

# Paper 4





# Emerging school structures and collective dynamics in spawning herring: a simulation study

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## Abstract

Schooling fish are known to display various collective behaviours depending on ecological context and life history situation. In Norwegian spring spawning herring (NSS-herring) (*Clupea harengus*) different trade-offs during the seasons of feeding, overwintering, migration and spawning are likely to influence school morphology and behaviour. In the field, school morphology and spatial distribution can be observed using acoustics and individual features such as length, age, stomach fullness and gonad maturation can be measured from biological samples. Nonetheless, in the field, we only record resulting patterns, not the mechanisms of how individual decisions and interactions lead to the observed formations. Individual based models (IBM) on the other hand, are promising simulation tools for investigating how low-level individual behaviour influences large-scale behaviour. We have used this approach with a rule based school model in order to gain understanding of how certain schooling dynamics and patterns can emerge during the spawning of NSS-herring. Response to predation and motivation towards spawning are added to the response to nearby fish. Simply by varying population size and how the motivation towards spawning is synchronised between fish with different gonad states we find different responses of the system in terms of school morphology and dynamics. With high behavioural synchronisation, the system is mainly represented by one integrated school, whereas low degree of synchronisation gives a system with frequent split-offs of small schools. An intermediate degree of synchronisation leads to a more complex situation with schools or layers in a dynamic vertical contact and formation of vertical 'hourglasses' or cylindrical shaped schools. This suggests that the degree of motivational synchronisation between individuals in a school will determine whether or to what degree a school splits into different components or remains integrated. Furthermore, distinct and characteristic formations may be generated and maintained through mere differences in spawning motivation. We also find that with increasing population size there are new system behaviours emerging, not present with lower population size. Larger populations lead to horizontal extension of the pre-spawning components resulting in a double layer system where vertical bridges connecting the two layers are established. The cylindrical bridges are truly emergent properties of the system, formed and maintained by ovulating and spent herring moving across these structures. Similar school formations with vertical connections have been observed acoustically in spawning herring schools. Our results demonstrate that the presence of collective mechanisms in social aggregations like fish schools is likely to have significant influence on emerging large-scale patterns.

*Keywords:* schooling dynamics, school model, individual based models, spawning herring, collective behaviour, emergent patterns

## Introduction

Aggregate and group behaviour are found in different social animals including mammals, birds, insects and fish (Parrish and Edelman-Keshet 1999). From modern system biology, large societies of animal aggregations containing thousands or millions of individuals are understood as leaderless decentralised systems. The organised group level behaviour emerging in these societies is understood as self organising from the local interactions between individuals (Camazine et al. 2001; Couzin and Krause 2003). Schooling in fish is a good example of self-organized group behaviour, where collective behaviour emerges as a result of numerous fish simultaneously responding to the movement of neighbouring fish and the local environment (Parrish et al. 2002).

In the large marine ecosystems of the world more than 4000 species of pelagic fish are schooling, and several solitary species swarm as juveniles (Shaw 1978). For a better understanding of the dynamics of schooling fish we need to build knowledge that link the individual interactions and decisions within a school to the collective behaviour seen in large schools of fish. Obligatory schooling fish like herring live their lives in a constant context of social interaction. This implies that even if the fish are driven by internal motivations (hunger, fear, reproduction, migration) and respond to environmental factors like predation, food, temperature and light, the local decision will always to some degree be influenced by the actions of the nearby individuals within the school. The kind and degree of interaction taking place may therefore have a major influence on the emerging school patterns. This mechanism of how individual interactions leads to school patterns is poorly known, as field observations are mainly able to monitor resulting patterns, not the mechanism itself. Keeping in mind that such individual interactions are of a nonlinear nature, we are facing a complex system, which is not trivial to understand from observations alone. Several fields of research including social science, biochemistry, communication networks, system ecology and economics are dealing with similar problems of understanding emergent system properties from the interactions between distributed agents or entities/nodes (Auyang 1998). A common approach to deal with such complex systems is the application of IBM's or agent-based models (ABM) (Grimm 1999). The strength of this model approach lies in the ability to explore the link between individual behaviour and emerging system behaviour. Several studies have applied IBMs able to simulate fish schools from individual behavioural rules (Aoki 1982; 1984; Huth and Wissel 1992; 1994; Reuter and Breckling 1994; Romey 1996; Vabø and Nøttestad 1997; Inada 2001; Couzin et al. 2002; Inada and Kawachi 2002; Parrish et al. 2002; Couzin et al. 2005; Viscido et al. 2005). The early models of schooling fish were typically focused on the model's ability to produce realistic schooling behaviour by comparing properties like cohesion, nearest neighbour distance and polarization with lab experiments (Huth and Wissel 1994). Some models have focused on the collective responses of fish schools (Couzin et al. 2002; Inada and Kawachi 2002; Couzin et al. 2005). Few studies, however, have applied such models to investigate collective behaviour in an ecological context, where schooling behaviour is influenced by the external environment and internal motivational state of the fish. A review of different models of schooling fish is presented in Parrish et al. (2002).

We present here a model framework of schooling fish applied on the ecological context of herring during spawning. Our model is not a predictive model but rather of an exploratory or heuristic type, aiming at the elucidation of possible essential mechanisms through manipulations of the model parameters. The model is based upon the classical type of fine scale rule-based school models (Reynolds 1987; Huth and Wissel 1992; Viscido et al. 2005). Our rationale for doing so is the assumption that the direct interactions between fish, taking place on a fine temporal and spatial scale, is essential in a model aiming at understanding the collective behaviour emerging in spawning herring. We add motivation as a parameter independent for each individual and a subsequent response to spawning and predation. The model is applied to the ecological scenario where one school of pre-spawning herring enters the spawning site. As time goes by, each fish develops its internal gonad state and switches to new gonad stages from given criteria followed by motivational changes. This creates a challenging collective system, where interacting individuals with motivational differences enter the stage. We expect various effects to appear at the group level, and hence monitor all school activity and dynamics. We track number and shape of schools, how and how often they split and merge, for how long each school persists, and how well individuals with different motivations are sorted into different schools. From general knowledge of collective behavior, we expect the group behavior to be dependent on the number of individuals in the group. As a main question we ask: what kind of collective dynamics should one expect to see in our modelled system as a function of population size and degree of motivational synchronisation?

## Materials and methods

### Biological background

Herring spawn once a year over a well-defined period, a reproduction mode sometimes termed *synchronism* (Le Clus 1979). They are adapted to a life in the pelagic, but unlike most pelagic fish they have demersal spawning (Blaxter and Hunter 1982). The preferences for both spawning substrate and spawning depth vary from population to population (Runnström 1941; Blaxter and Hunter 1982; Haegele and Schweigert 1985). In this study we use the behaviour of NSS-herring as a reference. They deposit the spawn directly on hard bottom and prefer spawning depths of 30-250 meters (Runnström 1941). The whole process of spawning from the building-up of gonads to the deposition of eggs takes several months, but most herring have reached maturation when they arrive at the spawning grounds (Iles 1984). Before herring are said to be ripe and the deposition of eggs can start, a short pheromone induced period of spermiation and ovulation occurs (Gillis et al. 1990). For simplicity we merely refer to this period as ovulation in the model definition. After ovulation the release of milt from a male initiates the act of spawning in both sexes (Stacey and Hourston 1982). NSS-herring spend from 1-7 days at the spawning site (Johannessen 1986; Axelsen et al. 2000; Skaret et al. 2003), but at least for Pacific herring, the emptying of gonads for a single fish may be completed within 2-4 hours (Holliday 1958).

The great challenge for herring at the spawning site lies in maximising the chances of a successful reproduction without being eaten. The engagement in spawning necessarily results in a reduced alertness towards predators, and gadoids like cod and saithe feeding on the herring are abundant near the bottom at the spawning grounds (Høines et al. 1995; Høines and Bergstad 1999). The bottom is not only a general high-risk predation zone, herring school organisation also becomes less appropriate for avoidance manoeuvres when they position themselves close to the bottom (Axelsen et al. 2000). Much of the elaborate schooling dynamics observed at the spawning ground has therefore been explained as the behavioural outcome of a trade-off between predation and reproduction (Nøttestad et al. 1996; Axelsen et al. 2000; Skaret et al. 2003). This may seem a straightforward trade-off but it does in a collective setting become more complicated. The motivation of herring to go down will change according to maturation state (Nøttestad et al. 1996), and the maturation state is not fully synchronised between individuals within a school or population. We aim at incorporating both a realistic trade-off between reproduction and survival and various degrees of conflicting individual motivations in our simulations in order to explore the resulting collective behaviour.

### The Model

#### 1. General model structure

We adapt an individual based modelling approach, IBM (Grimm 1999), defining a system consisting of  $N$  individual fish ( $i=1,2,..,N$ ), released in a continuous 3 dimensional space. The physical space is bounded by a cylindrical volume with fixed boundary, defined by a given radius and depth. The top and bottom of this cylinder represent the

water surface and sea bottom. A cubic grid of cells covers the cylindrical volume, each cell containing reference indexes to the individuals present in the cell. This enables monitoring of schools and a fast spatial algorithm speeding up the simulation substantially. Time is modelled in discrete steps. Predation pressure follows a vertical profile following the depth of the cylinder. During a simulation all individuals are initially placed randomly within a 4 m diameter sphere at the centre of the cylinder, initiating the system as one school. The swimming behaviour of each fish is modelled by combining interaction with nearby fish, response to predation and seeking towards the bottom to spawn. The internal gonad state is represented by a continuous value varying through four behavioural stages (mature, ovulation, spawn, spent) determining the motivation of the fish towards spawning and predation. Individuals are initialised as pre-spawners (mature).

## 2. *The individual based model*

Our IBM is rule-based and similar to school models used in earlier studies of schooling fish and can be thought of as belonging to the type of models first introduced by Huth and Wissel (1992; 1994). Our model, however, is defined in continuous 3D space and the responses of the fish are acceleration of swimming velocity (not only direction change). We also introduce a model framework able to combine schooling behaviour with reaction to predation and motivation towards spawning. The motivation towards spawning is controlled by the internal gonad state (see section below). The main assumptions for the model are based on an abstraction of the biological background. The model is defined on the level of individual fish, determining the action of each fish during each time step. The action calculated by our IBM is the change in swimming velocity, i.e. acceleration, from one time step to the next. The acceleration ( $\mathbf{a}_i^t$ ) of each fish,  $i$ , during each time step,  $t$ , is based on a combination of the behavioural rules. This acceleration response gives the change in position ( $\mathbf{p}_i$ ) and velocity ( $\mathbf{v}_i$ ) of each fish, through the standard dynamic equations:

$$\mathbf{v}_i^t = \mathbf{v}_i^{t-dt} + \mathbf{a}_i^t \cdot dt \quad (1)$$

$$\mathbf{p}_i^t = \mathbf{p}_i^{t-1} + \mathbf{v}_i^{t-dt} \cdot dt + \frac{1}{2} \cdot \mathbf{a}_i^t \cdot dt^2 \quad (2)$$

where  $dt$  is the duration of a time step. Vectors are indicated by **bold** notation.

### 2.1 *Rule combination*

The IBM is defined as a combination of five behavioural rules each generating an acceleration vector ( $\mathbf{a}_k$ ) as a response.

$\mathbf{a}_0$ : Avoid crashing into boundaries (bottom, surface, cylinder walls),

$\mathbf{a}_1$ : Social repulsion

$\mathbf{a}_2$ : Social attraction

$\mathbf{a}_3$ : Move towards bottom to spawn

$\mathbf{a}_4$ : Avoid predation.

