

AWAIT IN THE PELAGIC: HERRING COMPROMISING REPRODUCTION
AND SURVIVAL WITHIN A VERTICALLY
SPLIT SCHOOL

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ABSTRACT

The spatio-temporal dynamics of the spawning process were investigated in shallow waters (~50 m) for a single medium sized school (~5 tons) of Norwegian spring spawning herring (*Clupea harengus*). School dynamic parameters, e.g school area, density, vertical extension, shape and movements observed with sonar and echosounder were related to biological parameters such as gonad maturation and stomach fullness obtained from gillnet samples throughout the spawning process.

Prior to spawning, extended cylindrical school shape indicated different depth preferences of individual herring within the school. As the majority of the fish became ripe, the school segregated vertically into one pelagic component contracting to a tight ball and one demersal component spreading out on the bottom. The two components kept close contact (2-30 m vertical distance), interchange of individuals being allowed through temporal rejoinings. The school completed spawning within three days. After spawning, the two components rejoined to form a loose flake feeding at the surface. Herring fed both prior to and after spawning. Predatory fish (gadoids > 50 cm) were present in the area.

The trade-off between survival and reproduction prior to, during and after spawning may have caused spawning substrate, predators and food to act as vertically splitting forces on the school. Ripe individuals must descend to the bottom substrate to spawn, whereas immature and spent individuals may have preferred to stay in the pelagic environment for safety and feeding reasons. Schooling fish have traditionally been considered to make one out of three behavioural decisions: *stay*, *join* or *leave*. For an obligate schooling species like herring, *leave* might not be an alternative unless a large group can leave together or there are other schools near-by. A fourth strategy, *await*, without losing contact with the rest of the school, is suggested from this study. Reasons why individual spawning is not more synchronised are discussed.

Keywords: Herring, spawning, school, vertical split, collective decisions, synchronisation, feeding.

INTRODUCTION

Herring (*Clupea harengus*) is adapted to a pelagic lifestyle (Harden Jones, 1968; Blaxter, 1985; Froese and Rechlin, 1992) and utilises the pelagic environment for feeding and protection by making extended horizontal and vertical migrations (Fernö et al., 1998). Schooling behaviour commences at the larval stage and persists throughout the lifespan (Breder, 1976; Blaxter and Hunter, 1982; Blaxter, 1985; Fuiman and Magurran, 1994; Domenici and Batty, 1997). The individuals swim in a synchronised and polarised manner, minimising the risk of predation (Pitcher, 1983) and have an extensive repertoire of predator responses (Pitcher and Wyche, 1983; Pitcher and Parrish, 1993; Vabø and Nøttestad, 1997).

Herring spawn demersally (Runnström, 1941; Devold, 1963), thereby modifying their pelagic lifestyle and regular schooling pattern. Pacific herring (*Clupea palassi*) spawn on seaweed and kelp (Hay, 1985), whereas Norwegian spring spawning herring (*Clupea harengus*) use coarse gravel and rocks (Runnström, 1941; Polder, 1961) with no other shelter than the school. Unless schools are in contact with the bottom, spawners will have to leave the school to distribute their spawning products on the bottom substrate, and fewer potential escape routes, difficulties to perform coordinated group manoeuvres and reduced dilution effect (Pitcher and Parrish, 1993) may cause the fish to be more vulnerable to predators than in the pelagic. If spawning substrate is limited and patchily distributed (Runnström, 1941) the fish also have to be relatively stationary during spawning, and the weak predator response in this situation (Mohr, 1964; Johannessen, 1986) may further increase the risk of predation.

Individual herring should therefore be expected to spend a minimum of time at the bottom and benefit from coordinated spawning. Although Baltic herring typically spawn in multiple waves (Aneer et al., 1983; Ware and Tanasichuk, 1989 a and b; Rajasilta et al., 1993), Atlantic herring is capable of spawning in just one batch (Bowers and Holiday, 1961) and spawning is thus potentially quite rapid (minutes to hours) at an individual level. In spite of this, field studies indicate that spawning of a school of Atlantic herring takes from one (Furevik, 1976; Johannessen, 1986) to several (Aneer et al., 1983; Kjørsvik et al., 1990; Nøttestad et al. 1996) days. There is no apparent reason why the spawning grounds should represent an optimal location concerning predation risk or feeding opportunities, and over time, predators can be attracted (Toresen, 1985 and 1991; Høines et al., 1995) and planktonic food resources may deplete (Nonacs et al., 1994). It is generally believed that herring start feeding shortly after spawning (Parson and Hodder, 1975; Messieh et al., 1979; Crawford, 1980; Slotte, 1993 and 1996; Huse and Ona, 1996; Nøttestad et al., 1996). Spent herring remaining at the spawning grounds may thus encounter high predation pressure and sub-optimal feeding conditions, and a crucial question could be why the individuals in a herring school do not spawn more synchronously. If each individual choose time and location of spawning in accordance with its own state regardless of the other school members, the school should be expected to split into multiple subgroups. This could however increase the risk of predation (Pitcher and Parrish, 1993), and herring should be expected to compromise reproduction and survival.

At the spawning grounds off Karmøy in south-western Norway, Nøttestad et al. (1996) observed spawning herring both as a continuous layer on the bottom and as distinct schools above the bottom. However, the school dynamics throughout the spawning process are not known. Our aim was to monitor the behaviour of a herring school throughout spawning. This requires an appropriate observation method. Ideally, one should study a single school with no interference from other schools. We combined the use of sonar and echosounder to resolve the three-dimensional school

dynamics. In order to relate the observed behaviour to different stages of the spawning cycle, the maturation state and stomach fullness was recorded from gillnet samples from the school throughout the period.

MATERIALS AND METHODS

The investigation was carried out in Bildøy bay in south-western Norway, in the period April 25-29, 1994. A single school of herring was observed acoustically between 10:00 and 16:00 (local time) every day, using the 96 GRT research vessel R/V "Hans Brattstrøm" (University of Bergen). The vessel is equipped with a multi-beam scanning sonar (Kaijoo Denki KCH 1827) and a single-beam echosounder (Simrad EQ 50). The sonar, set for rotated directed transmission (RDT), was transmitting on 20 out of 48 rod elements in sequence for each ping, emitting 164 kHz pulses with 12-30 ms total duration at 100-300 m range. Beam width (acoustical axis ± 3 dB) was 4.0° horizontally and 6.5° vertically. Reception was in sectors, 90 sectors completing a 180° sweep. The transducer head was tilted mechanically (1° steps). The echosounder transmission frequency was 49 kHz, pulse duration ranging from 0.3-1.0 ms at 50-300 m range. Beam width was 8.0° alongship and 13.0° athwardship.

A survey was daily conducted south of Bildøy in order to map the presence of other schools in the vicinity (figure 1). The observed school was tracked at a distance of 50-100 m, primarily, but low echo intensity and navigational problems caused some variance (25-250 m). The sonar image was recorded on video tape (13 hours). Tracks shorter than 10 minutes were disregarded in order to minimise potential vessel avoidance (bursts). Freeze-frames of the sonar image were analysed every 1 min, obtained when the sonar image was the least affected by bottom echoes or noise within an interval of ± 5 seconds. If no acceptable image was observed within the 10 second interval, data were not collected. Altogether 397 samples out of approximately 500 were accepted.

Horizontal area (a) of the school was measured on the freeze-frames using a light pen, corrected for tilt angle distortion (Misund, 1991), and compensated for distance-induced bias using linear regression ($R^2=0.11$, $p<0.001$ (uncompensated); $R^2=0.00$, $p>0.05$ (compensated)) (Axelsen, 1997):

$$\text{School area} = a \cdot s^2 \cdot \cos(\epsilon) - (d \cdot b) \quad (\text{m}^2) \quad (1)$$

where s = scaling factor,
 ϵ = tilt angle,
 d = vessel to school distance, and
 b = linear regression coefficient.

The circularity of the school (Gerlotto et al., 1994) was calculated as:

$$\text{Circularity} = 100 \cdot (p / (4\pi \cdot s \cdot a))^{-1} \quad (\%) \quad (2)$$

where p = school perimeter.

Relative density (%) was defined as the extent of the overall school area covered by the core (the densest part of the school, indicated red on the sonar screen).

GPS positions of the school were calculated using the position of the vessel, the vessel to school bearing and the distance from the vessel to the surface projection of the school. Swimming speed ($\text{m}\cdot\text{s}^{-1}$) was calculated using the distance and time-lap between consecutive school positions. To minimise bias caused by altering swimming direction, observations with more than two minutes time-lap were excluded. Net displacement velocity ($\text{m}\cdot\text{s}^{-1}$) was calculated as swimming speed from the first to the last school position each day. For comparison, centre depth was calculated from the sonar measurements as:

$$\text{Centre depth (sonar)} = (d \cdot \sin(\epsilon)) - td \quad (\text{m}) \quad (3)$$

where td = transducer depth (1 m); and from the echosounder measurements as:

$$\text{Centre depth (echosounder)} = D_{\min} + (0,5 \cdot V_{\text{sounder}}) \quad (\text{m}) \quad (4)$$

where D_{\min} = minimum depth of the school, and

V_{sounder} = vertical extension of the school.

