Self-Organized Shape and Frontal Density of Fish Schools

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Abstract

Models of swarming (based on avoidance, alignment and attraction) produce patterns of behaviour also seen in schools of fish. However, the significance of such similarities has been questioned, because some model assumptions are unrealistic [e.g. speed in most models is constant with random error, the perception is global and the size of the schools that have been studied is small (up to 128 individuals)]. This criticism also applies to our former model, in which we demonstrated the emergence of two patterns of spatial organization, i.e. oblong school form and high frontal density, which are supposed to function as protection against predators. In our new model we respond to this criticism by making the following improvements: individuals have a preferred 'cruise speed' from which they can deviate in order to avoid others or to catch up with them. Their range of perception is inversely related to density, with which we take into account that high density limits the perception of others that are further away. Swarm sizes range from 10 to 2000 individuals. The model is three-dimensional. Further, we show that the two spatial patterns (oblong shape and high frontal density) emerge by self-organization as a side-effect of coordination at two speeds (of two or four body lengths per second) for schools of sizes above 20. Our analysis of the model leads to the development of a new set of hypotheses. If empirical data confirm these hypotheses, then in a school of real fish these patterns may arise as a side-effect of their coordination in the same way as in the model.

Introduction

Individual-based models of repulsion/attraction and alignment among agents have often been used to investigate schooling among fish (e.g. Warburton & Lazarus 1991; Huth & Wissel 1992; Romey 1996; Couzin et al. 2002; Kunz & Hemelrijk 2003). A number of patterns of swarming in these models closely resemble those found in real swarms (Huth & Wissel 1994; Hiramatsu et al. 2000; Couzin et al. 2002; Kunz & Hemelrijk 2003; Hoare et al. 2004; Hemelrijk & Kunz 2005). A criticism of these models is, however, that they are based on unrealistic assumptions regarding control of speed (fixed with random error), the range of perception (too large to

be considered local) and the school sizes (which are small). Thus, even when empirical data of real fish are similar to patterns in the model, their significance is unclear (Parrish & Viscido 2005). This criticism may also apply to our previous models, in which we studied school shape and structure (Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005).

Therefore the aim of this paper is, first, to develop a new model without these shortcomings and, second, to develop testable hypotheses for the mechanisms underlying the school shape and the structure in real schools of fish. In our earlier model, we worked on the origin of the oblong shape and high frontal density of fish schools (Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005). These patterns are

thought to function as protection against predation, because predators are supposed to attack mainly the front of schools. The oblong shape is thought to reduce the size of the most dangerous part which is the frontal area (Bumann et al. 1997) and to diminish the chance of detection by predators (Partridge et al. 1980). Furthermore, high frontal density is assumed to arise because individuals hide behind each other to shield themselves from predators (Bumann et al. 1997; Krause et al. 1998). Because it seems unlikely that individual fish have an idea of group shape and frontal density, we developed in an earlier model an explanation for the formation of these complex patterns by self-organization (Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005). We showed that an oblong school shape and a high frontal density arises by self-organization as a side-effect of the behavioural rules of coordination. Our earlier model suffered, however, from the shortcomings mentioned by Parrish & Viscido (2005).

Therefore, the first aim of this paper is to study whether in a more realistic model these patterns of the organization of schools still emerge. As is usual in these models, individuals follow three main rules: they avoid others that are close by, they align to others up to an intermediate distance and they are attracted to individuals further away (Huth & Wissel 1994; Couzin et al. 2002, 2005; Croft et al. 2003; Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005; for a recent review see Reynolds 1987; Reuter & Breckling 1994; Parrish & Viscido 2005). We develop an improved model as follows: first, instead of fixing the speed at a certain value with random error, we give individuals control over their speed in a more natural way. They move at a cruise speed (Videler 1993) towards which individuals return after speeding up to catch up with others or slowing down to avoid collision; we investigate two cruise speeds that are typical of real fish, slow (two body lengths per second or 2 BL/s) and fast (4 BL/s) (Videler 1993). Second, perception usually includes all group mem-

bers, but in our new model we make perception more local, namely individuals are unlikely to perceive those that are hidden behind others. We model this by making their range of perception flexible. It is reduced when the local density of individuals is high, and it increases, when the density is low. Third, in our new model we create schools of a larger range of sizes (10-2000) than has ever been studied before in this kind of model. Finally, the model is made three-dimensional (3D).