These rules are combined using a priority scheme, executed in their listed order until the accumulated acceleration  $|\mathbf{a}_i^t|$  reaches a maximum acceleration ( $a^{\max}$ , Table 1).

$$\mathbf{a}_i^t = \mathbf{a}_0 \cdot \mathbf{a}^{\max} + \mathbf{a}_1 \cdot \mathbf{a}_1^{\text{avail}} + \mathbf{a}_2 \cdot \mathbf{a}_2^{\text{avail}} + \mathbf{a}_3 \cdot \mathbf{a}_3^{\text{avail}} + \mathbf{a}_4 \cdot \mathbf{a}_4^{\text{avail}} + N \cdot \eta \quad (3)$$

Each term in this equation represents a rule, and is added subsequently as long as the available acceleration  $\mathbf{a}_k^{\text{avail}} > 0$ . The acceleration available after the  $k-1$  other rules have been applied, is therefore:

$$\mathbf{a}_k^{\text{avail}} = \mathbf{a}^{\max} - \left| \sum_{m=0}^{k-1} \mathbf{a}_m \cdot \mathbf{a}_m^{\text{avail}} \right| \quad (4)$$

It follows from this that  $\mathbf{a}_0^{\text{avail}} = \mathbf{a}^{\max}$ . For instance, if there is a full response on repulsion, i.e.  $|\mathbf{a}_1|=1.0$ , the succeeding rules have no available acceleration.  $N$  represents stochastic noise ( $|N|=|\mathbf{a}_i^t|$ ), which is always applied, giving perturbation on the final acceleration vector where  $\eta$  is the amount of noise (Table 1). When fish are solitude, responses to predation or spawning are not applied. Then a “random turn” search rule is applied (Vabø et al. 2004). This rule enables the fish to gradually turn to the left or right during a time interval, then altering direction, and so forth until contact with other fish is attained.

## 2.2 Motivation and response

Each behavioural rule,  $k$ , defines the response as a unit vector ( $\mathbf{u}_k$ ) pointing in the accelerated direction, multiplied by a response factor ( $f_k \in [0,1]$ ). The response factor is a function of situation (density, depth, distance to a neighbour etc.) and defined differently from each rule. In addition a fish may have a specific motivation towards the influence the rules represents. The motivation factor ( $m_k \in [0,1]$ ) then determines the maximum applied response to the influence in question. The final rule acceleration  $\mathbf{a}_k$  is therefore less or equal to a unit vector and can be expressed:

$$\mathbf{a}_k = f_k \cdot m_k \cdot \mathbf{u}_k \quad (5)$$

The true acceleration response (in units of  $\text{ms}^{-2}$ ) from each rule is then  $\mathbf{a}_k \cdot \mathbf{a}_k^{\text{avail}}$  as in (3). The motivation towards avoiding boundaries and schooling is always 1.0. Motivation towards spawning, and predation are functions of internal gonad state ( $s$ ), hence we replace  $m_3$  and  $m_4$  with the notations  $M_s^{\text{Sp}}$  ( $M_s^{\text{Sp}} \in [0,1]$ ) for spawning and  $M_s^{\text{Pr}}$  ( $M_s^{\text{Pr}} \in [0,1]$ ) for predation respectively. They reflect a trade-off between avoiding predation and spawning thus we apply  $M_s^{\text{Pr}} = 1.0 - M_s^{\text{Sp}}$  in all stages except for spent herring where spawning motivation is turned off ( $M_3^{\text{Sp}}=0$ ), but  $M_3^{\text{Pr}}$  is in this stage kept at the value of  $M_2^{\text{Pr}}$ , which is fixed to 0.1 (Table 1).  $M_1^{\text{Sp}}$  (ovulation) is set to vary linearly between the  $M_0^{\text{Sp}}$  (mature) and  $M_2^{\text{Sp}}$  (spawn) and  $M_1^{\text{Pr}}$  changes accordingly (Figure 1).

## 2.3 Gonad state development

Around spawning, herring go through four phases: *mature*, *ovulation*, *spawn* and *spent*. These are implemented as four different behavioural states reflecting discrete gonad maturation stages. The gonad state increases continuously within these stages ( $s \in [0,4]$ ), except in the first stage (mature) where it is fixed (Figure 1). In the mature stage each fish has a given probability of switching to the ovulation phase. During ovulation ( $1.0 \leq s < 2.0$ ) each individual can switch into the spawning stage with a given probability if a generated

Gaussian random number  $N(2.0, 0.3)$  is below the current gonad state, provided that the fish is within 1 meter from the bottom. When the closest neighbour is spawning, this probability increases by a factor of 100. Note that this is the only case when fish are explicitly influenced by the state of other fish. If the gonad state during ovulation reaches  $s=1.99$  without switching to spawning, the gonad state stops increasing. During spawning ( $2.0 \leq s < 3.0$ ),  $s$  increases whenever the fish is within 1 meter from the bottom and twice as fast as during ovulation. An individual automatically enters the spent stage when  $s > 3.0$  and  $s$  continues to increase until the simulation stops. The rate of the physiological process of gonad state development has been speeded up considerably in our simulations in order to capture the physiological development within 1 simulated hour (36 000 time steps). However, this rate of change is still slow in comparison with the time scales determining changes, stabilisation and organisation of spatial distributions.

#### 2.4 Avoiding boundaries rule

When the position of an individual one second ahead in time will be less than two body lengths from the boundary, it responds by accelerating away from the boundary:

$$\mathbf{a}_0 = \begin{pmatrix} \mathbf{e}_\perp & \text{for } r_b < L \\ \frac{\mathbf{e}_\perp}{1 + d_b - L} & \text{for } L \leq r_b \leq 2 \cdot L + v_i \end{pmatrix} \quad (6)$$

where  $r_b$  is the distance from the boundary,  $L$  is one fish length,  $v_i$  swimming speed and  $\mathbf{e}_\perp$  is the unit vector away from the boundary.

#### 2.5 Schooling rules

The schooling behaviour of the fish is modelled using a combination of two rules: repulsion and attraction. These are *social rules* implementing how fish interact. Perception is limited by a specified perception range ( $\lambda$ ) and field of view ( $\phi$ ). Laboratory studies suggest that close behavioural interaction between fish is a function of distance squared or distance cubed (Partridge 1981). The repulsive response to nearby fish is therefore implemented as a function decreasing by distance cubed, resulting in high repulsion at close range and a rapid decreasing repulsion in a low responding (neutral) zone (Fig. 2). The presence of such a neutral zone has recently been identified in laboratory experiments (Tien et al. 2004). Attraction is defined to increase with distance following a square relationship expressing that fish within a school apply little attraction to their neighbours while peripheral individuals are increasingly attracted towards other fish (any object displaced away from an observer will appear to shrink as a function of distance squared). For each of  $N^{\text{obs}}$  observed neighbours, each fish (i) responds either with repulsion within a repulsion zone,  $R_{\text{rep}}$  or attraction outside this zone (Aoki 1982). However, if the local density ( $\delta_i$ ) exceeds a density threshold  $\delta^{\text{thr}}$ , attraction is not applied at all. In this way mainly peripheral individuals apply attraction towards other fish, while fish inside a school simply respond with repulsion or ignorance towards other fish. This enables the fish to exhibit individualistic tendencies like responding to the environment (Gueron et al. 1996). With a repulsion, attraction or no response applied to each neighbour, we have:

$$\mathbf{a}_1 = \sum_{j \neq i}^{N^{obs}} \frac{-\mathbf{e}_{ij}}{1 + \alpha^0 \cdot r_{ij}^3} \quad \text{for } 0 < r_{ij} \leq R_{rep} \quad (7)$$

$$\mathbf{a}_2 = \sum_{j \neq i}^{N^{obs}} \frac{\mathbf{e}_{ij}}{1 + \alpha^1 \cdot (r_{ij} - R_{rep})^{-2}} \quad \text{for } R_{rep} < r_{ij} \leq \lambda \text{ and } \delta_i < \delta^{thr} \quad (8)$$

The responses are normalised if necessary, i.e.  $\max |\mathbf{a}_1| = 1.0$  and  $\max |\mathbf{a}_2| = 1.0$ .  $\mathbf{e}_{ij}$  is the unit vector from fish,  $i$ , towards fish,  $j$ ,  $r_{ij}$  is the corresponding distance.  $\alpha^0$  and  $\alpha^1$  are fixed positive constants (Table 1). In terms of equation 5, the expression in (7) and (8) represents  $f_{1j} \cdot \mathbf{u}_{1j}$  and  $f_{2j} \cdot \mathbf{u}_{2j}$  respectively, as response and response direction are calculated for each neighbour ( $j$ ). Our repulsion and attraction rules reflect smooth transitions in behavioural response to variations in distance and are illustrated in Figure 2. The social interaction rules are independent of internal state.

Observing surrounding fish and responding accordingly are only done with a 50% probability at each time step, i.e. with a time step of 0.1 s each fish responds to other fish 5 times per second on average. This introduces a stochastic element representing periods of ignorance, similar to a “swim and glide” behaviour commonly observed in fish. If a fish has been ignorant for more than 0.5 seconds it is forced to respond. Response to predation risk and spawning motivation is applied every time step.

### 2.6 Attraction towards spawning substrate rule

Spawning is the simplest rule with a unit vector ( $\mathbf{u}_3$ ) always pointing straight down. The strength of the acceleration response towards spawning is therefore only determined by the motivation,  $M_s^{Sp}$ , which is a function of gonad state. The initial motivation,  $M_0^{Sp}$ , is a parameter explored in the simulations.

$$\mathbf{a}_3 = M_s^{Sp} \cdot \mathbf{u}_3 \quad (9)$$

### 2.7 Response to Predation rule

Predation risk is implemented as a vertical profile following Beer’s law of light attenuation by depth,  $d$ , (Aksnes and Giske 1993; Aksnes and Utne 1997). We have set the corresponding response factor,  $f_4$ , scaling the response to predation equal to this predation risk profile:

$$f_4 = \left( \begin{array}{ll} e^{(\kappa \times d)} & \text{for } 0 < d < D_{2/3} \\ e^{(\kappa \times d)} + \frac{d - D_{2/3}}{D - D_{2/3}} & \text{for } d \geq D_{2/3} \end{array} \right) \quad (10)$$

$D$  is the total depth and  $D_{2/3}$  is the depth at two-third of the total depth. The predation risk increases linearly up to 1.0 close to the bottom. The rule determining the response to predation checks the changes in predation risk between the current depth of the fish vs. the depth of the fish one second ahead (given the velocity of the fish). The responding

unit vector ( $\mathbf{u}_4$ ) points straight up or down, in the same vertical direction as the fish is swimming if predation risk decreases or in the opposite vertical direction if predation risk increases. The response to predation is a function of both depth and motivation (gonad state):

$$\mathbf{a}_4 = M_s^{\text{Pr}} \cdot f_4 \cdot \mathbf{u}_4 \quad (11)$$

### 3. Measurements

Using a “virtual ecologist” approach, we measure and monitor a range of different parameters at the individual as well as school level. The individual level parameters are recorded as averages and standard deviations for the whole population for each simulated minute. Schools are monitored every simulated second. All measurements are automatically saved to disk for later analysis during each simulation.

#### 3.1 Individual level metrics

Three different measures are recorded, including 1) Final gonad state, 2) Duration of ovulation, 3) Predation risk.

Predation risk ( $P$ ) is a function of the number of individuals within one meter ( $N_I$ ), school size ( $S^{\text{sc}}$ ) and the predation profile (Eq.10) in the following way:

$$P = \frac{1}{2} \cdot p^{\text{Pr}}(d) \cdot \left( a \cdot \left( 1 - \left( \frac{N_I}{20} \right)^3 \right) + b \cdot \left( 1 - \frac{S^{\text{sc}}}{20} \right) \right) \quad (12)$$

where  $a=0$  for  $N_I > 20$ , otherwise  $a=1.0$ . Similar  $b=0$  for  $S^{\text{sc}} > 20$ , otherwise  $b=1.0$ .