Altogether 72 echograms from the time period of the sonar recordings were analysed. Single fish echoes from larger fish in the immediate vicinity of the school were interpreted as fish predators. Four different shape categories, discriminated according to horizontal to vertical extension ratio were defined, whereas various amoeba-like shapes that were not persistent over time and deviated from the other categories were classified as "Amorphous" (table 1). Horizontal school extension may have been subject to some random error caused by variation in passage speed, but the speed was relatively constant and the margins between the various categories were large.

The school was sampled using four gillnets aligned in one chain (25 m long and 4 m high) with 32-34 mm meshes (stretched at 5 kg pressure). The nets were set each day around 16:00 in the vicinity of the school and collected around 09:00. Setting depth was 40-50 m. Total length (10 mm groups) and wet weight (0.1 g resolution) of the herring was measured. Stomach fullness was graded 1-5, 1 corresponding to empty and 5 to full, and gonad maturity index classified according to the 8 point ICES maturity scale (Anon., 1962).

Plankton in the surface water was sampled at the end of the study to investigate available prey species and obtain a rough estimate of the zooplankton density. Altogether 8 parallel vertical plankton hauls were worked in the upper 6-10 meters of the water column in the vicinity of the school, using a Juday-sampler with circular opening (60 cm diameter) and 180 μm meshes. Two CTD-profiles were taken, one in the Bildøy Bay and one in the connecting fjord system. A standard weather report was provided from the nearest meteorological field station (DNMI, Flesland).

RESULTS

Weather conditions were generally stable. The wind direction was predominately south-western, with wind force 5-8 $\text{m}\cdot\text{s}^{-1}$. Total wave height did not exceed 30 cm. It was generally clouded (1/8-4/8). The surface layer (upper 50 cm) was relatively brackish (25-30 psu), salinity steadily increasing towards the bottom (33 psu). It was cold, coastal water in the area, with low temperature

in the entire water column (5.2-5.6 °C). The zooplankton density in the upper 10 meters was about 90 mg·m⁻³ (total dry weight), dominated by juvenile stages of *Calanus finmarchicus*. Juveniles of *Pseudocalanus* sp., *Acartia* sp., *Temora* sp. and *Oithona* sp. and eggs from various species were present in the samples as well.

In each gillnet sample, 5-10 gadoids such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*), all > 50 cm (total length), were entangled. The number of herring in the samples ranged from 7 to 71. Length of the herring sampled ranged from 250 to 360 mm (average ± SD (mm) = 305 ± 19) and weight from 148 to 363 g (average ± SD (g) = 232 ± 45). The samples were dominated by fish from 3 to 5 years of age, but 6, 7 and 11 years old individuals (from the strong 1983 year class) were also present.

The two sexes were evenly present in the samples (49.8 % males and 50.2 % females, n=133). The distribution of the gonad maturation indexes in the samples demonstrated a gradual development from dominance of early stage maturing individuals to dominance of spent individuals throughout the period (figure 2). In the first sample, all the herring was maturing or ripe, whereas only 10 % of the herring in the last sample was in a pre-spawning state, the remaining 90 % being running or spent. Fish at all maturation stages had food in their stomachs, but there was a positive correlation between stomach fullness and maturation stage ($r=0.19$, $p<0.05$). Linear regression demonstrated only a weak, but significant ($R^2=0.04$, $p<0.05$), increase of stomach fullness with increasing maturity stage.

Only one herring school was recorded, exclusively observed inside the Bildøy Bay. The size of the school was estimated to 3-5 tons, or roughly 15.000-20.000 individuals. Echosounder recordings the first day revealed that the school divided into two vertically segregated components, one pelagic and one demersal. Only the pelagic component could be detected by the sonar, and the sonar parameters therefore exclusively refer to this part of the school. Vertical extension, minimum-, maximum- and centre depth was only calculated for the pelagic school component, whereas school shape was considered for both pelagic and demersal component, if identified. The vertical extension of the layer of spawning fish at the bottom (Carpet, see later) was estimated to approximately 2 m.

During the following three days, the distance between the components varied from 2-30 m, but was mainly 10-20 m. The two subgroups were consequently aligned vertically and rejoined temporarily (20 out of 59 occasions). When divided, thin connections between the components could sometimes be observed. Towards the end of the period, the components rejoined to form a 5-10 m thick surface layer.

Net displacement velocity was highest prior to spawning (0.20 m·s⁻¹ the first day), lowest as spawning commenced (0.01 m·s⁻¹ the second day) and increased towards the last day of the period (0.14 m·s⁻¹ the last day). School area was relatively low the first two days (~240 m²) but increased the last three days (~550 m²). Swimming depth and vertical extension decreased steadily throughout the period, from about 25 m and 22 m the first day to about 10 m and 8 m the last day, respectively. The relative density of the school was significantly higher on average prior to spawning (41 % the first day) than after spawning (25 % the last day) ($p<0.001$; Mann-Whitney U- test, Bonferroni correction of α - level). Swimming speed and circularity on the other hand showed little variation. An overview of sonar and echosounder parameters is given in table 2.

The change of school shape (figure 3) throughout the period supports this explanation, as the school underwent a transformation from being stretched out vertically prior to spawning, splitting vertically as spawning commenced, and finally joining to form a horizontally prolonged flake at the surface after spawning. The most common category or combination of categories was "Cylinder" the first day (47 %), "Amorphous/Carpet" the second day (42 %), "Ball/Carpet" the third day (30 %), "Cylinder/Carpet" (24 %) and "Flake/Carpet" (19 %) the fourth day and "Flake" the fifth day (48 %). The shape categories were associated with different depth intervals (Tukey HSD test with unequal n, $p < 0.001$) (table 1). The school dynamics throughout the spawning process are illustrated schematically in figure 4.

DISCUSSION

Representativity of the observations

Using both sonar and echosounder permitted us to closely follow the spatial and temporal dynamics in a herring school throughout the spawning period. The demersal school component was readily identified with the echosounder, despite potential problems with shadow effects and bottom echoes (Ona, 1990; MacLennan and Simmonds, 1992), whereas area, density and movements of the pelagic school could be described using the sonar. Although the school tended to be recorded deeper with the sonar than with the echosounder, possible due to sound wave refraction, the trends in the observations with the two instruments were the same. Vessel avoidance caused by noise from propellers and engines has been reported for Atlantic herring (Olsen et al., 1983; Misund, 1991; Misund and Aglen, 1992) and consequences for abundance estimation have been identified (Olsen et al., op. cit.; Fréon et al., 1992; Soria et al., 1996). There was, however, no relationship between vessel to school distance and depth of the school, and the echosounder did not indicate deeper school positions than the sonar or any diving activity. The vessel was thus considered to have negligible influence on the observed behaviour.

Classifying the gonad maturity index permitted us to study the behaviour of herring at different maturity stages. The gillnets were fishing from the bottom to four meters height, and the entire school may therefore not have been sampled. Although this may have caused a bias towards a higher frequency of ripe fish close to the bottom, the samples are believed to give a valid indication of the changes in maturity, as the gonad maturity of the fish increased gradually throughout the period.

Environmental factors may affect fish behaviour. Weather conditions were however stable, and the CTD profiles indicated cold, coastal water, which herring searches for prior to spawning (Runnström, 1941). The environmental conditions were thus typical for a spawning locality, and changes in behaviour could not have been triggered by sudden changes in the prevailing conditions.

No other schools were observed in the area, consequently no interactions between schools may have taken place. Our observations therefore show that isolated schools of spawning herring exist, even though Norwegian spring spawning herring generally gather in dense aggregations along the coast to spawn (Devold, 1963 and 1967; Dragesund, 1970; Dragesund et al., 1980; Nøttestad et al., 1996). Hence, our observations are first of all relevant for isolated schools. On the other hand, Slotte (1998) observed that herring spawning in shallow areas are distributed in demersal layers and pelagic schools, suggesting that our findings may be representative for the spawning dynamics at

the spawning grounds, even though some aspects of the behaviour may be modified by interactions between schools. Our observations were restricted to day-time, but Slotte (op. cit.) observed the same distribution pattern at night-time.

School shape

Prior to spawning, the shape of the school was mostly cylindrical, stretched out in the vertical plane. Although vertically extended fish schools exist (Wrzesinski, 1972), horizontally stretched schools are more common (Wrzesinski, op. cit.; Misund, 1993; Nøttestad et al., 1996). Individuals of different maturation stage may prefer different vertical positions in the water column, ripening fish searching downwards to descend to the bottom and early maturing and spent fish having preference for the pelagic environment. Yet, staying with the group may be more important than vertical position alone, and this may have caused the school to stretch out in the vertical plane without splitting.