Our second goal is to understand the origin of an elongated school form and high frontal density in the model and to translate this understanding into testable hypotheses. For this, we extend the analysis of the results far beyond that of our earlier model. For instance, we study the density of the core and the tail of the swarm and the location of the core of the swarm and investigate these measurements in relation to group size and speed. In this way, we develop detailed model-based hypotheses that may be used to verify whether in real fish an oblong school form and high frontal density may appear as a side-effect of coordination in a similar way as in the model.

Methods

The model consists of artificial fish that move in an unbounded 3D world that is continuous and homogeneous, i.e. without structure (Figs 1a, 2a). Each individual is characterized by its position, r, its scalar speed, v, and its orientation in space. Its orientation is indicated by its forward direction, e_x, its sideward direction, e_y and its upward direction, e_z, which it changes by rotations around these three principal axes, e_x, e_y and e_z (roll, pitch and head) (Fig. 1a) as in the model by Reynolds (1987). Movement of individuals is calculated from their speed and orientation. Time proceeds in discrete time steps. At each step Δt, all individuals are synchronously updated.
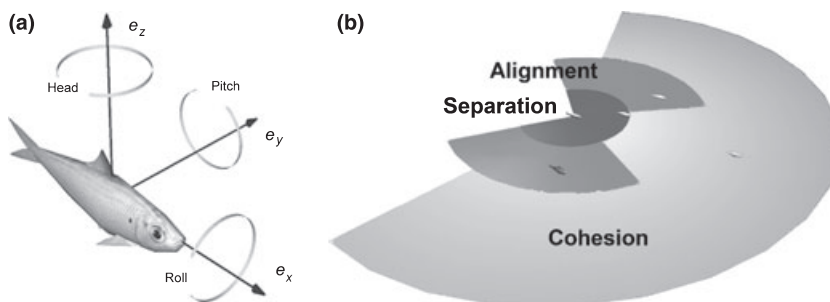

Fig. 1: (a) Local coordinate system. (b) Behavioural zones of separation, alignment and cohesion.

The behaviour of each individual is based on the position and direction of its neighbours in three overlapping behavioural zones (Fig. 1b). An individual is attracted to those in its cohesion zone; it also aligns its movement to others that are at medium distances away from it in its alignment zone and it avoids individuals that are close by in its zone of separation. For these three behavioural acts, cohesion, alignment and separation, the individual has a blind zone behind. This is larger for cohesion than for separation and alignment, because cohesion is supposed to be mediated visually only, whereas for separation and alignment the lateral line system may also be used. Because alignment is mainly performed through the lateral line system, it has also a blind area at the front (Partridge & Pitcher 1980).

The radius of perception (which equals the cohesion radius) decreases with local density in order to reflect the fact that individuals are influenced only by those they *can* perceive: when the local density is higher, their perception extends over a shorter distance than when it is lower. At a very high density this perception radius may even shrink below that of the default range of alignment (and thus shorten the range of alignment too) but it cannot become smaller than the separation range R_{min}. The new perception radius, $R(t+\Delta t)$, is calculated as linear interpolation of the current radius $R(t)$ and a density-dependent term:

$$R'_i = R_{max} - n_w \cdot n(t)$$

$$R_i(t+\Delta t) = max\{R_{min}, (1-s) \cdot R(t) + s.R'\}; \quad s = n_i \cdot \Delta t \quad (1)$$

where n(t) is the number of perceived neighbours at time t. The parameter n_w indicates the influence of a single neighbour and n_i controls the smoothness of the radius adaptation. Note that this adaptable view is supported by empirical evidence for a relatively fixed number of interactants in starling flocks (Ballerini et al. 2007).

The behaviour of an individual is calculated as a Newtonian net steering force as follows. It consists of the sum of the three 'social' steering forces (separation, alignment and cohesion) plus additional terms for the control of speed, the correction of unrealitisc pitch and roll angles and random noise (Equation 7).