#### 3.2 Monitoring of schools

Every simulated second the system is scanned in order to detect schools. A cubic grid of 208124 cells,  $80 \times 80 \times 80$  cm each, covers the cylindrical volume ( $84780 \text{ m}^3$ ) keeping track of which fish are occupying each cell. A school is registered if a region of space contains more than 5 individuals within an interconnected chain of nonempty cells. Each simulated second, this algorithm compares the identified schools with the previously identified schools allowing us to track the formation of new schools and monitor the development of persistent schools. At each simulated minute, various metrics are recorded for each existing school. The total number of schools produced during a simulation is also recorded. School dynamics is monitored through the detection of different events, which can occur to a school. These events are: 1) Appear, 2) Split 3) Join 4) Leave and 5) Merge. A school appears if more than five loose individuals not part of a school aggregate. A school splits into two new schools if more than 20% of the fish in the original school leave. If  $< 20\%$  leave, a new school forms provided that more than 5 fish leave, but the original school is recorded as the same school subjected to a “leave” event. If a school increases with less than 20% it experiences a “merge” event, else, two schools join forming a completely new school. Schools are therefore born either through “appear”, “join” or “split”. The type and frequency of events help us characterise the behaviour of the system.

### 3.3 School metrics

Different metrics are recorded for each school including: 1) Size (number of fish), 2) Vertical extension, 3) Horizontal extension, 4) Age, 5) Standard deviation of gonad stage (mixing), 6) Events.

#### 3.3.1 Mixing

The standard deviation of the discrete gonad stage of the fish within a school is denoted the mixing. Mixing is therefore the inverse of sorting by gonad stage. If all fish within a school have the same gonad stage, e.g. spent, the standard deviation is zero and there is no mixing, i.e. there is perfect sorting. The mixing parameter measured at each time step, is the average of all schools present weighted by the number of individuals in each school.

#### 3.3.2 School shape

The school algorithm classifies each school as belonging to one of five different school shapes, determined by the ratio ( $\mu$ ) between the vertical and horizontal extension of the school. We have extended and slightly modified the classification given by Axelsen et al. (2000), into five different types of shapes: Flake ( $\mu \leq 0.33$ ), Ellipsoid ( $0.33 < \mu \leq 0.75$ ), Ball ( $0.75 < \mu \leq 1.25$ ), Short cylinder ( $1.25 < \mu < 2.0$ ) and Long cylinder ( $\mu \geq 2.0$ ). The first two categories are grouped together as flat shaped and the last two as cylinder shaped in our results section.

### 3.4 System metrics

Measures at the level of the system include the total number of schools produced during a simulation, the frequency of small schools ( $< 10\%$  of population size) occurring and the number of schools present. In order to have a measure of the characteristic school size during a simulation we calculated a sort of relative school size ( $S_{rel}$ ). The measure is defined by :

$$S_{rel} = \sum_{s=0}^{N^{Sc}} S^{Sc} \cdot \frac{S^{Sc}}{N^2} \quad (13)$$

where  $N^{Sc}$  is the number of schools,  $N$  population size and  $S^{Sc}$  school size. If there are two equal sized schools then  $S_{rel}=0.5$ . If most fish are in a large school the relative school size will be close to 1.0. For instance if  $N^{Sc}=6$  and  $N=1000$  where 5 schools have size 20 and one school has size 900, then  $S_{rel}=0.812$ .

### Simulation settings

We have investigated three versions of the model, of which two were preliminary versions. This was done to see the range of various system behaviours and then formulate a more general as well as simplified model when exploring the collective behaviour more systematically. The first model runs used a discrete shift in gonad state from  $M_0^{Sp}$  to  $M_1^{Sp}$  while in the final model  $M_1^{Sp}$  gradually changed linearly from  $M_0^{Sp}$  towards  $M_2^{Sp}$ . A second version of the model used a density dependent response factor modulating each individual's acceleration towards the bottom substrate and response to predation as a function of the number of surrounding neighbours. Lessons from the preliminary model runs are briefly reported. The final model version investigates the behaviour of the

system as a function of  $M_0^{Sp}$  and population size (Table 2). All fixed model parameters are summarised in Table 1.

## Results

Our results are based on a quantitative analysis of individual and school metrics as well as a qualitative evaluation of overall system behaviour. The simulated system can be understood as containing three levels of behaviour; individual- (model definition), school- (emerging group) and emerging system-behaviour. Our main focuses are how variation in initial motivation for spawning ( $M_0^{Sp}$ ) and population size affect school dynamics and global system behaviour. We recognise a general trend in the global response of the system which we have chosen to classify into three different system types; “*split-off system*” System 1, “*dynamic connected system*” System 2 and “*integrated system*” System 3. Figures 3a-c and 3f-h show the mixing of schools according to gonad stage and the numbers of produced schools typical for the three systems. The characteristics of these three systems are described in the following:

### ○ **System 1: SPLIT-OFF SYSTEM**

The system is characterised by unstable dynamics where small schools or groups of ovulating individuals split off like droplets from a larger pre-spawning component to start spawning. The small schools are often well sorted, but overall there are several smaller leaps in the mixing parameter following splits (increased sorting) and joins of schools (decreased sorting). There is generally good sorting in the first part of a run. There are frequent events of splits, joins, leaves and merges in the system. Typically there are several schools present at the same time. The pre-spawning and spawning components are separated.

### ○ **System 2: DYNAMIC CONNECTED SYSTEM**

This system is characterised by high vertical plasticity where two separate layers or components of the same school structure continuously connect and disconnect. The two components consist of spawning herring at the bottom and pre-spawners (mature) herring some meters above bottom where ovulating herring are represented in both layers and responsible for establishment of contact between the two. In the second half of the simulation, spent herring also participate in the establishment of connections, as they are motivated to move up. System 2 is identified from the sudden leaps in the sorting parameter as well as the high number of registered events and new schools due to the subsequent splitting and joining of the same group of fish (Fig 3b and g). The pre-spawning and spawning components are dynamically connected.

### ○ **System 3: INTEGRATED SYSTEM**

In this system mainly one large school is formed, persistent as one unit through the mature, ovulation and spawning phase. Then spent herring form small schools, which split off and leave the bottom area. Before spent herring appear, there are few or no events in this kind of system and hence no schools produced (Fig 3h, Fig 5). The sorting is also low (Fig 3c). The vertical extension of this system is low, indicated by the low value of the form parameter (Table 3). The pre-spawning and spawning components are integrated.

In the first preliminary model version where motivation for spawning changed in discrete steps we mainly found the kind of behaviour typical for System 1. In the second model version explicitly incorporating density dependency, high density dependence drove the system towards hesitation resulting in a more integrated behaviour (System 3) and disabling very small schools to approach the bottom. System 2 appeared for lower or intermediate density dependency. Our final model version captures all three types of system behaviour, and we removed the density dependence making our model simpler and easier to analyse. Our implementation of the school model results in certain school characteristics, which are not within the focus of our study but briefly reported in order to give readers a signature of the school behaviour for comparison with similar models and real observations. These metrics include speed  $0.35 \pm 0.08 \text{ ms}^{-1}$ , average nearest neighbour distance  $0.44 \pm 0.14 \text{ m}$ , average density  $2.73 \pm 0.97 \text{ m}^{-3}$ , average collisions per minute  $0.014 \pm 0.028$  and degree of polarization  $89.52 \pm 40.18^\circ$ . The values are means over all individuals averaged over 60 measurements (including average standard deviation) during one simulation with  $N=500$  and  $M_0^{\text{Sp}}=0.05$ . Density will tend to increase slightly for large population sizes.

Table 3 summarises the results of all simulation runs, including three groups of simulation trials. Most measurements presented in Table 3 describe school characteristics; number of schools, age, shape, size, school events and mixing within schools. Only spawning success are measurements at the individual level. Simply by varying the initial spawning motivation for the standard number of individuals,  $N=500$  in the first simulation trial, the three different systems reveal their characteristics through a combination of various measurements of school dynamics. Figure 3 also shows the degree of mixing and school production characterising the three different systems. System 3 reveals itself by the very low number of schools emerging in the first half of the simulation (Fig 3h), the very low number of small schools (<10%), and the high maximum age of schools (Table 3). In addition schools are mainly flat shaped since the motivation and therefore the depth preference are quite similar for mature, ovulating and spawning herring. System 3 is unmistakable for  $M_0^{\text{Sp}} \geq 0.4$ . Since all fish are integrated in one school until spent herring appear, the mixing in System 3 simply follows the gradual development of gonad state where the maximum is reached half the way through the simulation when all gonad stages are present (Fig 3c). When spent herring appear they split off from the bottom layer forming separate schools without mixing with pre-spawners and thereby causing distinct drops in the mixing. This increases the sorting in the second half of the simulation (Fig. 3c). For lower values of  $M_0^{\text{Sp}}$  maturing herring await higher up in the water column mixing with spent herring through the simulation. For  $M_0^{\text{Sp}}=0.35$  the system is in the transitions between System 3 and System 2, resembling System 3 in terms of number of schools in the first half and number of small schools as well as maximum school age. The total number of schools, however, is more than five times higher than for  $M_0^{\text{Sp}} \geq 0.4$  and there is a significant number of cylindrical shaped schools and a high frequency of Split and Join. This leads us to System 2, which dominates in the small range  $0.25 \leq M_0^{\text{Sp}} \leq 0.3$ . The total number of schools emerging for these values of  $M_0^{\text{Sp}}$  is dramatically higher than for other values of  $M_0^{\text{Sp}}$  (Fig 3g). Despite this, the number of small schools is very low, as the high school count comes from subsequent vertical splitting and rejoining of larger schools forming cylindrical

structures. This is confirmed by the high number of cylindrical shaped schools (30%) for  $M_0^{Sp}=0.3$  and the fact that more than 90% of the events are Splits or Joins (column “frequency of events”). Most events therefore lead to new schools and Figure 5 illustrates how the number of events is maximised around  $M_0^{Sp}=0.3$ . Another consequence of this dynamics is that schools are short lived (since two schools joining create a completely new school), and we find that the mean and maximum school age values are very low. Summing up, System 2 is distinctively identified in Table 3 through the five columns: total number of schools, mean/max school age, ratio of cylindrical shapes and frequency of Split/Join events. In addition, the dynamical contact also leads to sudden leaps and subsequent drops in the mixing, characteristically only for System 2 (Fig. 3b). The main characteristic of System 1 is the unstable school dynamics where small schools or groups of fish leave the pre-spawning layer. We see that the number of small schools is significantly higher for  $M_0^{Sp} \leq 0.2$  in Table 3. This relates to the number of schools present which also is high compared to System 2 and 3. Further, due to the frequent leaving and merging of small groups of fish in System 1 where an event of Merge per definition does not result in two new schools produced as with Split, there are more school events than the total number of schools produced (column “frequency of events”). Since ovulating fish rapidly split off from the pre-spawning layer the sorting in the first half of the simulation is very good in System 1 (Fig 3a).