Cylindrical shape on the first day was followed by predominately amorphous shape the next day. At this point, the school divided in two vertically distinct components. The amorphous shape may result from reduced synchrony and polarity in the school (Pitcher and Parrish, 1993) as individuals were about to break out of the pelagic school to spawn on the bottom. The following Tight Ball formation of the pelagic school component could have been caused by individuals searching for the centre of the school for protection (Pitcher and Wyche, 1983; Parrish, 1992; Fréon et al., 1993; Pitcher and Parrish, 1993).

Partial vertical school split

Traditionally, schooling fish has been thought to make one out of three alternative behavioural decisions: *stay*, *join* or *leave* (Pitcher and Parrish, 1993). For an obligate schooling species like herring, *leave* might not be an alternative unless other schools to *join* are present in the vicinity, or individual fish can coordinate leaving. We suggest that a fourth strategy, *await*, without losing contact with the group, might be involved when compromising the trade-off between reproduction and survival in a spawning herring school.

The most interesting observation in this study was the partial split of the school into one pelagic and one demersal component. We could not take samples from the different divisions, but we assume that the demersal component was dominated by spawning fish and the pelagic component of pre- and postspawners. There were no indications that spent individuals left the school. No echoes outside the school characterised as herring were detected, and the estimated school area actually increased throughout the spawning period, presumably because the school flattened out. Although split into two components, the school seemed to remain one unit during spawning. The observed connection between the components is interpreted as fish descending to the bottom to spawn and fish ascending after spawning. This connection may be seen as a confusion zone with low levels of synchrony and polarity due to differences in individual behaviour (Pitcher and Parrish, 1993, Pitcher et al., 1996) inducing searching towards safer parts of the school. The connection was discontinuous, suggesting that individuals moved between the compartments in groups, decreasing the risk of predation.

School splitting has earlier only been observed in the horizontal plane (Pitcher et al., 1996). In contrast to schools splitting horizontally (Pitcher and Parrish, 1993; Nøttestad et al., 1996; Pitcher et al., 1996; Misund et al., 1997), the two vertical components remained vertically aligned during spawning. It has been observed that schools in the pelagic have remained in contact between

splitting and rejoining events (Pitcher et al., 1996), but these connections lasted much shorter (minutes) than the contact observed between the two divisions of the spawning school (days). Contact between school components may be more readily facilitated for spawning schools splitting vertically close to the bottom, since the bottom restricts downward movements and the spawning substrate is spatially restricted.

The finding that pre-spawning and post-spawning herring do not stay on the bottom supports the assumption that staying demersally is associated with costs. Predation is considered the primary evolutionary force shaping schooling behaviour in pelagic fish species (Fuiman and Magurran, 1994). The predation risk is presumably higher close to the bottom because of restricted possibilities to escape and the large area to volume relationship (Parrish, 1992) in the horizontally flattened spawning layer (Carpet) compared to the pelagic school (Ball). During the herring spawning period several piscivores and benthivores have been reported to show diet shifts, abandoning their normal prey in favour of herring eggs and herring (Høines et al., 1995) and we observed potential predators close to the herring school both acoustically and in the gill-net samples.

Although feeding prior to spawning has been reported for spring spawning herring (*Clupea harengus*) in Minas Basin, Nova Scotia (Bradford and Iles, 1992), it has generally been believed that herring do not feed prior to spawning but start shortly after (Parson and Hodder, 1975; Messieh et al., 1979; Crawford, 1980; Slotte, 1993 and 1996; Huse and Ona, 1996; Nøttestad et al., 1996), presumably due to the change in trade-off between reproduction prior to and after spawning (Nøttestad et al., op. cit.). The present study however demonstrates that Atlantic herring may feed both prior to and after spawning. The vertical distribution of zooplankton is not known, but herring should improve feeding conditions by migrating to the depth with maximum feeding opportunities, and after spawning the spent school formed a loose feeding flake at the surface. The relatively high food concentrations may have permitted the herring to filter-feed (Gibson and Ezzi, 1985 and 1992). Using this feeding technique, a pelagic herring school may combine predator defence and feeding (see Magurran, 1993), and feeding at spawning grounds may thus depend largely on food concentration and availability.

During the spawning act, herring must keep in contact with the bottom to shed their eggs on appropriate substrate. Hence, costs and benefits of staying at the bottom should change throughout the spawning period, varying between fish of different maturation stages. This conflict between individual fish within the school could partly be resolved by forming vertical divisions. The gradual ascent of the pelagic component illustrates the dynamics of the process over time, and may be explained by an increasing proportion of spent fish and decreased attraction to the bottom. Individual position preferences in fish schools have earlier been postulated (Magurran, 1993) and to some extent observed (Krause, 1993), but to our knowledge this is the first observation of a fish school where individuals of different states move apart, yet holding contact for a period of several days.

Ripening fish waiting above the spawning substrate to spawn is not unexpected, but why would post-spawners not leave the area? Although herring may seldom occur in schools of optimal size (Fernø et al., 1998), the pelagic spawning schools observed by Nøttestad et al. (1996) were of about the same size as the school observed in the present study. A reduction of school size below a certain threshold could be strongly selected against, and at this point, the risk of predation could increase markedly because of lower probability of detecting an approaching predator, less protection by

dilution and reduced ability to perform coordinated evasive actions (Pitcher and Parrish, 1993). Herring often move between schools of different size and composition (Pitcher et al., 1996), but are not likely to leave a school unless there are other schools to join (Fernö et al., 1998). Even if the optimal situation differs between individual fish, a school of herring often make collective decisions and remain one unit (Fernö et al., op. cit.). Spent individuals may thus do better remaining in the school, paying the costs of reduced feeding opportunities and generally higher predation risk compared to more preferable sites.

A comparison between this study and an extensive field study on the aggregation pattern of Norwegian spring spawning herring (Slotte, 1998) confirms that our observations of herring divided into a demersal layer and pelagic schools are representative for the general pattern of spawning behaviour in shallow areas in south-western Norway. Herring in shallow spawning areas off Karmøy stay in dense schools both day and night with no apparent vertical migrations (Slotte, op. cit.); whereas at the deeper (100-200 m) spawning grounds off Møre, herring is observed in dense layers on the bottom during the day and dispersed pelagically at night. Elevated visually mediated predation in shallow areas may explain why herring stay in dense vertically aligned schools close to the bottom. Predation may thus be a key factor inducing vertical school splitting.

Duration and timing of spawning

The school in the present study completed spawning in three days. This is in accordance with previous studies indicating that herring spawning takes from one (Furevik, 1976; Johannessen, 1986) to several (Aneer et al., 1983; Kjørsvik et al., 1990) days, and the present study is to our knowledge the first direct study of the entire spawning period. Nøttestad et al. (1996) suggested that schools migrate in, spawn and migrate out again on a 4-6 day basis at the Karmøy spawning grounds, but they had no observations on single schools throughout the spawning process. The duration of spawning influences the residential period in the spawning area and thereby the assessment of the spawning stock (Axelsen and Misund, 1997).

Individual herring should be expected to spend a minimum of time at the bottom, thus benefiting from coordinated spawning. Evidently, Atlantic herring is capable of spawning quickly (Harden Jones, 1968), even in one batch (Bowers and Holiday, 1961), but the literature is inconclusive concerning the duration of individual spawning. The high fraction of maturing individuals at maturity stage 4 and 5 on the first two days and the high percentage of spent individuals on the third day in the present study indicates that herring can develop from stage 5 to stage 7 in one or two days.

The duration of the spawning period may to a certain extent be influenced by school size. Pacific herring distribute their spawning products repeatedly in brief periods, and small schools (10-20 individuals) have in laboratory experiments been demonstrated to complete spawning more rapidly (3 hours) than larger (100-200 individuals) schools (12 hours) (Stacey and Hourston, 1982). A high number of individuals may have less synchronised maturation and take longer to spawn. Available area of spawning substrate could be a limiting factor for school size, and variations in school size and available spawning substrate can thus cause variations in the duration of spawning.

The cluster tendency of schools at the spawning grounds may also influence duration of spawning. In a situation with several schools in the vicinity (Nøttestad et al., 1996), spent individuals from different schools could reorganise in new pelagic schools. Mean residence time at the spawning grounds for an individual fish could in this case be reduced.

We have argued that there are costs involved in staying at the bottom and that herring can benefit from forming a pelagic component. However, if the school is to remain one unit, fish in the pelagic must keep in contact with the fish on the bottom, and this may restrict the herring moving to more favourable locations. Although a spawning period of three days represents a considerable degree of synchronisation compared to the total duration of the spawning period in Norwegian spring spawning herring (about four weeks) (Devold, 1967; Johannessen et al., 1995), a crucial question could thus be why a herring school needs three days to accomplish spawning. Reorganisation of schools by splits and joins (Pitcher et al., 1996) can decrease variation in maturity stage within a school, but availability of other suitable schools can be restricted, and there could also be constraints in the mechanisms leading to splitting and joining (Fernö et al., 1998). The maturing process could be synchronised by pheromones (Scott, 1994), and spawning could be triggered by an external stimulus such as sperm release, as suggested by Stacey and Hourston (1982). The time that individuals in a school have been in contact can however vary, and a prerequisite for release of milt to induce spawning is that the fish are mature. Hence, even if there is a selection pressure to synchronise maturation, this does not necessarily have to result in a perfect timing of spawning. The strength of the selective forces is also uncertain. The costs of waiting in the pelagic have not been quantified. In addition, all individuals in a school may not be able to spawn simultaneously. Spawning involves selection of spawning substrate (Holliday, 1958) and the area of suitable substrate may be limited. The male releases milt into the water around the female with no evidence of pairing (Ewart, 1884; Holliday, 1958; Aneer et al., 1983; Stacey and Hourston, 1982), but individual herring has been observed to dive rapidly towards the bottom to distribute the spawning products (Aneer et al., op. cit.; Ware and Tanasichuk, 1989 a and b). The spawning layer in the present study was estimated to be about two meters thick and all fish could not be in contact with the bottom at the same time.