To avoid collision with n_s others that are in its separation zone, individual i perceives a steering force f_{si} to move in the opposite direction of the average direction of others that is inversely weighted by the distance at which it perceives the others:

$$d_{si} = -\frac{1}{n_s} \sum_{j=1}^{n_s} \frac{r_{ij}}{|r_{ij}|^2}; \quad f_{si} = w_s \frac{d_{si}}{|d_{si}|} \quad (2)$$

where d_{si} is the preferred direction of separation, and $r_{ij} = (r_j - r_i)$ is the vector pointing towards neighbour j. The influence of a neighbour declines with its distance to the acting agent as has been suggested by Reynolds (1987) and been implemented by others (Reuter & Breckling 1994; Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005).

As regards the n_a neighbours in its alignment zone, individual i perceives a steering force, f_{ai}, to align with the average forward direction of them:

$$d_{ai} = -\frac{1}{n_a} \sum_{j=1}^{n_a} e_{xj}; \quad f_{ai} = w_a \frac{d_{ai} - e_{xi}}{|d_{ai} - e_{xi}|} \quad (3)$$

d_{ai} is the alignment direction of individual i, e_{xi} and e_{xj} are the vectors indicating the forward direction of individuals i and j.

Further, individuals are attracted by a steering force f_{ci} to the centre of gravity (i.e. the average x, y, z position) of the group of n_c individuals located in their cohesion area:

$$d_{ci} = -\frac{1}{n_c} \sum_{j=1}^{n_c} \frac{r_{ij}}{|r_{ij}|}; \quad f_{ci} = w_c \frac{d_{ci}}{|d_{ci}|} \quad (4)$$

Here, the calculated directions of alignment, d_{ai} and of attraction, d_{ci} are identical to those of the model by Couzin et al. (2002).

Note that the social steering forces f_s, f_a and f_c all have the form of a unit vector multiplied by a weighting factor. The weighting factors w_s, w_a and w_c prioritise the importance of these forces with collision avoidance being decisive (Table 1).

The social steering forces also have a length, which may cause individuals to slow down (e.g. to avoid collisions) or to speed up (e.g. to catch up). However, each individual prefers to swim at cruise speed v_0 and deviations from this are reduced by a compensating force (Helbing & Molnar 1995):

$$f_{speedi} = \frac{1}{\tau}(v_0 - v)e_{xi} \quad (5)$$

where the ''relaxation time'' τ is the characteristic time scale for the return to cruise speed.

During migration real fish do not show large pitch angles over longer periods and they virtually never roll. This feature is absent in a 2D model, but when representing the three-dimensional orientation of individuals, we had to apply downward pointing forces (negative global z-direction) to rotate the fish back into a horizontal plane:

Table 1: Summary of model parameters. The unit of length is one body length (BL) and the unit of mass is one body mass (BM)

Parameter	Unit	Symbol	Value(s) explored
Number of individuals	1	N	10-2000
Time step	s	Δt	0.05
Zone of separation			
Radius	BL	R_{min}	2
Blind angle back	Degrees	–	60
Zone of alignment			
Maximum Radius	BL	–	5 (adaptive)
Blind angle back	Degrees	–	60
Blind angle front	Degrees	–	60
Zone of cohesion			
Maximum Radius	BL	R_{max}	15 (adaptive)
Blind angle back	Degrees	–	90
Cruise speed	BL/s	v_0	2; 4
Weights			
Separation	$BL^2 \cdot BM/s^2$	w_s	10
Alignment	BM/s^2	w_a	5
Cohesion	BM/s^2	w_c	9
Relaxation time	s	τ	0.2
Pitch control	$BL^2 \cdot BM/s^2$	w_{pc}	2
Roll control	$BL^2 \cdot BM/s^2$	w_{rc}	5
Random noise	$BL^2 \cdot BM/s^2$	$|f_\zeta|$	0.5
Max. force	$BL^2 \cdot BM/s^2$	f_{max}	3

$$f_{pci} = -w_{pc}(e_{xi} \cdot z)z; \; f_{rci} = -w_{rc}(e_{yi} \cdot z)z. \quad (6)$$

A random component, f_ζ, is added to the sum of these forces to reflect that decision making in animals is subject to stochastic effects (such as sensory error and undefined motivational influences). The net steering force, f_{neti}, is then given by:

$$f_{neti} = \{f_{si} + f_{ai} + f_{ci} + f_{speedi} + f_{pci} + f_{rci} + f_\zeta\}. \quad (7)$$

If this net steering force f_{neti} exceeds a maximum magnitude f_{max}, it is rescaled to f_{max}, thus limiting the maximum acceleration to 3 body lengths per second^2 or 3 BL/s^2 (for default parameters, see Table 1).