We are particularly interested in the characteristics of System 2 since the school structures emerging here display interesting similarities with observations in the field (Figure 8). Our second simulation trial therefore varies population size with initial spawning motivation fixed at  $M_0^{Sp}=0.3$ . For small population sizes ( $N < 200$ ) there is a tendency that the two school components (lower spawning layer and upper layer) are not able to establish vertical contact like they are with  $N=500$ . This results in several small schools present at the same time. The System 2 type of behaviour, where two school components continuously connect and disconnect in the vertical therefore vanishes for small population sizes. The low population size, however, results in less horizontal extension and thus frequent occurrences of short and long cylinders as ovulating herring stretch the pre-spawning school downward. In Figure 6 this is evident from the high height-to-area ratio. Due to the low population size most school events are also Split and Join. In simulation trial two, the dynamic connected system behaviour characterising System 2 appears for intermediate population sizes ( $200 \leq N \leq 2000$ ) and is at a peak for  $N=500$  and  $N=1000$ . For  $N=500$  the average number of schools present (1.62) tells us that there are more often two schools than one, while for  $N=1000$  there is more often one connected school (1.34). In both cases there is an extensive dynamic contact where about 90% of school events are Split and Join (Table 3). Notably for  $N=1000$  small schools (<50 fish) are completely absent, i.e. we mostly have two major school components connecting and disconnecting. For  $N \geq 2000$  the system becomes more permanently connected for long periods of time, pushing the average number of schools present down towards 1.0 (Table 3). The total number of schools emerging drops accordingly. For  $N=4000$  we therefore have mainly one school present (1.05) connecting the system completely for long periods of time, resembling System 3 behaviour. The relative school size is consequently close to 1.0. In Figure 4a this is illustrated through barely any school production in the time period between 10-40 minutes for  $N=4000$ . The cylindrical school

shape typical for System 2 for  $N=500$  is also largely replaced by one flattened school. The flat shapes we see with high  $N$ 's emerge as a response to the narrow vertical area of low predation defined by the predation profile (Figure 2). With an increasing population size the fish will squeeze out horizontally within the preferred low-predation belt (Fig 6). For the even larger population size of  $N=8000$  an even more connected system may be expected, but in fact the system is less connected producing more schools than for  $N=4000$  (Fig 4a). This is directly related to the horizontal expansion of the pre-spawning layer. Larger population sizes lead to a new and unexpected kind of parallel system behaviour that shows up even more pronounced in the third simulation trial.

Our third simulation trial investigated how the most apparent System 1 configuration ( $M_0^{Sp}=0.05$ ) would respond to changing population size. Table 3 shows this in rows 19-27. Our expectations were that by simply increasing the population size, we could move the system from System 1 towards a dynamic connected system (System 2) and further towards an integrated system (System 3). We were partly wrong in this assumption. For these simulations there is a systematic increase in number of schools emerging, schools present and school events as a function of population size (Table 3 and Fig 4b). The frequency of cylindrical shaped schools is also relatively high. There is always a direct connection between the number of schools present and the number of small schools. These measures increase for larger population sizes as opposed to the second simulation trial ( $M_0^{Sp}=0.3$ ), where they almost vanished. What does this imply? Instead of moving towards a dynamic connected system, larger population sizes create parallel dynamics where small schools leave the upper layer from different locations simultaneously. For  $N=4000$  there are more than 5 schools simultaneously present on average. These schools must consist of one or two large schools and several small schools because the relative school size is still high (0.69, Table 3). If all schools were of similar size, the relative school size would be around 0.2. But there are also indications that the upper and bottom layer may be connected from time to time because the average school age is not very high for  $N \geq 2000$  indicating periodical contact. The high values of maximum school age are caused by the isolation of some small schools not merging with the major layers. In general, high school ages imply either isolation of schools or tight integration (System 3). Another effect of the parallel dynamics is the increasing portion of cylindrical shaped schools due to the schools forming vertical bridges between layers (Table 3). By plotting the 3-D spatial distribution we can clearly see how such a system is parallel dynamically connected (Figure 7e). This is as if a System 2 kind of behaviour occurred simultaneously at different locations. We ran one simulation with 16000 fish pushing our computational limits, to see if the system finally approached System 2 or 3 behaviour. The outcome was rather an even more parallel system, doubling the total number of schools produced, number of small schools and number of schools present.

The increasing horizontal extension of the pre- and post spawning layers emerging for larger population sizes in the second, but especially in the third simulation trial, relates to the combination of system depth and the applied predation profile. Figure 6 illustrates this flattening of the schools as a function of population size. The narrow vertical predation risk zone defined around 2/3 depth increases for larger system depths (Fig 2). For compression we therefore included further simulation trials with extended system

depths and large population sizes. The last two rows in table 3 show simulations for 90 m system depth. The number of schools produced was similar to the third simulation trial for large  $N$  (Fig 4b and c), but these simulations with extended depths revealed even new surprising system behaviours in terms of vertical dynamics (Fig 7d). Instead of making contact between pre-spawning and spawning layers even more rare with the distance between layers extended from 10 m to 30 m, the opposite was the case. Interestingly, the system initially behaves as System 1, but as ovulating herring become abundant, one large cylinder connecting the two layers establishes. This hourglass morphology is amplified by herring entering the spent stage and kept for several thousand time steps in the simulation run (Fig 7d).

Even if our focus is emerging schooling dynamics, we have measured individual parameters reflecting the spawning performance (last columns Table 3). The total success reflects predation pressure given by positioning in the water column, school size and density. The first simulation trial therefore simply reflects vertical positioning of post spawners resulting from differences in  $M_0^{Sp}$ . When post spawners are situated closer to the bottom (System 3) the overall predation risk is increased while the duration of ovulation is reduced. In the second and third simulation trials we are able to see the effects of population size on spawning success since motivation is fixed. In general, low population sizes ( $N \leq 200$ ) perform badly in terms of spawning success (Table 3). The final gonad state is lower and fish spend more time in the ovulating phase. Larger population sizes tend to increase spawning success until a certain level is reached for  $N \geq 1000$ . The effect of population size is thus substantial. We see, for instance, that the total spawning success is 2.5 times higher for 1000 fish than for 100 fish in the third simulation trial.

## Discussion

In this study we have demonstrated interesting characteristics in the dynamics of spawning herring schools by using a relatively simple individual based school model incorporating response to predation and spawning. Simply by varying the population size and the difference in trade-off between spawning and predation in pre-spawning and spawning herring, we learn three main lessons: First, the behavioural synchronisation of herring with different gonad states is likely to determine whether or to what degree schools will split and sort into separate units or remain unified. Second, the population size or school size has a significant influence on the emerging school structures and dynamics. There are new levels of organisation emerging for large population sizes ( $N \geq 1000$ ) not present with low population sizes ( $N \leq 200$ ). Third, emergent properties including sorting of individuals with similar gonad states into separate schools or layers, or the establishment of dynamic large-scale structures do not require explicit coding in the model. Even in a simplified model system, complex group behaviour emerges.

Our concept of motivational synchronisation relates to the motivational difference between pre-spawners and spawners in the trade-off between spawning and predation. One may speculate why the physiological gonad state of herring entering the spawning ground is not perfectly synchronised in the first place to prevent the motivational conflict between pre-spawners and spawners. Having in mind that all natural systems contain variation and taking into account that the building up of gonads takes about six months (Iles 1984), a variation of a few days in timing should be expected. Field observations indicate that spawning in herring takes between one (Johannessen 1986) and several (Axelsen et al. 2000; Skaret et al. 2003) days, probably reflecting the variation in gonad stage. In addition there are different age groups entering the spawning site at different times (Slotte et al. 2000). Given that there are differences in gonad state in the system, behavioural synchronisation between pre-spawners, ovulating and spawning herring (high values of  $M_0^{Sp}$ ) leading to one integrated school may still seem an optimal solution. However, in this scenario mature herring, still not ready for ovulation have to spend much time in the high-risk predation zone close to the bottom. Our first simulation trial demonstrates this, giving low predation based spawning success in System 3 where mature and early ovulating herring are situated close to the bottom (Table 3). On the other hand, with low degree of synchronisation our simulations predict separation between pre-spawners and ovulating herring. This may also be disadvantageous, as mature herring about to switch into ovulation, would benefit from having contact with the spawning layer. An intermediate scenario where the herring compromise their motivation with the behaviour of the school might be the most favourable in an evolutionary context. In the most comprehensive field study concerning schooling behaviour of spawning herring, extensive vertical structures connecting a pelagic and a demersal component were observed during several days (Axelsen et al. 2000). A collective strategy of “await in the pelagic” was suggested, with pre-and post-spawners residing higher up in the water column where predation pressure is assumed to be less, without losing contact with the spawning component. One large school containing 15-20000 individuals was followed through a five-day period and vertical structures with explicit contact were observed the first two days and the fourth day, while during the third day there was a vertical split into

two components (Axelsen et al. 2000). We find it particularly interesting that our simulations demonstrate that with a moderate behavioural synchronisation between pre-spawners and spawners ( $M_0^{Sp} \sim 0.3$ ) the system behaviour bears clear similarities with the observations in the field: one school splits into two components or layers keeping a dynamic vertical contact. Acoustic recordings from such vertical structures in the field are given in Figure 8. Our results suggest that such structures are able to emerge as a result of collective behaviour without the need for individual fish to be aware of the larger school structure, a possible second school component, the state of neighbouring fish or to execute any “strategy” regarding preferable school behaviour.

Several simulation studies on schooling fish have typically used a few fish (10-100) to simulate the principal mechanisms leading to schooling (Aoki 1982; Huth and Wissel 1992; Huth and Wissel 1994; Inada 2001; Inada and Kawachi 2002; Parrish et al. 2002). The results presented in such studies mainly focus on measures like nearest neighbour distance, cohesion and polarisation, which are possible to compare to laboratory studies where similar numbers of fish are used (Huth and Wissel 1994). Some studies investigate variations in collective behaviour for different model settings (Couzin et al. 2002) and varying population size (2-128 fish) (Viscido et al. 2005). We are interested in the understanding of emergent school structures for large number of individuals in an ecological context. In our simulations, we find entirely new kinds of system behaviour emerging with very large population sizes. This strongly suggests that in large aggregations like in herring during spawning there are collective effects, which can not emerge in a simulation with 100 individuals or in a small laboratory. This is a highly important recognition. The number of individuals is by itself an essential factor determining the behaviour of the system as a whole. The parallel dynamics emerging in our third simulation trial with large population sizes demonstrates this principle. A group of 100 fish with the same trade-off and behavioural rules obviously cannot generate such dynamic spatial structures. There are additional implications of these large-scale structures. An important recognition of pattern formations involving social aggregations is that the nonlinearity inherent in such interactive systems couples various scales together (Flierl et al. 1999). This means that not only does small-scale behaviour shape large-scale patterns, large-scale structures also influence individual behaviour (top-down). The establishment of vertical bridges between layers enables ovulating herring to climb down across the vertical structure and spent herring to climb up without waiting for a separate small school to form. Individual behaviour is in this way influenced by the large-scale structure, and importantly their influenced behaviour represents a positive feedback maintaining the existing structure. Similar positive feedback mechanisms are well-known features of self-organised social systems, for instance the lane formations in ants maintained by attractive pheromones deposition in the track (Deneubourg et al. 1989). Such systems can be thought of as having a collective response adapted to the environmental conditions, executed by interacting individuals.

It is important to emphasize that the influence of the environment is an essential aspect contributing in forming the complex school structures we see for large population sizes. When fish in a school only interact with neighbouring fish, principal characteristics of schooling may very well be revealed through laboratory studies or simulation studies

using a few fish. It is the environment (the predation profile) acting on individuals with different spawning-predation trade-offs, which set the conditions in which new system behaviours can emerge for larger population sizes. With no environmental influences our simulations would produce spherical shaped schools regardless of population size. This role of the environment for pattern formation in self-organised social systems is well recognised in other fields of biology (Camazine et al. 2001). Our last additional simulation trials with extended system depth of 90 m demonstrate dramatic effect on the collective response of the system. Even if the motivational synchronisation is the same as in the third simulation trial, the deeper low-risk predation zone around  $D_{2/3}$  (60 m) allows for more spherical shaped schools, which effectively reduces the parallel dynamics seen in simulation trial three. With the extended system depth the pre-spawning and spawning layers are 30 m apart instead of 10 m, apparently making contact even more difficult given the same population size. To our surprise, the system instead emerged into forming one major cylindrical bridge across the 30 m depth, first consisting of ovulating herring, then amplified by spent herring ‘climbing’ the bridge upwards. Interestingly this “super cylinder” emerges as a response to the combination of population size, motivational synchronisation and environmental constraints without changing individual level behavioural rules.