An alternative explanation is that perfect synchronisation is not selected for, but that the costs and benefits of spawning may vary over time and depend on when other individuals spawn. Herring often lay their eggs in thick layers (Runnström, 1941) and eggs in lower layers can suffer both slow developmental rate (Johannessen, 1986) and high mortality (Taylor, 1971). Thus, delaying spawning and depositing the eggs in the uppermost layers may be beneficial in terms of reproductive success. On the other hand, waiting too long to spawn may be risky as well, and individual herring suffer a certain risk of being taken by a predator before spawning. There is often strong competition within a species, the best strategy depending on what other individuals are doing (Smith, 1982). The situation for spawning herring is however unstable concerning both population size (Anon., 1998), with resulting competition for spawning substrate, and the abundance of predators (Bergstad et al., 1991; Dragesund, 1995; Høines et al., 1995), potentially decreasing the consistency of the selection pressure. Though speculative, this game theoretical approach remains an alternative explanation of the imperfect timing of spawning.

Concluding remarks

The changes over time in school area, depth, shape and vertical extension observed in this study demonstrate the dynamics of a spawning herring school. Individual state differences within a school seem to be reflected in individual position preferences influencing school shape, eventually leading to partial vertical school splitting. Fish schools forming distinct, stable subgroups is to our knowledge a new finding. Despite conflicts between individuals, schooling fish can compromise their demands and remain in contact during a period of three days. This illustrates how strongly individual fish in a school depend on each other, especially when there are no other schools to *join*

near-by, fish breaking away in small groups presumably having a high risk of predation. This explains the observation that herring stay at the spawning grounds in a suboptimal locality with respect to predation and food, *awaiting* in the pelagic for the other fish in the school to spawn, and supports the suggestion that a school of herring generally makes collective decisions even if the optimal situation differs between individuals (Fernö et al., 1998).

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REFERENCES

- Aneer, G., Florell, G., Kautsky, U., Nellbring, S., and Sjöstedt, L. 1983. *In-situ* observations of Baltic herring (*Clupea harengus membras*) spawning behaviour in the Askö-Landsort area, northern Baltic proper. *Mar. Biol.*, 74: 105-110.
- Anon. 1962. Recommendations adopted by the Herring Committee. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* (Append.), 1: 71-73.
- Anon. 1996. Report of the northern pelagic and blue whiting fisheries working group. ICES C.M. 1996/Assess: 14. 33 p. + figs. and tabs.
- Anon. 1998. Report of the Marine Resources. *Fisken og Havet*, Special edition 1, 1998. Institute of Marine Research, Bergen. 152 p.
- Axelsen, B.E. 1997. Stimdynamikk hos sild (*Clupea harengus*) under gyting. Cand. Scient. thesis, University of Bergen. (Norwegian) 95 p.
- Axelsen, B.E., and Misund, O.A. 1997. Schooling dynamics of spawning herring (*Clupea harengus*) in a bay in south-western Norway. *Proceedings of the 7th Russian/Norwegian Symposium: Gear Selection and Sampling Gears*. Murmansk, June 1997. pp.: 65-76.
- Bergstad, O.A., Røttingen, I., Toresen, R., Johannessen, A., and Dragesund, O. 1991. Return of Norwegian spring spawning herring (*Clupea harengus*) to historical spawning grounds of south-western Norway. ICES C.M. 1991/H:24 Pelagic fish committee.
- Blaxter, J.H.S., and Hunter, J.R. 1982. The biology of the clupeoid fishes. *Advances in Marine Biology* 20: 1-224.
- Blaxter, J.H.S. 1985. The herring: A successful species? *Can. J. Fish. Aquat. Sci.*, 42 (1): 21-30.
- Bowers, A.B. and Holliday, F.G.T. 1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus*) *Mar. Res.*, 5. 16 p.
- Bradford, R.G., and Iles, T.D. 1992. Unique biological characteristics of spring spawning herring (*Clupea harengus*) in Minas Basin, Nova Scotia, a tidally dynamic environment. *Can. J. Zool./ Rev. Can. Zool.*, Vol. 70(4): 641-648.
- Breder, C.M. Jr. 1976. Fish schools as operational structures. *Fisheries Bulletin U.S.* 74: 471-502.

- Crawford, R.H. 1980. A biological analysis of herring from the Atlantic coast of Nova Scotia and Eastern Northumberland Strait. Manuscript Thec. Rep. Ser. N. S. Department of Fisheries Halifax 80-03.
- Devold, F. 1963. Life history of the Atlanto-Scandian herring. Rapport et procès-verbaux des réunions. Conseil international pour l'Exploration de la Mer 154: 98-108.
- Devold, F. 1967. The behaviour of the Norwegian tribe of Atlanto-Scandian herring. FAO Fish. Rep., 62: 534-549.
- Domenici, P., and Batty, R.S. 1997. Escape behaviour of solitary herring (*Clupea harengus*) and comparisons with schooling individuals. Mar. Biol., 128: 29-38.
- Dragesund, O. 1970. Factors influencing year-class strength of Norwegian spring spawning herring (*Clupea harengus*). FiskDir. Skr. Ser. HavUnders., 15: 381-450.
- Dragesund, O., Hamre, J., and Ulltang Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. p. -v. Reun. Cons. int. Explor. Mer, 177: 43-71.
- Dragesund, O. 1995. Recruitment and trophic interaction between oceanic fish populations and coastal stocks. Pp. 305-322 in: Skjoldal, H.R., Hopkins, C., Erikstad, K.E., and Leinaas, H.P. (eds). Ecology of fjords and coastal waters. Proceedings of the Mare Nor Symposium on the Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam.
- Ewart, J.C. 1884. Natural history of herring. Rep. Fishery Bd Scotl., 2:61-73.
- Fernö, A., Pitcher, T. J., Melle, V., Nøttestad, L., Mackinson, S., Hollingworth, C., and Misund, O.A. 1998. The challenge of the herring: Making optimal collective spatial decisions. Sarsia 83: 149-167.
- Fréon, P., Gerlotto, F., and Soria, M. 1992. Changes in school structure according to external stimuli: description and influence on acoustic assessment. Fish. Res., 15: 45-66.
- Fréon, P., Gerlotto, F., and Soria, M. 1993. Variability of *Harengula* spp. School reactions to boats or predators in shallow waters. ICES Mar. Sci. Symp., 196: 30-35.
- Froese, R., and Rechlin, O. 1992. Synopsis of biological data on (*Clupea harengus*), ICES assessment units 22 and 24, using the fishbase format. ICES C.M. 1992/J:40 Pelagic Fish Committee.
- Fuiman, L.E. and Magurran, A.E. 1994. Development of predator defences in fishes. Rev. Fish Biol. Fish.: 146-183.
- Furevik, D.M. 1976. Beskrivelse av adferd i gyteperioden og undersøkelser på de tidlige stadier hos sild (*Clupea harengus*) i Lindaaspollene. Cand. Real. thesis, Norges Fiskerihøgskole/ University of Bergen. 79 p.
- Gerlotto, F., Fréon, P., Soria, M., Cottais, P.H., and Ronzier, L. 1994. Exhaustive observations of 3D school structure using multibeam side scan sonar: potential use for school classification, biomass estimation and behaviour studies. ICES C.M. 1994/B:26, Ref. D.
- Gibson, R.N., and Ezzi, I.A. 1985. Effect of particle concentration on filter- and particulate feeding in the herring *Clupea harengus*. Mar. Biol., 88: 109-116.
- Gibson, R.N., and Ezzi, I.A. 1992. The relative profitability of particulate and filter feeding in the herring *Clupea harengus*. J. Fish. Biol., 40: 577-590.
- Harden Jones, F.R. 1968. Fish Migration. Edvard Arnold Ltd., London. 325 p.

