teleost fishes* (ed. Pitcher, T. J.) 364-439 (Chapman & Hall, London, 1993).
9. Misund, O. A., Aglen, A. & Frønæs, E. Mapping the shape, size, and density of fish schools by echo Integration and a high-resolution sonar. *ICES J. Mar. Sci.* 52, 11-20 (1995).
10. Gerlotto, F. & Paramo, J. The three-dimensional morphology and internal structure of clupeid schools as observed using vertical scanning multibeam sonar. *Aquat. Living Resour.* 16, 113-122 (2003).
11. Krause, J., Butlin, R. K., Peuhkuri, N. & Pritchard, V. L. The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biol. Rev.* 75, 477-501 (2000).
12. Gueron, S., Levin, S. A. & Rubenstein, D. I. The dynamics of herds: From individuals to aggregations. *J. Theor. Biol.* 182, 85-98 (1996).
13. Couzin, I. D., Krause, J., James, R., Ruxton, G. D. & Franks, N. R. Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* 218, 1-11 (2002).
14. Vabø, R. & Skaret, G. Emerging school structures and collective dynamics in spawning herring: a simulation study. *Ecol. Modell.* (submitted).
15. Blaxter, J. H. S. & Hunter, J. R. The biology of the clupeoid fishes. *Adv. Mar. Biol.* 20, 1-224 (1982).
16. Høines, Å. S. & Bergstad, O. A. Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. *J. Fish Biol.* 55, 1233-1257 (1999).
17. Axelsen, B. E., Nøttestad, L., Fernö, A., Johannessen, A. & Misund, O. A. '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 (2000).
18. Nøttestad, L. et al. Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus* L) in a coastal spawning area. *Sarsia* 80, 277-284 (1996).
19. Gillis, D. J., McKeown, B. A. & Hay, D. E. Physiological and histological aspects of late oocyte provisioning, ovulation, and fertilization in Pacific herring (*Clupea harengus pallasii*). *Can. J. Fish. Aquat. Sci.* 47, 1505-1512 (1990).
20. Hay, D. E. Effects of delayed spawning on viability of eggs and larvae of Pacific herring. *T. Am. Fish. Soc.* 115, 155-161 (1986).
21. Foote, K. G., Knudsen, P., Korneliussen, R. J., Nordbø, P. E. & Røang, K. Postprocessing system for echo sounder data. *J. Acoust. Soc. Am.* 90, 37-47 (1991).
22. MacLennan, D. N., Fernandes, P. G. & Dalen, J. A consistent approach to definitions and symbols in fisheries acoustics. *ICES J. Mar. Sci.* 59, 365-369 (2002).
23. Rao, J. N. K. & Scott, A. J. The analysis of categorical data from complex sample-surveys: chi-squared tests for goodness of fit and independence in 2-way tables. *J. Am. Stat. Assoc.* 76, 221-230 (1981).

**Acknowledgements** We thank D. Tjøstheim, V. Hjellvik and K. Korsbrekke for statistical advice and A. Fernö, A. Johannessen, L. Nøttestad and R. Vabø for comments. The project was supported by grants from the Norwegian Research Council to E. Johnsen and G. Skaret.

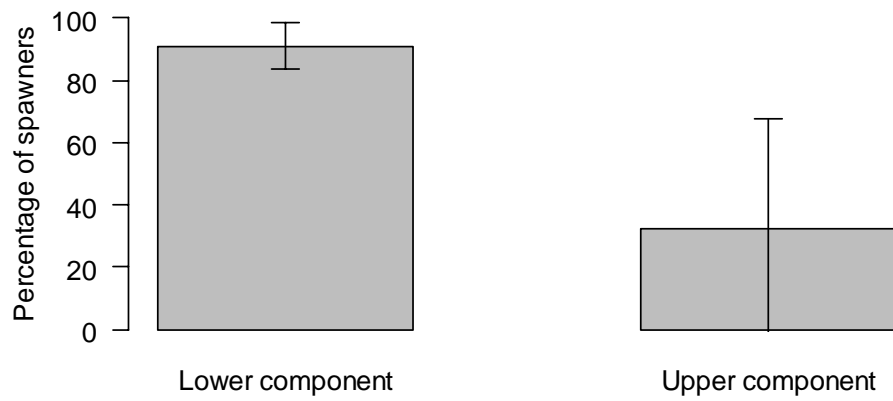


**Figure 1. Gonad maturation state of herring in the upper and lower components of an acoustically displayed hourglass formation.** **a**, Acoustic echogram displaying herring recordings coloured according to density. Ping number refers to each transmitted sound pulse fixed at a rate of  $1 \text{ s}^{-1}$ . The trawl path is represented by black lines ( $\alpha$ =pelagic and  $\beta$ =bottom) corresponding to covered ping numbers and average trawling depth. Frequency histograms of the three herring maturation states pre-spawning (Pre), spawning (S) and post-spawning (Post) are given in histograms above their appurtenant tow. **b**, Geographical survey track (grey line) with ping numbers covered and trawl path corresponding to (a). Time elapsed between the midpoints of  $\alpha$  and  $\beta$  is approximately 30 minutes.