Population size also affects the spawning success in our simulations. This is clearly seen in the second and third simulation trials where a dilution effect increases the predation related total spawning success for increasing population sizes until  $N=1000$ . Further, the final gonad state, reflecting the ‘connectivity’ in the system, basically shows that for small population sizes fish have more difficulties going through the different stages. Small schools are also more unstable leading to separation in the horizontal plane further disabling contact. Since the switching from ovulation to spawning explicitly is coded to have a higher probability if the nearest neighbour is already spawning, fish in larger schools will have a higher probability of switching from ovulation to spawning. This is because a larger school of ovulating herring after a given time will contain more spawners than a small school. There is a domino effect, and the result is higher throughput seen from the shorter duration during ovulation with increasing population size (last column Table 3).

Most simulation studies assume that all individuals are identical. When individuals are defined with different values of the rule parameters, simulation studies have shown that this produces sorting (Romey 1996; Couzin et al. 2002). This complies with empirical studies showing that fish shoals tend to be assorted by phenotypes including body length, species and body color (Hoare and Krause 2003). Fish within schools also tend to be close to others of similar size (Pitcher et al. 1986; Parrish 1989), or in multi-species groups to conspecifics (Parrish 1989). If variation in phenotypes is correlated with variation in behaviour, self sorting mechanisms have been suggested to explain the observed segregations (Couzin and Krause 2003). These authors also demonstrated this self-organized principle using a simulation model. The important discovery is that variation in behaviour between individuals can produce sorting without explicitly encoding complex recognition and decision-making capabilities (Couzin and Krause 2003). The results of our simulation trials support this conclusion. Our model fish are

neither able to observe or respond to the gonad state of local neighbours (except the nearest neighbour for ovulating herring being within 1 m from the bottom). The repulsion and attraction rules working between individuals are ignorant to the state of neighbouring fish. They only respond to the neighbour's position. Still, schools tend to be sorted by gonad state when they split. In addition, larger schools containing fish in various stages tend to be segregated into different vertical sections or layers. We have not explicitly quantified this vertical segregation within a school or layer, but it can be seen from the position plots (Fig. 7). Whenever sorting is emergent, it is essential that it is the difference in *behaviour* that produces sorting, whether this is imposed by variation in phenotypes or by motivation as in our case.

Our school model is defined relatively simple without explicitly including velocity matching as several basic school models do (Huth and Wissel 1992; Couzin et al. 2002). This could be criticized. On the other hand, some studies do insist on leaving out explicit velocity matching in the formulation of a school model (Parrish et al. 2002; Viscido et al. 2005). With a minimal school model we were able to incorporate spawning and predation and explore system behaviour within reasonable computational effort. We have used a high temporal resolution of 0.1 seconds in our model, which is essential in order to include individual interactions within a school properly. This sets computational limits to the total time period we can simulate for large population sizes. The physiological process of gonad state development has therefore been speeded up accordingly, enabling it to change from mature to spent within one simulated hour. The process is still slow compared to the temporal scale determining changes in the spatial distributions and vertical dynamics, e.g. a 30 cm fish moving at 1 BLs<sup>1</sup> would be able to move 30 meter vertically in a water column a hundred times during one hour. Since our focus is how school patterns emerge through variations in motivation and population size, we find the choice of simulation time justified. Our modelled herring and spawning area also introduce other simplifications of the real world and we deliberately ignore some factors that can influence schooling dynamics during spawning. Diel patterns in schooling have been observed in field studies from the spawning area (Skaret and Slotte in prep.; Brawn 1960; Skaret et al. 2003) probably as a result of the visibility influencing both schooling flexibility and predation pressure from visual predators. In our model we assume a permanent daytime situation. The predation profile follows Beer's law down to 2/3 of the total depth, which is no more than a curve describing the attenuation of light and thus reduction of visibility with depth (Aksnes and Giske 1993; Aksnes and Utne 1997). There is no distinction between sexes in our model even though there well may be differences in the spawning behaviour between males and females. In an ancient publication by Ewart (1884) sexual dimorphism in Atlantic herring is described with only the females touching the spawning substrate, but identical behaviour for both gender was observed in Pacific herring (Stacey and Hourston 1982). We also acknowledge other factors that may influence the spawning behaviour and schooling dynamics such as fish length, swimming abilities and visual range as well as environmental influences of temperature (Flierl et al. 1999), oxygen (Domenici et al. 2000) and current. Sensitivity analyses for these and other factors would have been appropriate, but outside the scope and capacity of this work.

As a conclusive remark, our main results are indeed relevant for NSS herring, but also provide new insight into possible mechanisms behind collective behaviour of fish schools in a more general sense. Cases of conflicting motivations within groups of social animals are not extraordinary and we show that they may not only initiate and maintain collective formations, but also that the formations may exhibit properties rendering them adaptive behaviours in nature. This is important for a deeper understanding of the morphology of schools (Gerlotto and Paramo 2003). We further argue that the ability to simulate large population sizes when modelling fish schools is imperative when investigating the mechanisms behind the formation of large collective formations and school morphology as observed in nature. With large populations we show that even minor changes to our relatively simple model system are enough to reveal the plasticity in school morphology and how it is dependent on individual motivation and surrounding environment. School morphology changed from a pure hourglass formation to a system with parallel dynamics merely through indirectly decreasing the range of preferred distribution depth for single fish. In an ecological context similar mechanisms may be relevant for shoals of fish in any motivational conflicting situation where the preferred vertical position is changing due to varying environmental factors.

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Table 1. Summary of all fixed model parameters. BL s<sup>-1</sup> is body lengths per second.

Parameter	Symbol	Value	Comment
<i>Simulation</i>			
Time step	dt	0.1 s	
Total simulated time	T	1 hour	Corresponds to 36000 time steps
<i>System</i>			
Cylinder radius		30 m	Cylinder volume=84780 m <sup>3</sup>
Total depth	D	30 m	The height of the cylinder
Grid cell size		0.8 m	
Light dampening factor	$\kappa$	-0.1	Used in Beer's law
<i>Individual parameters</i>			
Fish length	L	30 cm	
Max acceleration	$a^{\max}$	5 BL s <sup>-2</sup>	Corresponds to 1.5 ms <sup>-2</sup>
Maximum swimming speed	$v^{\max}$	2 BL s <sup>-1</sup>	Corresponds to 0.6 ms <sup>-1</sup>
Minimum swimming speed	$v^{\min}$	0.1 BL s <sup>-1</sup>	
Field of view	$\phi$	300°	
Visual range	$\lambda$	1.6 m	Equal to twice the grid cell size
State shift probability1	$\rho^0$	0.0006 s <sup>-1</sup>	Changing from mature to ovulation
State shift probability2	$\rho^1$	0.003 s <sup>-1</sup>	Changing from ovulation to spawning
Gonad state increment	ds	0.000833 s <sup>-1</sup>	Corresponds to 1.0 in 20 minutes.
Spawning motivation, spawn	$M_2^{\text{Sp}}$	0.9	
Predation motivation, spent	$M_3^{\text{Pr}}$	0.1	
Spawning motivation, spent	$M_3^{\text{Sp}}$	0.0	
Repulsion range	$R_{\text{rep}}$	90 cm	
Repulsion rule parameter	$\alpha^0$	100	
Attraction rule parameter	$\alpha^1$	0.1	
Density threshold attraction	$\delta^{\text{thr}}$	2.1 m <sup>-3</sup>	Based on local number of fish within 1 m
Noise parameter	$\eta$	0.05	

Table 2. *Overview of simulation trials.* The simulations are organised into three groups or trials. The first 100 simulations explore the behaviour of the system as a function of initial spawning motivation  $M_0^{Sp}$  with the standard population size. The other two groups of simulations explore the characteristics of two different system behaviours as a function of population size.

<b>Simulation trial group</b>	<b>Parameter values explored</b>	<b><math>M_0^{Sp}</math></b>	<b>Number of simulations</b>
1	500	0.05–0.50	100
2	50,100,200,1000,2000, 4000,8000	0.3	65
3	50,100,200,1000,2000, 4000,8000,16000	0.05	66

Table 3. *Results from all the simulation runs.* Each mean value represents an average of 10 simulation runs.  $M_0^{Sp}$  denotes spawning motivation for mature herring or initial spawning motivation during ovulation. Total number of schools emerging counts the schools from the whole simulation run, 1. Half only the first 30 minutes, and <10%, number of schools containing fewer than 10 % of total fish population if  $N \leq 500$ , and fewer than 50 individuals if  $N > 500$ . Schools pres denotes the mean number of schools simultaneously present counting each minute. Mean age school is the unweighted age average (in minutes) for a simulation run. The ratio between vertical and horizontal extension ( $r$ ) for the 3 shape categories is  $r \leq 0.75$  (Flat),  $0.75 \leq r \leq 1.25$  (Ball) and  $r > 1.25$  (Cylindrical).  $S_{rel}$  is a measure of the average relative school size in a simulation run with a value of 1 if one school comprises the whole population. Splitjoin is the ratio between the sum of the events ‘Join’ and ‘Split’ and the total number of events. The total spawning success is calculated as the mean duration in post-spawning stage divided by mean predation risk during the whole simulation run, FinSt is the gonad state at the end of the simulation run and DurOv is the duration of the ovulation phase. The Sorting is a measure of mixing of individual gonad maturation stages within a school with 0 being 100 % identical maturation stages or absolute sorting. Note that  $\sim$  SD is the *mean* standard deviation from the 10 runs whereas the standard deviation indicated by  $\pm$  is the standard deviation *between* the 10 runs. There is a total of 243 simulations in this table, each consisting of 36000 time steps.

\*The average is based on 5 simulation runs.

\*\*The average is based on 2 simulation runs.

\*\*\*Only 1 simulation run undertaken.

<sup>c</sup> Copied from the first simulation trial.