- Hooliday, F.G.T. 1958. The spawning of herring. *Scott. Fish. Bull.*, 10: 11-30.
- Huse, I., and Ona, E. 1996. Tilt angle distribution and swimming speed of wintering Norwegian spring spawning herring. *ICES J. mar. Sci.* 53: 863-873.
- Høines, Å., Bergstad, O.A., and Albert, O.T. 1995. The food web of a coastal spawning ground of the herring (*Clupea harengus*). Pp. 17-22 in: Skjoldal, H.R., Hopkins, C., Erikstad, K.E., and Leinaas, H.P. (eds). *Ecology of fjords and coastal waters. Proceedings of the Mare Nor Symposium on the Ecology of Fjords and Coastal Waters.* Elsevier, Amsterdam.
- Johannessen, A. 1986. Recruitment studies of herring (*Clupea harengus*) in Lindaaspollene, Western Norway, 1-3. *FiskDir. Skr. Ser. HavUnders.*, 18: 139-240.
- Johannessen, A., Slotte, A., Bergstad, O.A., Dragesund, O., and Røttingen, I. 1995. Reappearance of Norwegian spring spawning herring (*Clupea harengus*) at spawning grounds off southwestern Norway. Pp.: 347-363 in Skjoldal, H.R., Hopkins, C., Erikstad, K.E. and Leinaas, H.P. (eds.). *Ecology of Fjords and Coastal Waters*, Elsevier Science.
- Kjørsvik, E., Lurås, I.J., Hopkins, C.C.E., and Nilssen, E.M. 1990. On the intertidal spawning of Balsfjord herring (*Clupea harengus*). *ICES C.M. 1990/H:30 Pelagic Fish Committee.*
- Krause, J. 1993. Positioning behaviour in fish shoals - a cost-benefit analysis. *Journal of Fish Biology* 43: 309-314.
- Lambert, T.C. 1987. Duration and intensity of spawning in herring (*Clupea harengus*) as related to the age structure of the mature population. *Mar. Ecol. Prog. Ser.*, Vol. 39(3): 209-220.
- MacLennan, D.N., Simmonds, E.J. 1992. *Fisheries Acoustics.* Chapman and Hall, London. 325 p.
- Magurran, A.E. 1993. Individual differences in fish behaviour. Pp.: 441-477 in: Pitcher, T.J. (ed.), *Behaviour of Teleost fishes*, 2nd Ed. Chapman and Hall, New York.
- Messieh, S., Powles, M., and Cote, G. 1979. Food and feeding of the Atlantic herring (*Clupea harengus*) in the Gulf of St. Lawrence and adjacent waters. *Canadian Atlantic Fisheries Scientific Advisory Committee Res. Doc. 79/15*, Department of Fisheries and Oceans, Ottawa, Ont.
- Misund, O.A. 1991. Swimming behaviour of schools related to fish capture and acoustic abundance estimation. *Dr. Philos. Thesis*, University of Bergen. 132 p.
- Misund, O.A., and Aglen, A. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. *ICES J. mar. Sci.*, 49: 325-334.
- Misund, O.A. 1993. Dynamics of moving masses; variability in packing density, shape and size among pelagic schools. *ICES J. mar. Sci.*, 49: 325-334.
- Misund, O.A. A. Fernø, T.J. Pitcher and B. Totland. 1997. Tracking herring schools with a high resolution sonar. Variations in horizontal area and relative echo intensity. *ICES J. Mar. Sci.* 54:
- Mohr, H. 1964. Reaction of herring to fishing gear revealed by echosounding. In: *Modern Fishing Gear of the World. 2*, Fishing News (Books) Limited, London.
- Nonacs, P., P.E. Smith, A. Bouskila and B. Luttbeg 1994. Modeling the behaviour of the northern anchovy, *Engraulis mordax*, as a schooling predator exploiting patchy prey. *Deep-Sea Research II*, 41: 147-169.

- Nøttestad, L., Aksland, M., Beltestad, A., Fernö, A., Johannesen, A., and Misund, O.A. 1996. Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus*) in a coastal spawning area. *Sarsia*, 80: 277-284.
- Olsen, K., Angell, J., and Løvik, A. 1983. Quantitative estimations of the influence of fish behaviour on acoustically determined fish abundance. *FAO Fish. Rep.*, 300: 139-149.
- Ona, E. 1990. Physiological factors causing natural variations in acoustical target strength of fish. *J. Mar. Biol. Ass. U.K.*, 70: 107-121.
- Ona, E., and Mitson, R.B. 1996. Acoustic sampling and signal processing near the seabed: the deadzone revisited. *ICES J. mar. Sci.*, 53: 677-690.
- Parrish, J.K. 1992. Do predators 'shape' fish schools: interactions between predators and their schooling prey. *Netherlands Journal of Zoology*, 42 (2-3): 358-370.
- Parsons, L.S., and Hodder, V.M. 1975. Biological characteristics of south-western Newfoundland herring, 1965-71. *Resources Bulletin No. 11, International Commission for the Northwest Atlantic Fisheries, Dartmouth, N. S.*: 145-160.
- Pitcher, T.J. 1983. Heuristic definitions of shoaling behaviour. *Animal Behaviour* 31: 611-613.
- Pitcher, T. J. and C.J. Wyche 1983. Predator avoidance behaviour of sand-eel schools: why schools seldom split. Pp. 193-204 in: Noakes, D.L.G., Lindquist, B. G., Helfman, G.S., and Ward, J.A. (eds). *Predators and prey in fishes*. Junk, The Hague.
- Pitcher, T.J., and Parrish, J.K. 1993. Functions of shoaling behaviour in teleosts. Pp.: 364-439 in: Pitcher, T.J. *The Behaviour of Teleost Fishes*, 2nd ed. Croom Helm, London and Sidney.
- Pitcher, T. J., Misund, O.A., Fernö, A., Totland, B., and Melle, W. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. *ICES J. mar. Sci.*, 53: 449-452.
- Polder, J.J.W. 1961. Cyclical changes in testes and ovary related to maturity stages in The North Sea herring, *Clupea harengus*. *Archs neerl. Zool.*, 14: 45-60.
- Rajasilta, M., Eklund, J., Hänninen, J., Kurkilahti, M., Kääriä, J., Rannikko, P., and Soikkeli, M. 1993. Spawning of herring (*Clupea harengus membras*) in the Archipelago Sea. *ICES J. mar. Sci.*, 50: 233-246.
- 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, A.P., Liley, N.R., and Vermeirssen, E.L.M. 1994. *J. Fish Biol.*, 44: 131-147.
- Slotte, A. 1993. Norsk vårgytende sild (*Clupea harengus*). Bestandsstruktur og modningsutvikling under gytevandringen 1992. *Cand. Scient. thesis, University of Bergen. (Norwegian)*. 66.p.
- Slotte, A. 1996. Relations between seasonal migrations and fat content in Norwegian spring spawning herring (*Clupea harengus*). *ICES C.M.* 1966/H:11.
- Slotte, A. 1998. Patterns of aggregation in Norwegian spring spawning herring (*Clupea harengus*) during the spawning season. *ICES C.M.* 1998/J:32.
- Smith, J.M. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.

- Soria, M., Fréon, P., and Gerlotto, F. 1996. Analysis of vessel influence on spatial behaviour of fish schools using a multi-beam sonar and consequences on biomass estimates by echosounder. ICES J. mar. Sci., 53: 453-458.
- Stacey, N.E., and Hourston, A.S. 1982. Spawning and feeding behavior of captive Pacific herring (*Clupea harengus pallasii*). Can. J. Fish. Aquat. Sci., Vol. 39: 489-498
- Suuronen, P., Lehtonen, E., and Wallace, J. 1996. Avoidance and escape behaviour by herring encountering midwater trawls. Fish. Res., 29: 13-24.
- Taylor, F.H.C. 1971. Variation in hatching success in Pacific herring (*Clupea harengus pallasii*) eggs with water depth, temperature, salinity, and egg mass thickness. Rapp. p. -v. Reün. Cons. perm. int. Explor. Mer, 160: 34-41.
- Toresen, R. 1985. Predation on the eggs of Norwegian spring-spawning herring at a spawning ground outside the west coast of Norway in 1981. ICES C.M. 1985/H:55 Pelagic Fish Committee.
- Toresen, R. 1991. Predation on the eggs of Norwegian spring-spawning herring (*Clupea harengus*) on a spawning ground on the west coast of Norway. ICES J. mar. Sci., 48: 15-21.
- Vabø, R., and L. Nøttestad 1997. An individual based model of fish school reactions: predicting antipredator behaviour as observed in nature. Fisheries Oceanography 6: 155-171.
- Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J. Fish. Res. Bd Can., 35: 220-228.
- Ware, D.M., Tanasichuk, R.W. 1989a. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasii*). Can. J. Fish. Aquat. Sci., Vol. 46, 10: 1776-1784.
- Ware, D.M., Tanasichuk, R.W. 1989b. Biological basis of maturation and wave spawning in Pacific herring (*Clupea harengus pallasii*). The early life history of fish. Third ICES symposium in Bergen, October 3.-5., 1988. Blaxter, J.H.S., Gamble, J.C., and Westernhagen, H. von. (eds.), Vol. 191. 446 p.
- Wrzesinski, O. 1972. A study on schooling patterns of the Barents sea capelin and and North sea haddock. ICES C.M. 1972/B8. Gear and behaviour committee.