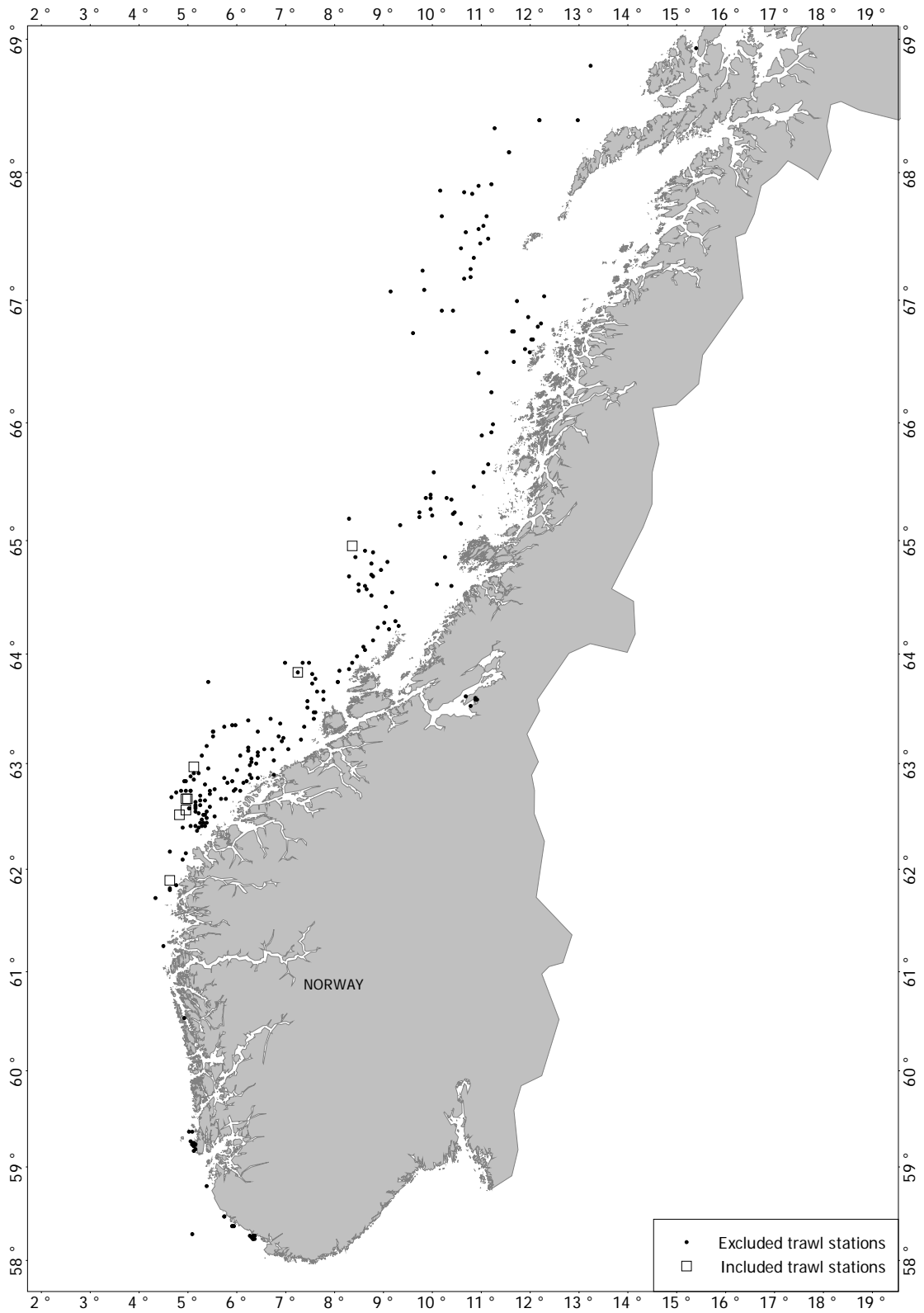




**Figure 2. Acoustic density profiles and appurtenant gonad maturation states and length distributions of herring. Lower, vertical distributions of nautical area scattering coefficient (NASC) of herring. Vertical resolution is 10 m and the NASC-values are sampled over a distance of 5 nautical miles with starting position of trawling within the third nautical mile. Black lines indicate average trawling depth relative to the density profiles. Middle-Upper, frequencies of the three herring maturation states pre-spawning (Pre), spawning (S) and post-spawning (Post) and length distributions of herring by trawl sample.**



**Figure 3. Overall percentage of spawners in upper and lower component of the hourglass formations.** The confidence bands are based on the design-adjusted Rao-Scott likelihood test taking into account clustering effects.



**Figure 4. Map showing all available trawl stations from the herring spawning survey (N=260).**