		No. of schools emerging			Schools pres		Age school			Shape school			
$M_0^{Sp}$	N	Total	1.Half	<10%	Mean	~ SD	Mean	~ SD	Max	Flat	Ball	Cyl	
0.05	500	130.0 ± 52.4	60.1 ± 20.0	12.4 ± 7.9	2.28	0.62	3.9	7.2	20.34 ± 2.81	0.90 ± 0.04	0.04 ± 0.01	0.07 ± 0.03	
0.1	500	117.1 ± 12.0	72.0 ± 15.1	10.1 ± 4.0	2.16	0.55	4.2	7.2	20.58 ± 3.69	0.91 ± 0.04	0.03 ± 0.01	0.06 ± 0.03	
0.15	500	124.2 ± 50.6	66.0 ± 50.1	6.3 ± 3.3	2.15	0.53	3.7	5.8	17.13 ± 6.63	0.93 ± 0.04	0.02 ± 0.01	0.05 ± 0.03	
0.2	500	140.9 ± 15.5	74.2 ± 10.6	3.4 ± 2.5	2.01	0.47	2.1	3.0	11.41 ± 6.00	0.91 ± 0.04	0.03 ± 0.02	0.05 ± 0.03	
0.25	500	251.9 ± 20.4	134.3 ± 25.9	2.0 ± 2.4	1.84	0.45	1.0	1.4	6.35 ± 1.70	0.78 ± 0.03	0.09 ± 0.02	0.13 ± 0.03	
0.3	500	657.6 ± 82.5	324.9 ± 47.3	2.5 ± 3.9	1.62	0.62	0.4	1.0	6.98 ± 1.27	0.63 ± 0.04	0.07 ± 0.03	0.30 ± 0.03	
0.35	500	158 ± 33.4	3.3 ± 1.8	0.1 ± 0.3	1.49	0.54	1.9	5.0	28.43 ± 1.15	0.66 ± 0.02	0.06 ± 0.02	0.28 ± 0.02	
0.4	500	33.9 ± 11.1	4.6 ± 4.1	0.8 ± 1.1	1.55	0.53	5.9	8.9	28.57 ± 3.88	0.93 ± 0.03	0.02 ± 0.02	0.05 ± 0.01	
0.45	500	21.6 ± 3.4	3.1 ± 1.9	0.7 ± 0.5	1.54	0.52	11.4	13.4	28.13 ± 1.40	0.97 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	
0.5	500	20.7 ± 5.7	2.7 ± 1.3	1.3 ± 0.7	1.58	0.57	13.4	20.0	37.84 ± 6.86	0.98 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	
0.3	50	31.7 ± 16.1	16.8 ± 10.2	0.0 ± 0.0	2.41	0.77	12.0	13.4	30.69 ± 6.36	0.41 ± 0.05	0.11 ± 0.04	0.49 ± 0.07	
0.3	100	132.8 ± 32.2	81 ± 21.8	0.7 ± 0.8	3.00	1.22	4.3	6.0	15.04 ± 3.93	0.56 ± 0.04	0.11 ± 0.02	0.33 ± 0.05	
0.3	200	367.2 ± 72.9	232.7 ± 38.6	7.0 ± 5.8	2.89	1.40	1.9	3.2	9.63 ± 1.72	0.68 ± 0.06	0.08 ± 0.02	0.25 ± 0.05	
0.3	1000	568.7 ± 50.3	230.6 ± 37.0	0.0 ± 0.0	1.34	0.47	0.5	1.6	11.76 ± 1.53	0.72 ± 0.03	0.06 ± 0.03	0.22 ± 0.04	
0.3	2000	274.9 ± 29.4	83.2 ± 28.9	0.0 ± 0.0	1.14	0.34	1.2	2.8	15.22 ± 2.57	0.80 ± 0.04	0.19 ± 0.04	0.01 ± 0.01	
0.3	4000	56.2 ± 25.0	10.8 ± 8.0	0.5 ± 1.3	1.05	0.15	6.3	8.1	22.85 ± 6.28	1.00 ± 0.02	0.00 ± 0.01	0.00 ± 0.01	
0.3	8000*	77.6 ± 60.7	42.0 ± 35.4	3.4 ± 2.2	1.32	0.45	10.0	19.4	49.58 ± 10.03	0.95 ± 0.07	0.02	0.02	0.03 ± 0.05
0.05	50	22.4 ± 17.0	13.1 ± 12.3	0.0 ± 0.0	2.30	0.77	15.8	13.1	29.32 ± 9.44	0.49 ± 0.06	0.10 ± 0.02	0.41 ± 0.07	
0.05	100	57.2 ± 29.2	24.2 ± 13.3	2.1 ± 1.4	3.31	1.27	9.3	9.4	18.25 ± 4.23	0.64 ± 0.05	0.10 ± 0.03	0.26 ± 0.04	
0.05	200	127.8 ± 66.5	44.9 ± 20.1	11.7 ± 5.4	3.64	1.63	5.1	7.4	16.15 ± 3.83	0.74 ± 0.05	0.08 ± 0.02	0.18 ± 0.05	
0.05	500 <sup>C</sup>	130.0 ± 52.4	60.1 ± 20.0	12.4 ± 7.9	2.28	0.62	3.9	7.2	20.34 ± 2.81	0.90 ± 0.04	0.04 ± 0.01	0.07 ± 0.03	
0.05	1000	218.8 ± 33.9	116.4 ± 26.2	10.3 ± 5.2	2.07	0.73	1.8	3.3	13.13 ± 4.44	0.93 ± 0.02	0.04 ± 0.01	0.04 ± 0.02	
0.05	2000	491.1 ± 132.7	324.6 ± 112.9	21.8 ± 6.9	3.10	1.44	1.4	4.1	15.06 ± 8.39	0.84 ± 0.07	0.05 ± 0.02	0.12 ± 0.06	
0.05	4000	1099.8 ± 254.5	745.2 ± 138.0	60.9 ± 9.4	5.35	2.97	1.3	3.8	18.57 ± 5.69	0.81 ± 0.04	0.05 ± 0.01	0.14 ± 0.03	
0.05	8000*	2280.8 ± 310.3	1549.8 ± 230.8	140.8 ± 23.4	10.61	6.02	1.2	3.6	23.15 ± 7.01	0.77 ± 0.06	0.06 ± 0.01	0.17 ± 0.06	
0.05	16000**	4720.0	3331.0	328.0	21.93	10.92	1.2	3.4	11.54	0.70	0.07	0.22	
0.05	4000**	711.0 ± 39.6	432.0 ± 47.7	43.4 ± 5.3	4.09	3.17	1.1	2.5	10.86 ± 2.64	0.44 ± 0.03	0.07 ± 0.03	0.48 ± 0.04	
0.05	8000***	1642.0 ± 39.6	1253.0 ± 144.2	126.5 ± 4.9	7.72	5.49	0.8	1.8	6.71 ± 2.78	0.40 ± 0.03	0.10 ± 0.00	0.51 ± 0.02	

Table 3 continued

$M_0^{Sp}$	N	$S_{rel}$	Frequency of events		Sorting		Spawning success				
		Mean	Total	SplitJoin	Mean	~ SD	Total	FinSt	~ SD	DurOv	~ SD
0.05	500	0.64 ± 0.17	255 ± 66	0.49 ± 0.07	0.42	0.14	130 ± 7	3.61	1.26	13.77	5.23
0.1	500	0.64 ± 0.15	243 ± 35	0.48 ± 0.06	0.42	0.17	127 ± 3	3.62	1.26	13.58	5.08
0.15	500	0.63 ± 0.17	213 ± 55	0.57 ± 0.08	0.42	0.18	121 ± 7	3.62	1.27	13.32	5.13
0.2	500	0.66 ± 0.16	196 ± 22	0.72 ± 0.08	0.43	0.20	113 ± 3	3.63	1.28	13.15	5.10
0.25	500	0.69 ± 0.18	299 ± 36	0.84 ± 0.05	0.45	0.22	100 ± 4	3.62	1.28	12.94	5.08
0.3	500	0.78 ± 0.21	706 ± 90	0.93 ± 0.04	0.53	0.25	93 ± 3	3.65	1.28	12.71	5.00
0.35	500	0.79 ± 0.22	167 ± 35	0.94 ± 0.04	0.64	0.25	85 ± 3	3.69	1.26	12.63	4.89
0.4	500	0.77 ± 0.23	44 ± 14	0.75 ± 0.10	0.63	0.25	75 ± 3	3.64	1.29	12.30	5.02
0.45	500	0.77 ± 0.22	38 ± 6	0.55 ± 0.06	0.62	0.25	75 ± 2	3.67	1.27	12.06	5.15
0.5	500	0.77 ± 0.23	42 ± 15	0.48 ± 0.06	0.63	0.26	76 ± 3	3.70	1.26	12.08	5.15
0.3	50	0.52 ± 0.24	31 ± 16	0.98 ± 0.03	0.39	0.09	28 ± 9	3.29	1.21	14.86	6.20
0.3	100	0.48 ± 0.24	151 ± 37	0.87 ± 0.09	0.39	0.11	53 ± 9	3.52	1.28	13.55	5.61
0.3	200	0.53 ± 0.24	412 ± 72	0.88 ± 0.06	0.41	0.14	77 ± 8	3.63	1.27	13.23	5.13
0.3	1000	0.87 ± 0.18	634 ± 32	0.90 ± 0.05	0.58	0.25	98 ± 3	3.68	1.26	12.94	4.91
0.3	2000	0.95 ± 0.12	354 ± 31	0.77 ± 0.05	0.63	0.26	102 ± 1	3.69	1.26	12.93	4.89
0.3	4000	0.99 ± 0.04	93 ± 51	0.61 ± 0.09	0.64	0.26	102 ± 1	3.69	1.26	12.94	4.89
0.3	8000*	0.99 ± 0.02	205 ± 164	0.40 ± 0.09	0.64	0.27	101 ± 0	3.67	1.27	12.84	4.97
0.05	50	0.51 ± 0.27	23 ± 17	0.79 ± 0.22	0.38	0.08	32 ± 17	3.03	1.24	18.88	11.19
0.05	100	0.47 ± 0.25	64 ± 31	0.84 ± 0.08	0.37	0.07	57 ± 12	3.38	1.29	15.25	6.75
0.05	200	0.49 ± 0.25	153 ± 65	0.81 ± 0.09	0.39	0.09	86 ± 10	3.56	1.21	14.42	5.31
0.05	500 <sup>C</sup>	0.64 ± 0.17	255 ± 66	0.49 ± 0.07	0.42	0.14	130 ± 7	3.61	1.26	13.77	5.23
0.05	1000	0.69 ± 0.18	392 ± 57	0.56 ± 0.05	0.45	0.19	137 ± 2	3.61	1.25	13.80	5.08
0.05	2000	0.72 ± 0.19	771 ± 186	0.63 ± 0.06	0.46	0.20	139 ± 5	3.62	1.26	13.83	5.15
0.05	4000	0.69 ± 0.20	1825 ± 273	0.60 ± 0.06	0.46	0.20	137 ± 1	3.61	1.24	13.82	5.12
0.05	8000*	0.66 ± 0.20	3842 ± 320	0.59 ± 0.04	0.45	0.18	137 ± 1	3.62	1.25	13.85	5.15
0.05	16000**	0.65	7610	0.62	0.44	0.17	138	3.62	1.26	13.83	5.13
0.05	4000**	0.72 ± 0.20	1103 ± 66	0.62 ± 0.02	0.41	0.21	174 ± 3	3.61	1.25	13.84	5.15
0.05	8000***	0.75 ± 0.00	2460 ± 42	0.67 ± 0.00	0.37	0.14	152 ± 0	3.56	1.20	14.54	5.17

<i>State shift</i>		stochastic ⇒	stochastic ⇒	continuous ⇒
<i>Gonad stage</i>	<i>Mature</i>		<i>Ovulating</i>	<i>Spawning</i> <i>Spent</i>
<i>Gonad State (s)</i>	0.9		1.0 → 1.99	2.0 → 3.0    3.0 →
<i>Spawn Motivation</i>	$M_0^{Sp}$		$M_0^{Sp} \rightarrow 0.9$	0.9    0.0

Figure 1. Overview of gonad state development and motivation toward spawning in relation to gonad stages. How the shifts between the one behavioural stage to the next are implemented, is indicated by the thick arrows at the top. The small arrows indicate that there is a linear increase of the value in the given behavioural stage. Simulations explore different values of  $M_0^{Sp}$ .