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TABLES AND FIGURES

Table 1 Vertical placement of the school components classified according to shape (n: number of observations; V: Vertical extension; H: Horizontal extension; Pel.: % pelagic observations; Dem.: % demersal observations; Vert.: Vertical extension).

Shape	Definition	n	Pel.	Dem.	depth ± SD	range	Vert. ± SD	range
Flake	V:H ≤ 1:5, pelagic	15	100	0	3.1 ± 1,5	2 - 8	5.3 ± 2,2	3 - 11
Ball	V:H = 3:4-5:4	16	100	0	11.8 ± 4,1	5 - 23	14.8 ± 3,9	8 - 24
Cylinder	V:H ≥ 3:1	20	90	10	20.8 ± 6,8	13 - 42	21.8 ± 5,8	13 - 36
Carpet ①	V:H ≤ 1:5, demersal	37	0	100	39.2 ± 9,7	25 - 59	2 *	
Amorphous	Others	20	55	45	28.7 ± 17	8 - 57	14.1 ± 8,9	3 - 34
All		108	69	31	24.6 ± 16	2 - 59	10.2 ± 9,0	2 - 36

① All recordings of "Carpet" were estimated to 2 m vertical extension (see text).

Summary of the results of the regression analysis. The dependent variable is the natural logarithm of the number of employees. The independent variables are the natural logarithm of the number of employees in the previous period, the natural logarithm of the number of employees in the previous period squared, the natural logarithm of the number of employees in the previous period cubed, the natural logarithm of the number of employees in the previous period to the fourth power, the natural logarithm of the number of employees in the previous period to the fifth power, the natural logarithm of the number of employees in the previous period to the sixth power, the natural logarithm of the number of employees in the previous period to the seventh power, the natural logarithm of the number of employees in the previous period to the eighth power, the natural logarithm of the number of employees in the previous period to the ninth power, and the natural logarithm of the number of employees in the previous period to the tenth power.

Variable	Coefficient	Standard Error	t-statistic	p-value
ln(EMP _{t-1})	0.95	0.02	45.00	<0.0001
ln(EMP _{t-1}) ²	-0.02	0.005	-4.00	<0.0001
ln(EMP _{t-1}) ³	0.0005	0.0001	5.00	<0.0001
ln(EMP _{t-1}) ⁴	-0.00005	0.00001	-5.00	<0.0001
ln(EMP _{t-1}) ⁵	0.000005	0.000001	5.00	<0.0001
ln(EMP _{t-1}) ⁶	-0.0000005	0.0000001	-5.00	<0.0001
ln(EMP _{t-1}) ⁷	0.00000005	0.00000001	5.00	<0.0001
ln(EMP _{t-1}) ⁸	-0.000000005	0.000000001	-5.00	<0.0001
ln(EMP _{t-1}) ⁹	0.0000000005	0.0000000001	5.00	<0.0001
ln(EMP _{t-1}) ¹⁰	-0.00000000005	0.00000000001	-5.00	<0.0001

Source: Author's calculations based on data from the U.S. Bureau of Economic Analysis, *Survey of Current Business*, Table A-10.

Table 2 School dynamic parameters from sonar and echosounder (SD: standard deviation).

Parameter		April 25	April 26	April 27	April 28	April 29	total
<u>Sonar</u>							
School area (m ²)	min	67	23	79	130	28	23
	max	541	930	1284	952	1513	1513
	mean	237	249	566	525	588	444
	SD	135	146	278	192	400	278
Relative density (%)	min	19	6	5	8	7	5
	max	71	58	69	75	50	75
	mean	41	28	37	38	25	33
	SD	16	11	15	12	11	14
Circularity (%)	min	41	24	23	39	31	23
	max	85	96	99	92	90	99
	mean	65	67	59	65	69	64
	SD	17	15	14	14	13	15
Swimming speed (ms ⁻¹)	min	0.20	0.07	0.07	0.04	0.08	0.04
	max	2.2	3.1	3.4	3.1	2.3	3.4
	mean	0.96	0.90	0.77	0.95	0.54	0.84
	SD	0.63	0.62	0.51	0.67	0.46	0.60
School depth (m)	min	13	1	3	1	1	1
	max	60	33	26	23	49	60
	mean	34	17	13	8.5	9.6	14
	SD	11	8.4	4.7	5.5	11.8	8.9
<u>Echosounder</u>							
School depth (m)	min	13	26	5	2	2	2
	max	28	45	24	22	42	45
	mean	20	37	13	9.7	8.2	14
	SD	4.5	10	4.8	7.5	9.7	10
Vertical extension (m)	min	13	22	8	3	4	3
	max	36	30	34	24	23	36
	mean	21	25	18	12	9.2	16
	SD	6.7	3.4	6.4	8.0	5.6	8.1

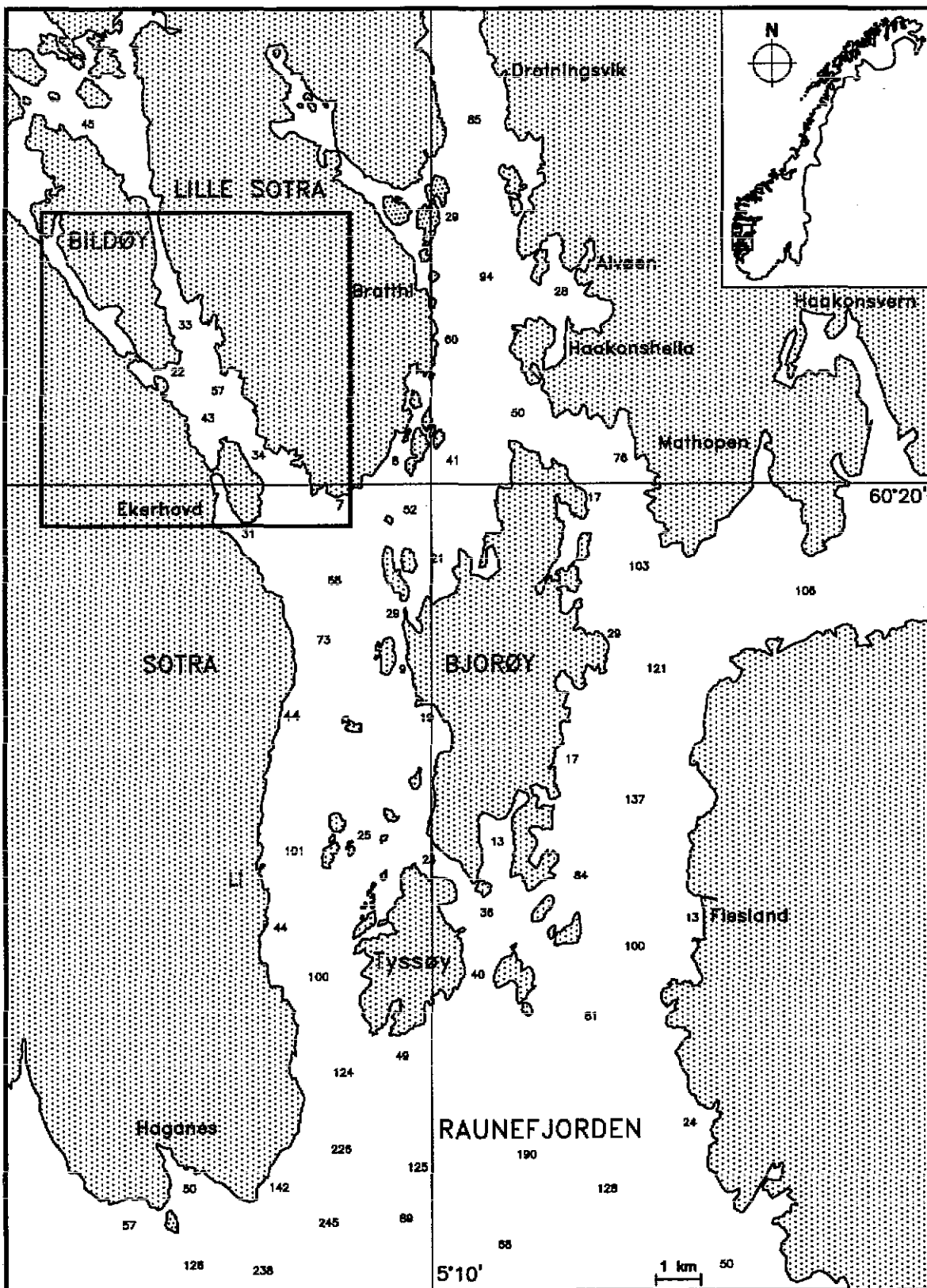
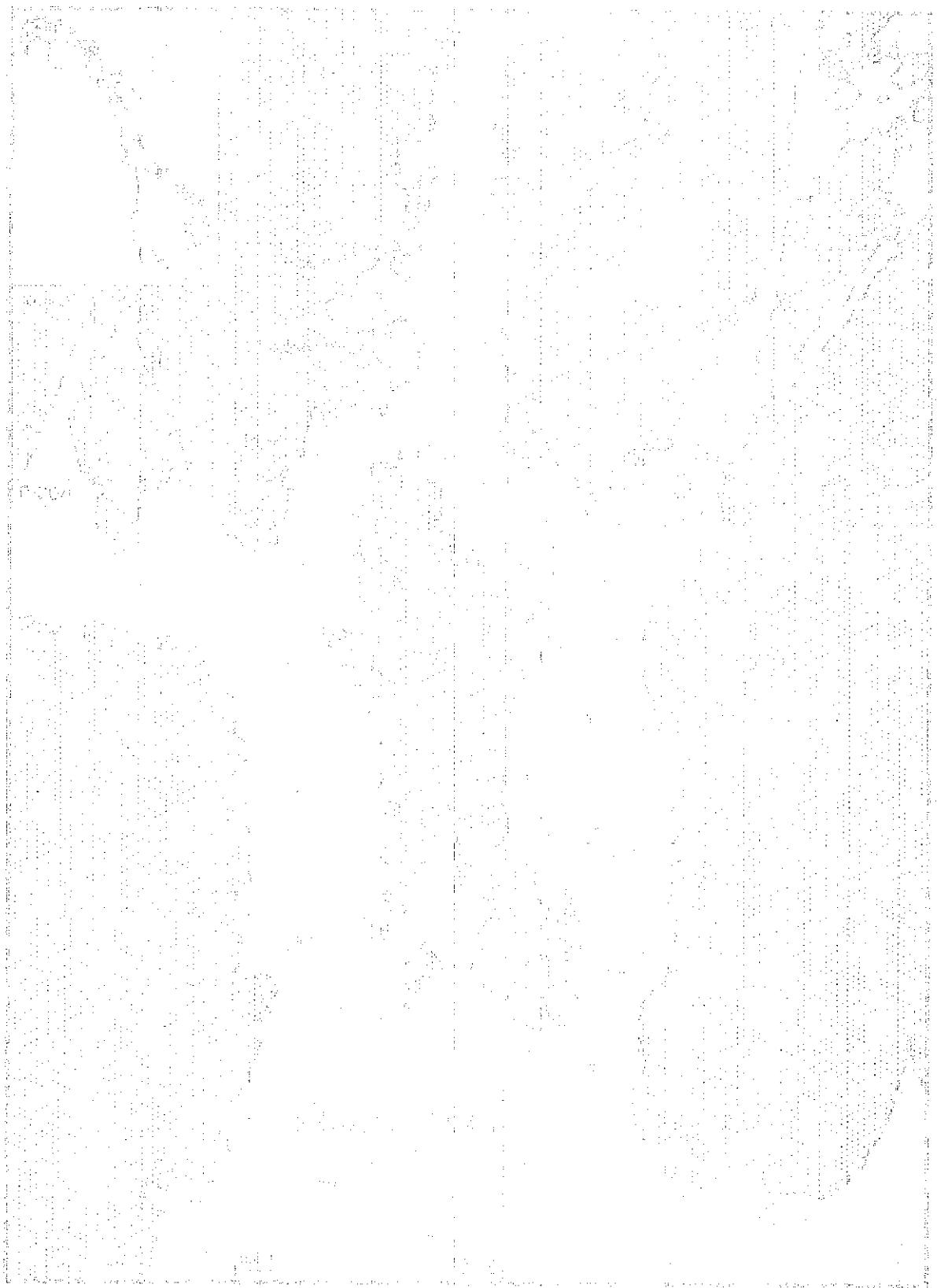