The model is implemented in C++. On a PC the program can handle up to 10.000 individuals in real-time. This is due to the use of a specific spatial-search method based on a Hilbert R-tree, to make individuals efficiently find their neighbours (Kamel & Faloutsos 1993, 1994). Because this method has been developed for static data, we have optimized the algorithm for the highly dynamic data of fish schools.

Starting Conditions

By default, individuals start in a spherical volume of radius 50 BL, at random locations while heading in random directions. Before the analysis of data is started the simulation is run for approximately 6000 time-steps to eliminate the influence of the initial condition.

To study the origin of an oblong form and a heterogeneous density distribution, we use a special starting condition, namely a school whose form is initially spherical. We create a spherical aligned school by running the simulation at a low relaxation time $\tau = 0.01$, so that the variance in speed becomes very small (of 0.002 BL/s compared to the default of 0.25 BL/s). Such a school becomes more and more spherical during turns (Hildenbrandt and Hemelrijk, in prep). Once the school is clearly spherical, we use it as a starting condition for a run with the normal variance in speed (of 0.25 BL/s).

Analysis of the Model

To quantify the form of the school, we create a bounding box around the school aligned to the average travelling direction (Fig. 2a). The elongation of the school is measured in two ways, a) by the length-width ratio of the bounding box and b) by the degree of circularity C (Axelsen et al. 2001) following equation 8:
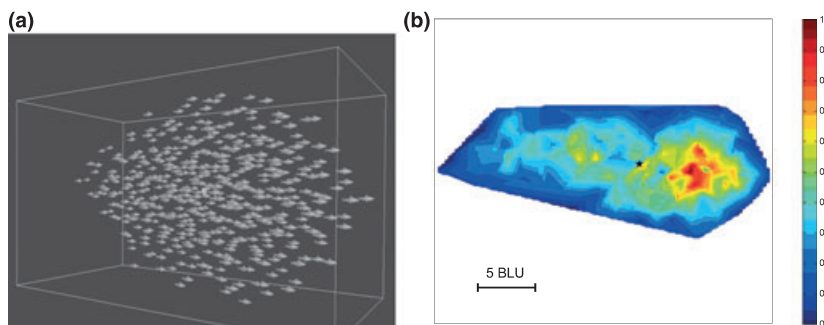

(a) **(b)**

Fig. 2: (a) Typical snapshot of the school within the bounding box. (b) Density distribution of its members. The school consists of 600 individuals that are moving at 2 BL/s. The stars indicate the locations of the centre of gravity. The density distribution is measured as the number of individuals in the cohesion region (BL^{-3}).

5 BLU

$$C = \frac{P^2}{4\pi \cdot A}$$

Here A represents the horizontal cross-sectional area of the school and P is its perimeter measured by the convex hull of the school which is the minimal envelope around the school (using the convhulln() function in Matlab, http://www.mathworks.com).

The spatial density distribution of the school is calculated as the distribution of the number of group members in the cohesion area of each individual, and the distance of each individual to its closest neighbour. It is calculated for a horizontal slice (one BL thick) through the middle of the height of the school determined along the vertical axis of the bounding box. The density is spatially interpolated and averaged over five consecutive time-steps.

To estimate the degree of frontal density, we use two measures, (a) the location of the centre of gravity of the school and (b) the location of the 'core' of the school. The core contains those 10% of the individuals which experience the highest local density (indicated in red in Fig. 2b). Its location is calculated as the center of gravity of the individuals belonging to the core. The degree to which the core is located towards the front is measured as its distance to the back of the school divided by the length of the bounding box. The tail is defined as the portion of the school which contains the 25% most rearward individuals. Statistics have been averaged over a simulation period of 3 minutes (which comprised 3600 time-steps) and over five replicas. We confine ourselves to five replicas, because between replicas the results appear to be similar. To test for significance of correlations and differences, we use only two-tailed tests of conservative, nonparametric statistics on the median values of 5 replicas (in order not to blow up the sample size).

Results

Our model produced both patterns of spatial organization: the form of the school appeared to be oblong, and the density was highest at the front. This held for both speeds and in all schools larger than 20 individuals.