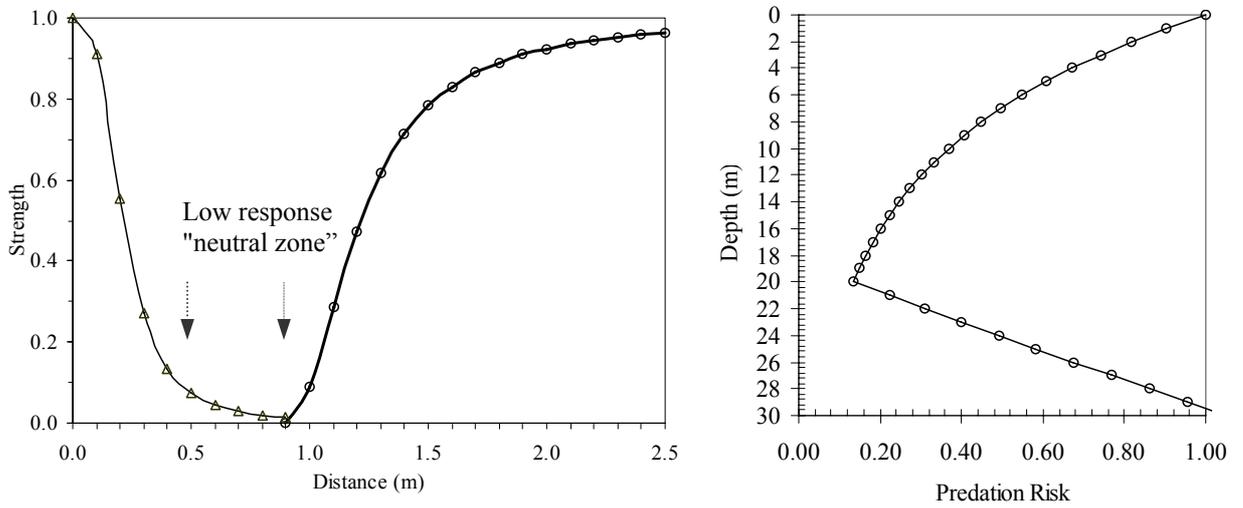


Figure 2. Model definitions for Left: The shape of the repulsion and attraction functions applied with repulsion as triangular marks and attraction as circular marks. Right: The predation risk profile applied, incorporating Beer's law of light attenuation by depth and adding a linear increase from 2/3 of total depth towards the bottom.

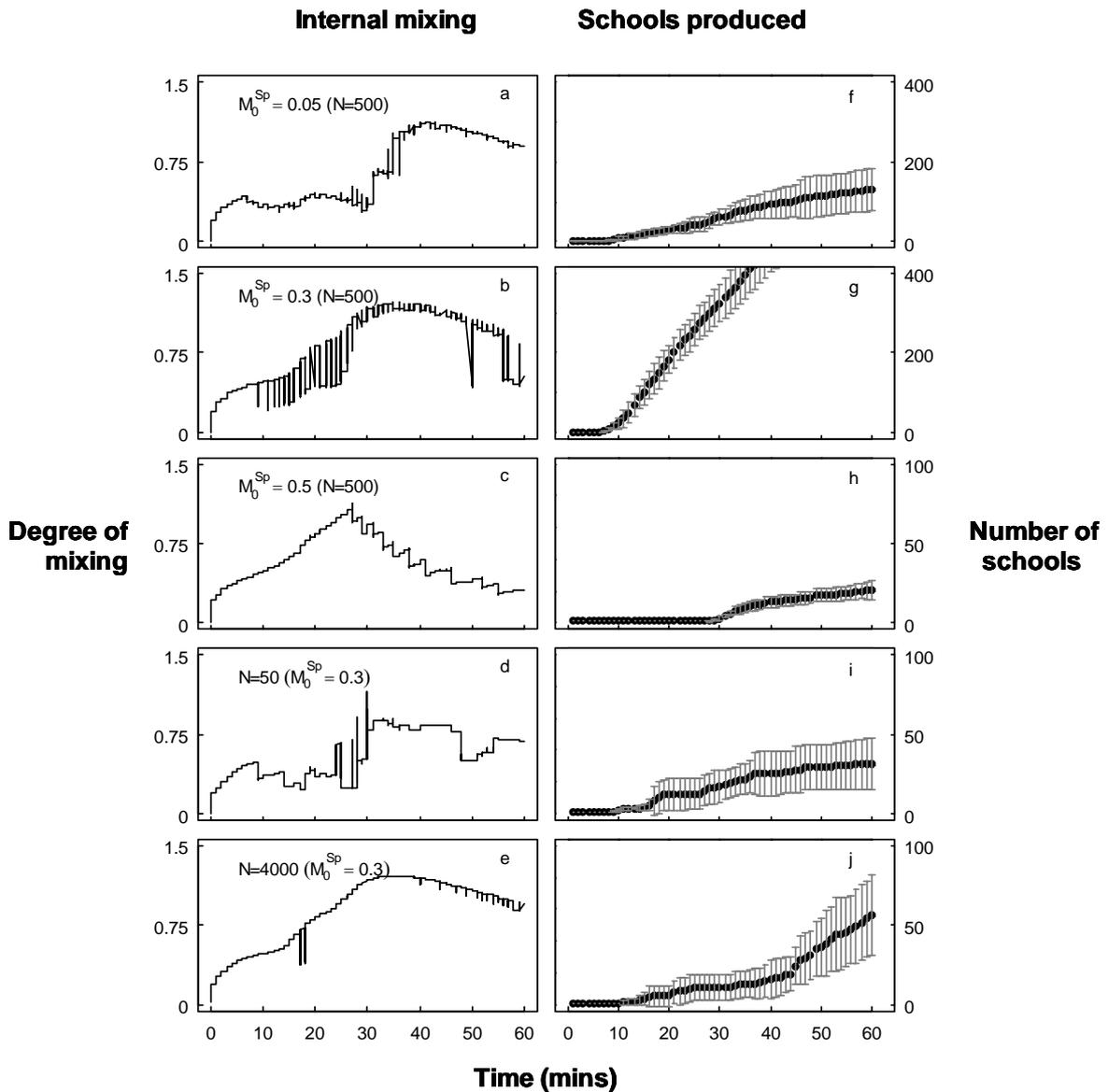


Figure 3. Mixing and school production ( $\pm$ SD) with 5 different simulation settings. The mixing refers to individual gonad maturation stage calculated as the standard deviation in each school and averaged over all the schools present weighted by school size. A value of 0 represents a school which is perfectly sorted by gonad stage. Each curve represents *one* typical simulation run with the given setting. The degree of mixing is measured each simulated second. School production is counted using a school detection algorithm (see text for details) scanning the system each simulated second. The mean school production over time is averaged over 10 runs. Note the differences in scaling for the number of schools produced.

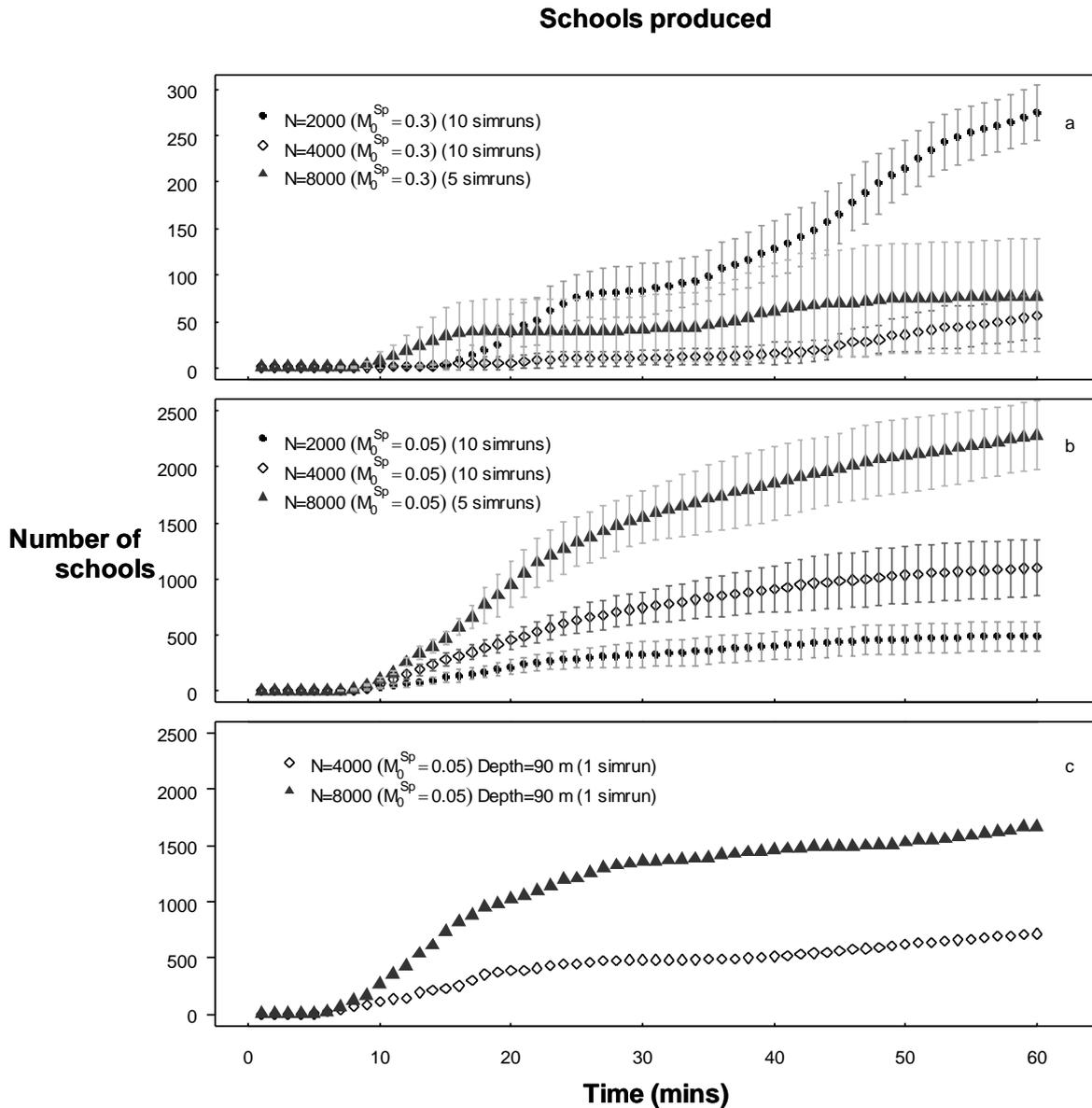


Figure 4. School production for simulation runs with high population numbers ( $N \geq 2000$ ). 4a and 4b show the school production from simulation settings with low and medium initial motivation towards spawning respectively ( $M_0^{Sp} = 0.05$  and  $M_0^{Sp} = 0.3$ ), whereas 4c shows results from runs with low initial spawning motivation using a cylinder height of 90 m as compared to the standard height of 30 m. Note the different scaling in 4a.

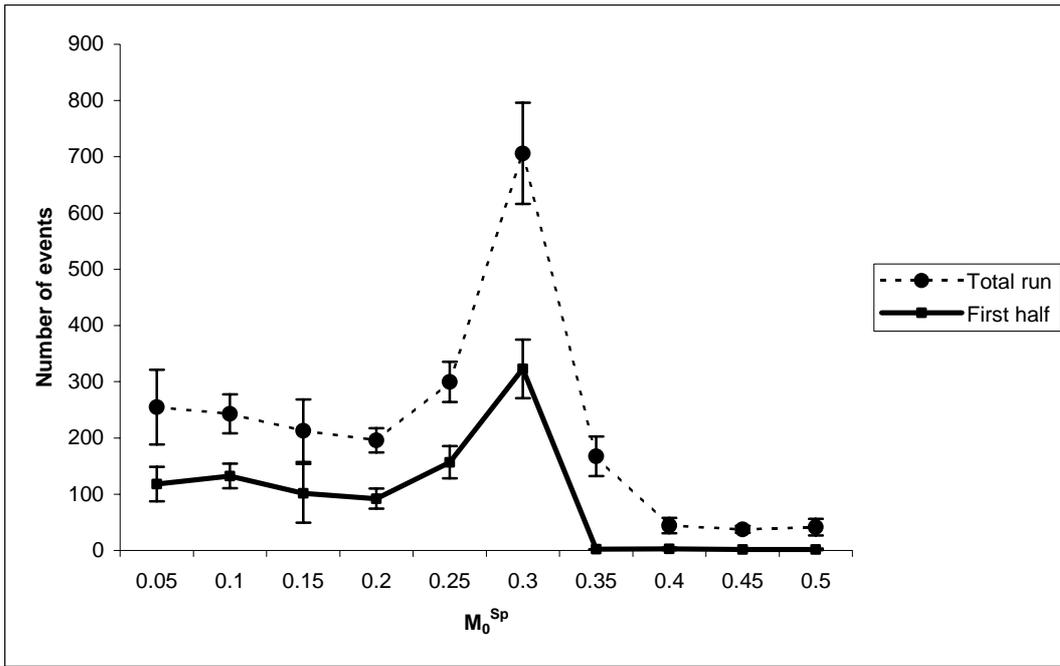


Figure 5. Number of events  $\pm$ SD during total and first half of standard simulation runs (N=500), as a function of initial motivation for spawning. Each value represents the mean of 10 independent simulations.