Figure 1 Map over the Bildøy area (□: study site, depths in m).



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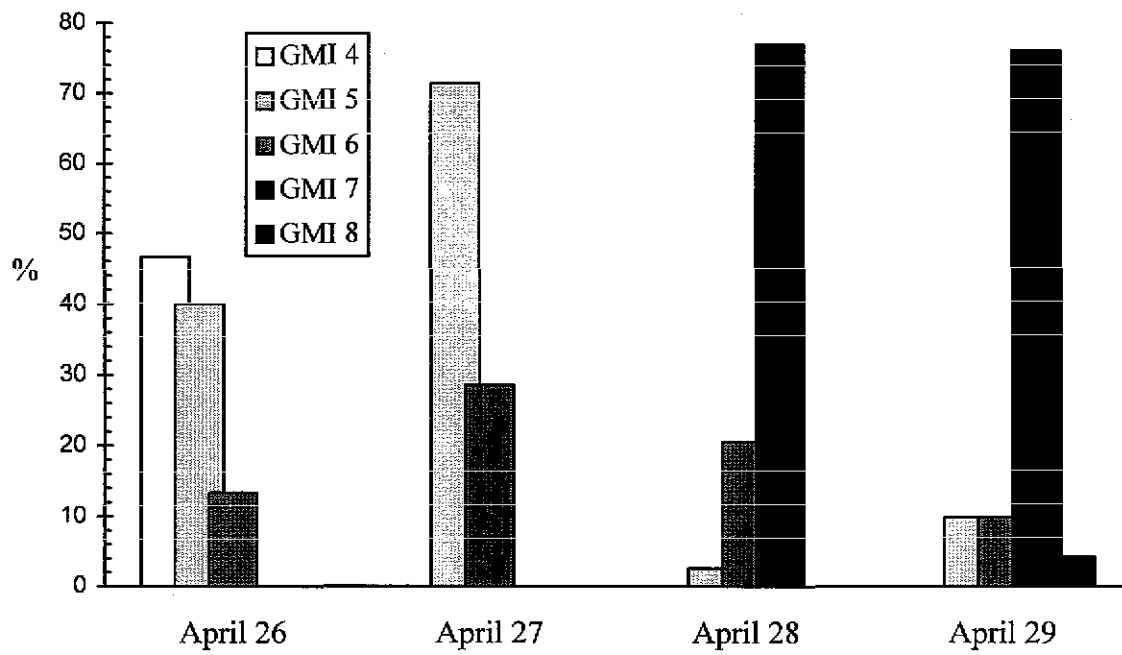
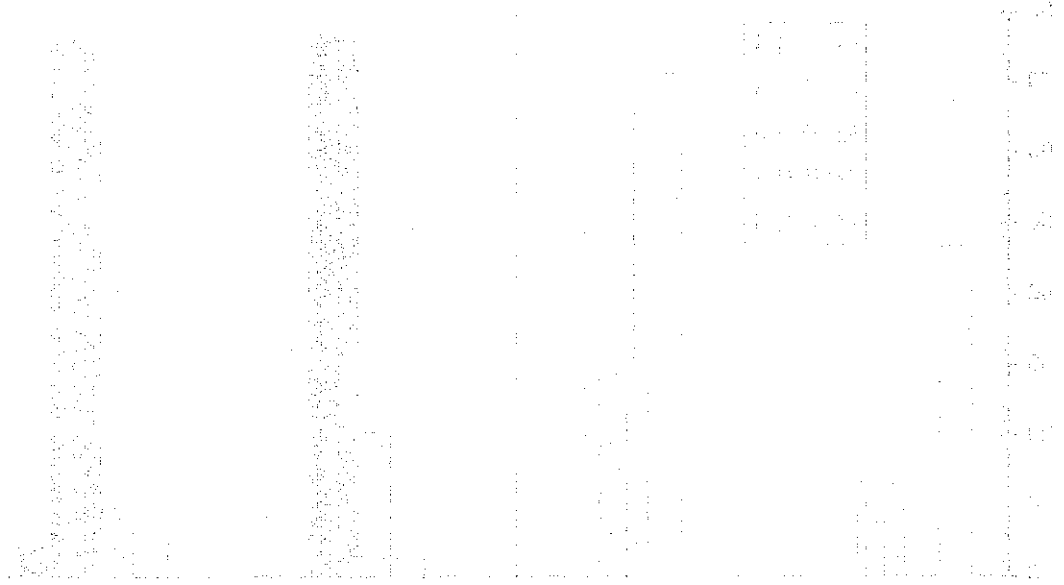


Figure 2 Gonad maturation indexes (GMI) (Anon., 1962) in the herring samples in percent (%).