To understand the origin of both patterns, we first performed a model experiment to get an understanding of their dynamic development. Second, we used this understanding to explain patterns at different group sizes and speed. To investigate the development of an oblong school from one that was spherical, strongly aligned and had the highest den-
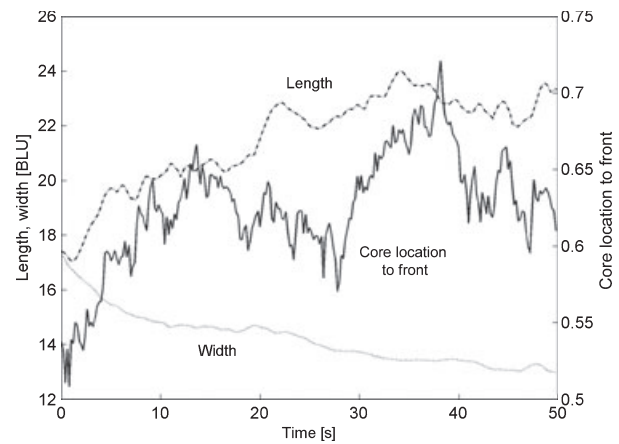

Fig. 3: Time series of a school in the transition from circular to oblong shape, its median length in BL, its width and the location of its core to the front (see text for the definition of the core). n = 600, cruise speed 2 BL/s (slow).

sity in the centre (see methods), we used a group of 600 slow individuals (2 body lengths per second or 2 BL/s). After the start the school began to elongate over time, and became narrower while the densest part shifted to the front (Fig. 3). This arose because individuals in trying to avoid collisions slowed down and thereby opened a temporary 'gap' in front of them, which, in turn, was taken up by lateral neighbours due to their sideward attraction. The length increased because a tail built up that was looser than the front (Fig. 2b). Stabilisation occurred within a simulation time of approximately one minute (after 1200 time-steps). The same happened at fast speed (data available on request).