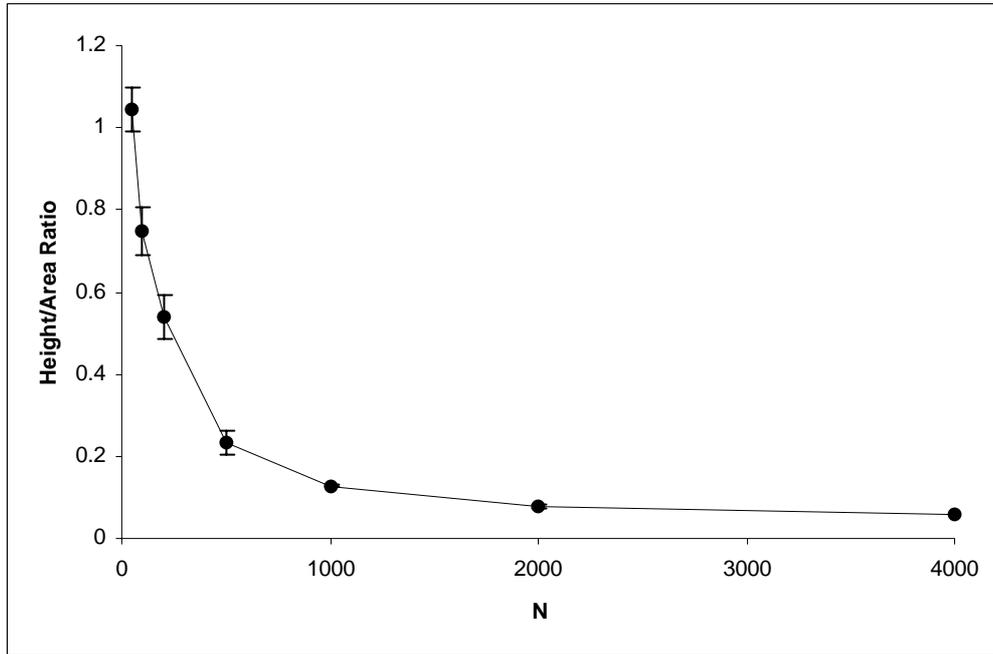


Figure 6. Mean ratio  $\pm$ SD between school height (m) and cross-section school area ( $m^2$ ) as a function of population size (N) with medium initial spawning motivation ( $M_0^{Sp}=0.3$ ). School area is given as  $\frac{1}{4} \times W \times L \times \pi$ , where W and L are the horizontal width and length of the school measured from above. The mean represents an average for a whole simulation run with samples taken every minute.

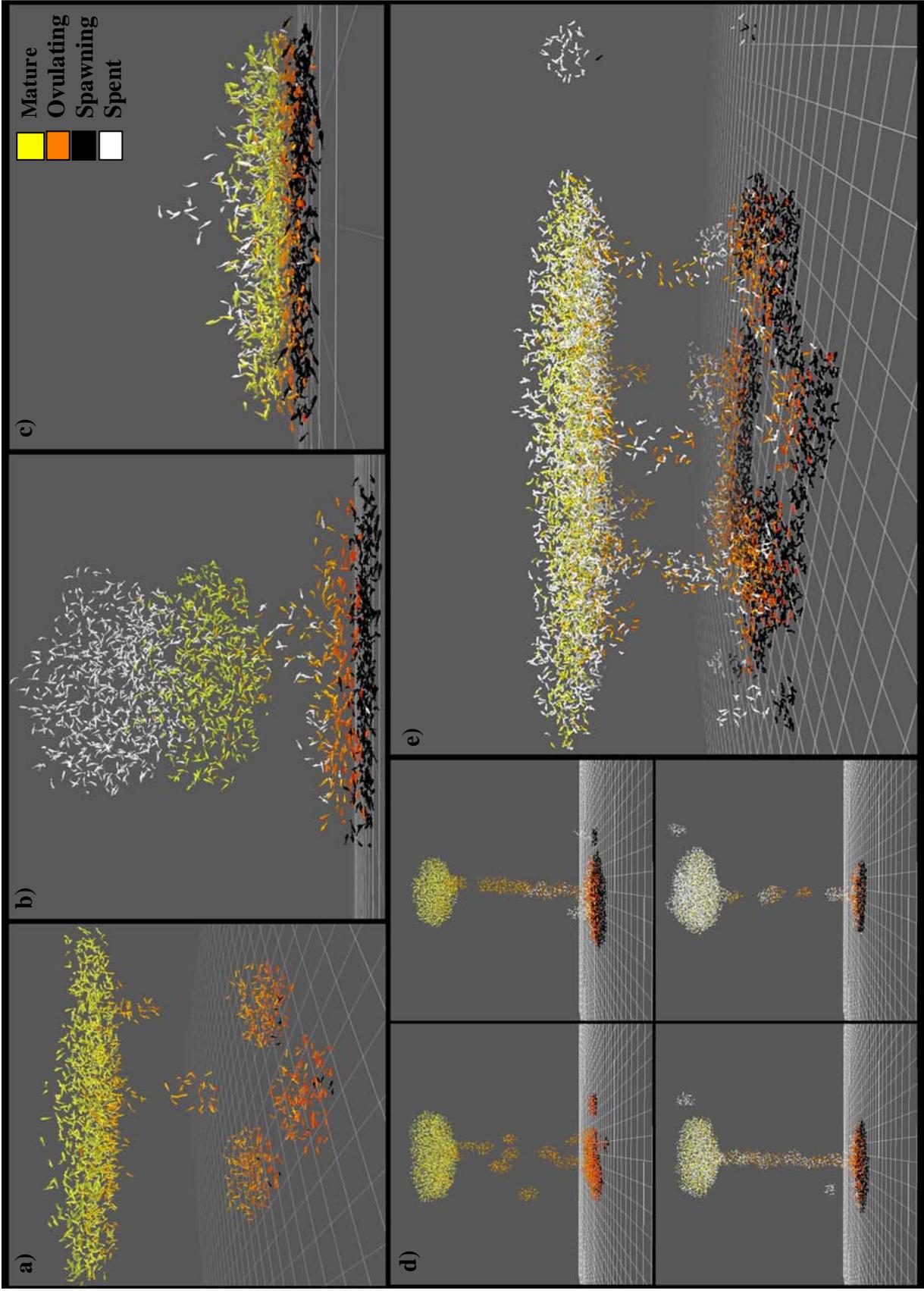


Figure 7. Illustration of different system behaviours. a) Split off system (System 1) with  $N=2000$  and  $M_0^{Sp}=0.05$  with 5 schools present. b) Dynamic connected system (System 2) with  $N=2000$  and  $M_0^{Sp}=0.3$ . c) Integrated system (System 3) with  $N=2000$  and  $M_0^{Sp}=0.5$ . In b) four different layers are indicated emphasizing the rich vertical structures emerging in System 2. In the contact zone ovulating herring are moving down, connecting with spent herring moving up. d) Emergent system behaviour for extended system depth,  $D=90$  m, for  $N=4000$  and  $M_0^{Sp}=0.05$ . The four frames (top left, top right, lower left and lower right) represent different times in the simulation at 16, 26, 36 and 48 minutes respectively. e) Parallel dynamics emerging for large population sizes and low behavioural synchronization,  $M_0^{Sp}=0.05$  and  $N=8000$ . This illustrates the horizontal extension of the pre-spawning layer occurring for larger population sizes. 10 different schools are present, but most are small while vertical bridges connect the pre-spawning layer with the spawning layer into one connected school. The vertical connections are established by ovulating and spent herring moving in opposite directions across the bridges. Colour indications: Mature herring (yellow), ovulating herring (orange to red), spawning herring (black) and spent herring (white).

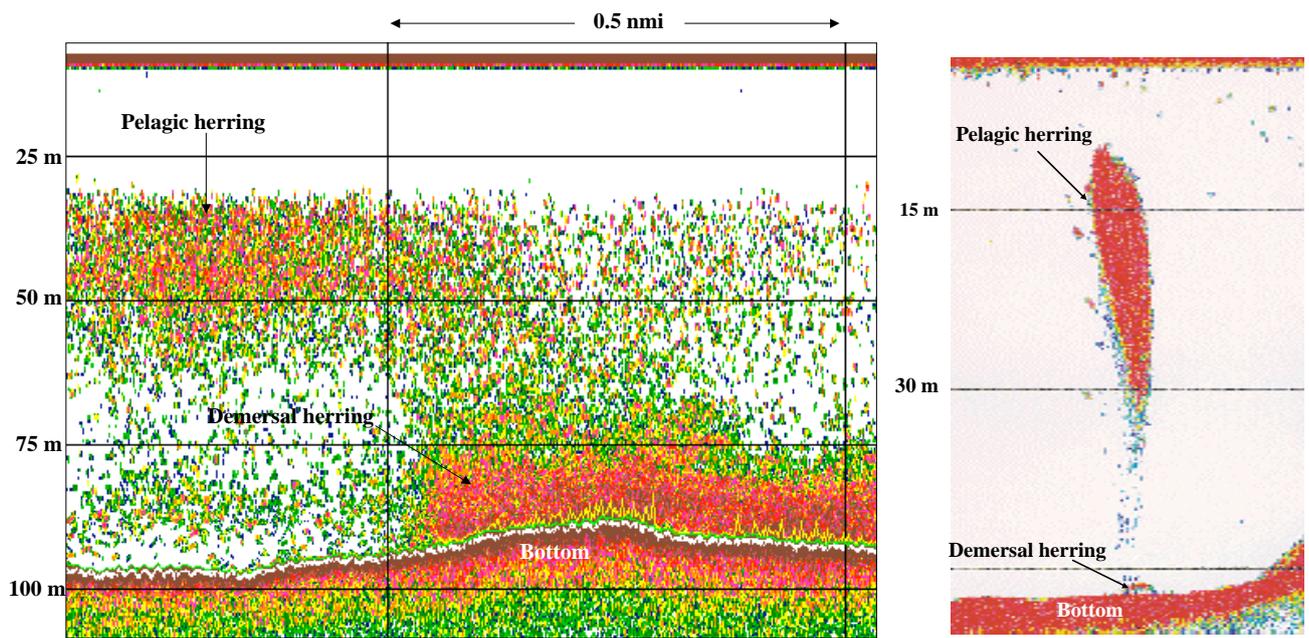


Figure 8. Left: Layers of herring and vertical split from main spawning area off Møre, Western Norway (Skaret and Slotte, in prep.). Right: Cylinder shaped and vertically split single school from spawning area (Axelsen et al., 2000).