1919

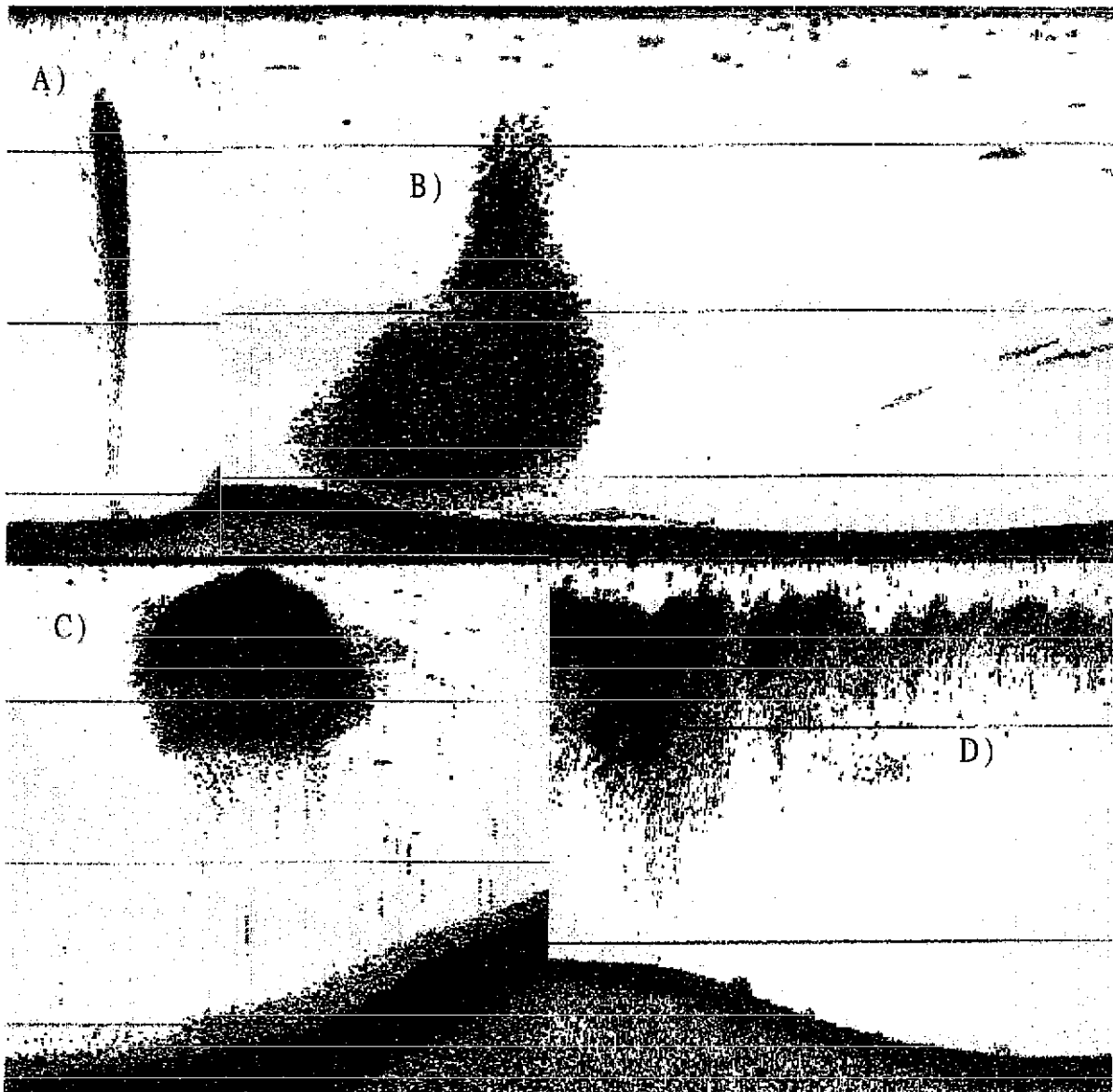


Figure 3 Different school shapes observed throughout the period: A) “Cylinder”, a thin connection can be seen towards the bottom (typically day 1 (and 4)); B) “Amorphous” (typically day 2); C) “Ball/Carpet” (typically day 3); D) “Flake” (typically day 5). Single fish targets can be seen underneath and next to the school (particularly in B). Bottom depth is about 50 meters in A)-C) and 20 m in D).

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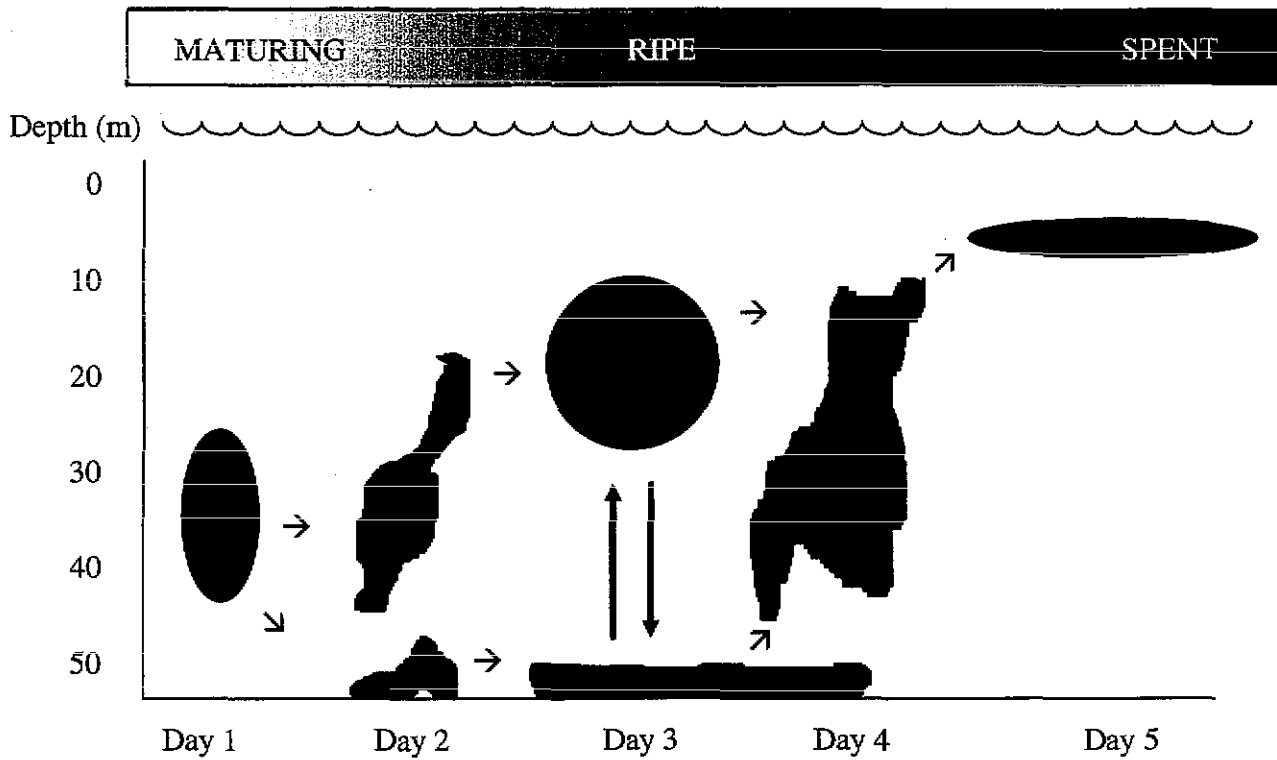


Figure 4 Schematic illustration of herring spawning dynamics.

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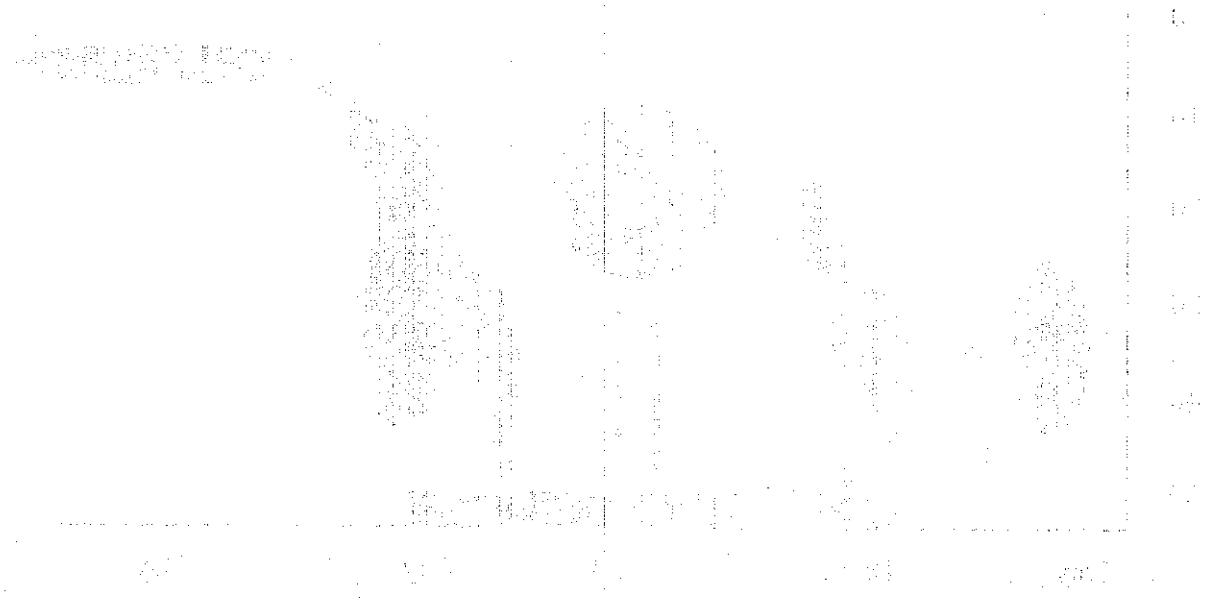


Figure 1. Structure of the protein-DNA complex.