This explanation made the effects of school size and speed understandable. First, with increasing school size, the density increased in the group and its core due to the greater attraction among the greater number of individuals (Spearman rank correlation, n = 10, complete group: $rho_{fast} = 1$, $rho_{slow} = 1$, $p = 0.00$, core: $rho_{fast} = 1$, $rho_{slow} = 1$, $p = 0.00$, tail: $rho_{fast} = 0.87$, $rho_{slow} = 1$, $p = 0.00$, Fig. 4a). With increasing group size the increase in density was strongest in the core and weakest in the tail as a consequence of difference in density between the two. As regards school form and frontal density, at larger school sizes, schools became more oblong and the core was located more to the front (Oblong: $rho_{fast} = 0.82$, $p = 0.01$, $rho_{slow} = 0.98$, $p = 0.00$, Core to the front: $rho_{fast} = 0.99$, $rho_{slow} = 0.95$, $p = 0.00$, Fig. 5). This arose because in large schools the higher density forced a higher number of individuals to fall back to avoid collisions, thus building up a longer tail. Note that at a school size of 2000, the
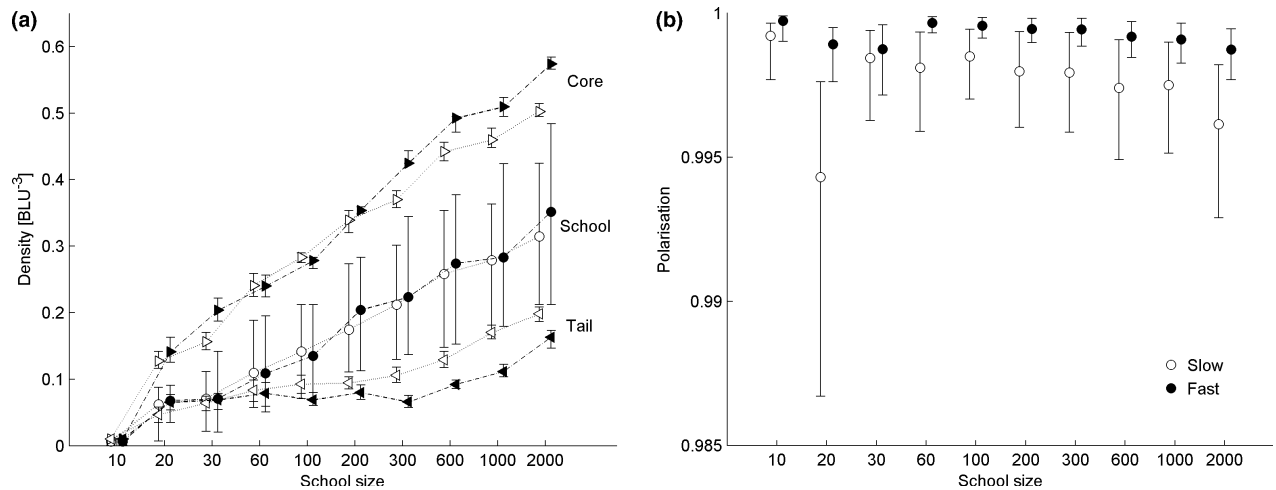
Fig. 4: (a) Density of core, tail and complete school vs. school size. (b) Polarisation vs. school size (medians and interquartile). Filled symbols: cruise speed 4 BL/s (fast). Open symbols: cruise speed 2 BL/s (slow). The value for polarisation for a group size of 20 individuals is unexpectedly low.
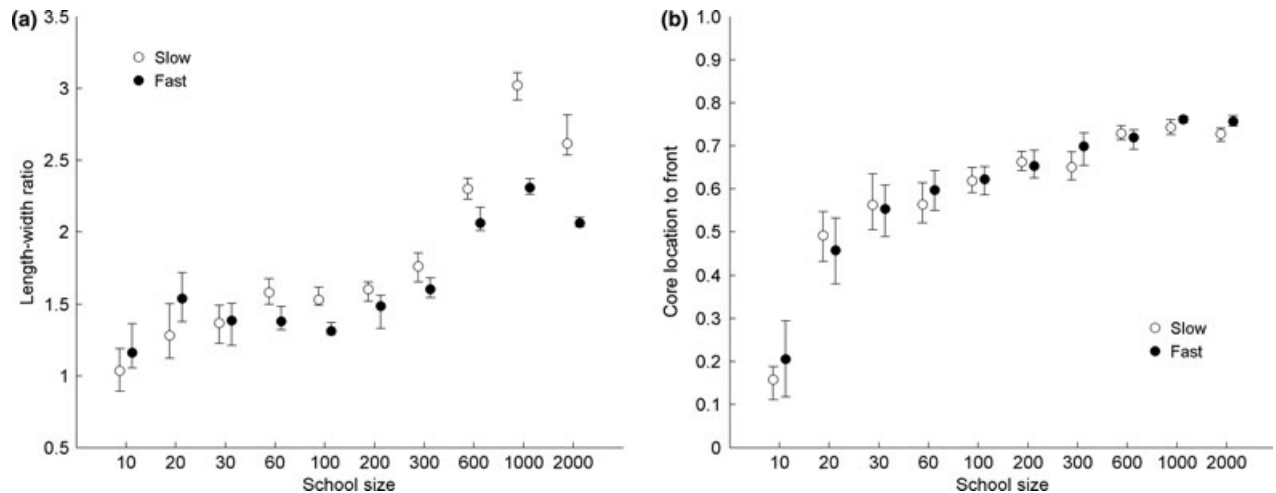

Fig. 5: (a) Length-width ratio and (b) location of the centre of gravity of the core to the front (median and interquartile).

shape became less oblong. This was caused by the form becoming irregular through the development of several dense kernels and 'amoeba-like pseudopodia'. Thus, the measures of length/width and frontal density were no longer useful, and therefore, we have not studied larger swarms.

Secondly, slower schools (N > 30) were more oblong (Wilcoxon matched-pairs signed ranks test on the median-values, n = 7, T = 28, p = 0.02, Fig. 5a). This is due to their weaker polarisation (Wilcoxon matched-pairs signed ranks test on the median-values, n = 10, T = 55, p = 0.00, Fig. 4b) which is caused by the greater ease with which slower individuals turn. Consequently, individuals

avoided each other more often and thus, they fell back more frequently, which resulted in a longer tail. Thirdly, when the school size was increased, the increase in density in the tail became greater in a slow school and core density was lower than in a fast school (Wilcoxon matched-pairs signed ranks test on the median-values of fast and slow schools, Density in Tail n = 10, T = 39, p = 0.05, Core density n = 10, T = 39, p = 0.02, Fig. 4a). This also was due to the lower degree of polarisation in slow schools. Due to the lower polarisation, more individuals had to avoid collisions by falling from front to back, thus decreasing the density of the core and increasing that of the tail.

Table 2: A list of model based hypotheses related to the origin of an oblong school form and high frontal density

Model-based hypotheses	Empirical data
1. Group size	
a. larger groups are denser	(Breder 1954; Keenleyside 1955; Nursall 1973; Partridge 1980; Partridge et al. 1980)
b. larger groups are more oblong	(Axelsen et al. 2001)
c. their densest core is located more forward	n.a.
d. their core is denser	n.a.
e. their tail (25% and 50% at back) is denser	n.a.
2. Cruise Speed	
a. Slower groups are less polarised	(Inagaki et al. 1976)
b. they are more oblong	(Partridge 1980)
c. their densest core is loser	n.a.
d. their tail is denser	n.a.

n.a., not available.

Similar results regarding the relationship of both patterns (oblong shape and frontal density) with group size and speed, are obtained when, (a) instead of using width divided by length to measure form, the degree of circularity is measured as is done by Axelsen et al. (2001) (see methods), (b) when, instead of the centre of gravity of the core, that of the complete school is computed, and (c) when, instead of using density, the nearest neighbour distance (NND) is calculated (data available on request).

Our results lead to the following hypotheses for real fish: Firstly, larger groups are expected to be denser than smaller ones (including their core and their tail); they are more oblong and their core is located more towards the front. Secondly, slower schools are less polarised, more oblong, their tail is denser and their core is less dense than in faster schools (Table 2).

Discussion

In the present paper, we have confirmed that both patterns (of oblong shape and of high frontal density) emerge as a side-effect of behavioural rules of coordination in a model of fish schooling in which speed control and perception is more realistically modelled. Furthermore, we find that larger groups are denser (conform models by Huth & Wissel 1992; Reuter & Breckling 1994) and more oblong and the core is located more to the front. Upon further

inspection of the data of our earlier model 'SchoolingWorld' (Kunz & Hemelrijk 2003), it appears that here too the centre of gravity of the swarm is located more frontally, as the size of the school increases. When the size of the group increases the school becomes more oblong. As to the absolute values, for group sizes of 20–100 in both models the location of the core is around 40% to the front and the length/width ratio is comparable in both models although it was a bit broader in our former model (1.2 BL) than in the present one (1.5 BL).

Thus, the two patterns appear to emerge in both models despite the differences between both models: SchoolingWorld is built in two dimensions, and fish have a fixed speed with random error and a global view. In it, these patterns emerged in pure groups of small as well as of large individuals (Kunz & Hemelrijk 2003), in mixed groups of both small and large individuals (Hemelrijk & Kunz 2005), as well as in mixed groups in which another rule has been added causing small individuals to avoid big ones or in which individuals prefer to be close to those of similar size (Hemelrijk & Kunz 2005). In our new model, speed and perception of others are controlled in a more natural way and, besides, it is implemented in 3D. Here, the oblong form and high frontal density arise for group sizes in the range of 30-2000 and at two speeds. Thus, the two spatial patterns are robust despite these different model representations. Whether the two patterns also develop in other individual-based models of schooling must still be studied.

The mechanism that caused the building up of high frontal density as suggested in the earlier model is not found in the new model (Hemelrijk & Kunz 2005). It was supposed to build up through a kind of traffic jam, because individuals at the front have no group members ahead of themselves, and, therefore, are attracted exclusively to those at either side. Consequently, the direction of their movement continuously varies (their turning rate was high), which reduces their speed relative to the forward direction of the school, resulting in a jam near the front, because the others behind them cannot slow down.

In our present explanation, the oblong school form develops because individuals slow down in order to avoid collisions. This way, they automatically move backwards in the swarm, while those that were formerly at their sides, move side wards together. The length of the school stabilises, because, individuals catch up again if they fall back too far. The number of individuals falling back is on average compensated by the number that is speeding up.

Note that this mechanism automatically results in the build-up of the highest density at the front: Because only a small percentage of individuals slows down, the density of individuals at the back of the school is less than at the front at both speeds. However, at higher speed individuals have to avoid collisions less often because the direction of the school is more polarised (Kunz & Hemelrijk 2003; Viscido et al. 2004) and consequently, at higher speed schools are shorter and relatively broader. At larger school sizes a relatively longer tail develops, because more individuals fall back due to the school's higher density. In an earlier model the origin of an oblong group shape arose similarly (Kunz & Hemelrijk 2003; Hemelrijk & Kunz 2005), even though individuals can not catch up with others because they move at constant speed with random error.

Is there empirical support for our results? First, schools are usually oblong (Pitcher 1980), but there are exceptions, such as parasitized schools (Ward et al. 2002). Partridge et al. (1980) describe for herring schools of 30 individuals, a length/width ratio of 1.2, which is close to our value of 1.5. Further, an oblong form and high frontal density of the shoal have been described specifically for juvenile roach (Bumann et al. 1997). Whether an oblong group shape and high frontal density also occurs in other taxa (such as birds, primates and ungulates) is unclear at present. Systematic studies are needed to clarify this. Second, there is extensive support for our conclusion that larger schools are denser (Breder 1954; Keenleyside 1955; Nursall 1973; Partridge 1980; Partridge et al. 1980). Larger schools of herring (*Clupea harengus*) are reported to be more oblong than smaller ones (Axelsen et al. 2001). Slower schools are less polarised (Inagaki et al. 1976) and Partridge and co-authors found that in saithe and cod slow schools are more oblong than faster ones (Partridge et al. 1980). Besides, a comparison of their data of different species shows that from herring via saithe to cod schools appear to become more oblong as their speed goes down. Partridge and co-authors explain changes of shape with speed in a way different from ours, namely by the need of the fish to avoid disadvantageous hydrodynamic effects and their wish to obtain optimal positions to monitor each other (which differs between different velocities). That slower schools are more oblong contradicts, however, the predictions by Breder (1959) and Radakov (1973), who argue that faster schools should be more oblong.

We did not analyse groups larger than 2000 individuals, because here pseudopodia developed and very dense kernels, which have been described also for very large schools of real fish (e.g. Gerlotto & Paramo 2003).

Even though similar patterns of oblong shape and high frontal density are found in real fish (Bumann et al. 1997), they may develop via other processes than described by our model. First, high density at the front may arise from competition for food, because hungry fish are located at the front (Krause 1993) and frontal positions are better for foraging (DeBlois & Rose 1996). However, this mechanism is insufficient to explain why oblong shape and frontal density appear also among satiated fish (Bumann et al. 1997).

Secondly, in real fish, movement through water may be more difficult at the front than at the back, because of hydrodynamic advantages at the back (Herskin & Steffensen 1998; Svendsen et al. 2003). Consequently, frontal individuals would slow down and frontal density would build up. However, hydrodynamic effects are supposed to be weak in species with the swimming style of 'burst-and-coast' where periods of active tail beating are interrupted by coasting periods (Fish et al. 1991). Therefore, this does not explain the oblong shape and frontal density in these species (Bumann et al. 1997).

It may be considered a shortcoming of our model that it only studies the consequences of simple rules of coordination. Real animals are naturally much more complex, they show reproductive behaviour, hunger *etcetera*. However, in a model it is important to confine the study to a minimal number of mechanisms, so that their effects become clear. Besides, the theory of self-organisation aims at finding the simplest explanation for a complex collective phenomenon (Couzin & Krause 2003). Furthermore, we obviously studied the models only in the parameter range (of size of dead angle, and relative contributions of the three behavioural acts) in which a travelling polarised school emerged, but not in the range of parameters that led to milling and to a confused swarm or a swarm that fragmented. A shortcoming of the model, and all others of this kind, is that vision is identical around the axis of movement, which implies that width and height of the school are identical, which is often not true in nature (Krause & Ruxton 2002). We will address this problem in future work.

Yet, despite all these objections, these models enable us to understand how both of these adaptive patterns (*viz.* oblong shape and high frontal density) may arise. To obtain empirical evidence details of the way in which collision is avoided should be

studied. Furthermore, if our model reflects the process of coordination of real fish, we may expect that in a single species larger schools (of individuals that ideally are identical in size, satiated regarding food, unparasitised, *etcetera*) should also be more oblong and their core should be located more to the front, and faster travelling schools should be broader and more polarised than slower ones (Table 2). It is now the turn of the empirical scientists to test our hypothesis that oblong school shape and high frontal density arise as a side-effect of coordination in schools of fish.

Acknowledgements

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