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Simulations of the social organization of large schools of fish whose perception is obstructed

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ABSTRACT

Individual-based models have shown that simple interactions among moving individuals (repulsion, attraction and alignment) result in travelling schools that resemble those of real fish. In most models individuals interact with all neighbours within sensory range which usually includes almost all the individuals of the school. Thus, it implies (almost) global perception. However, in reality in large groups, individuals will only interact with their neighbours close by, because they cannot perceive those farther away, since they are masked by closer ones. Here, we have developed a new model to investigate how such obstruction of perception influences aspects of social organization in schools of up to 10,000 individuals. We will show that in small schools of up to approximately 30 individuals group shape and density resembles that obtained with global perception, because in small schools hardly anyone is masked by others: school shape is oblong and the density is highest in the frontal half of the school. With increasing group size, from approximately 200 individuals onwards, internal density becomes variable over time, regions of high and low density develop at any location within a school, and group shape becomes more complex, in the sense that inward bounds and appendages occur more frequently. The complexity of shape and internal structure arises because, due to their limited perception, individuals interact relatively more locally in larger schools. In case of global perception, however, shape remains elliptical for all group sizes and in groups above 1000 individuals, the schools become unrealistically dense. In sum, our results show that obstructed perception in itself suffices to generate a realistic organization of large schools and that no extra rules for 'coping' with many individuals are needed.

1. Introduction

The flexible coordination of schools of fish, ranging from groups of a few individuals to vast aggregations of millions, has been an enigma for a long time. Recently computer models based on processes of self-organization (Camazine et al., 2001; Deneubourg and Goss, 1989; Hemelrijk, 2002, 2005) have shown that coordination among neighbours suffices to generate collective behaviour that resembles that of schools of fish (Aoki, 1982; Couzin et al., 2002; Niwa, 1994; Parrish and Viscido, 2005; Reuter and Breckling, 1994; Reynolds, 1987). Besides, such models may guide empirical studies. For instance, they have predicted that larger schools are denser and more oblong (Hemelrijk and Hildenbrandt, 2008; Hemelrijk and Kunz, 2005; Kunz and Hemelrijk, 2003). These traits are supposed to be interconnected, schools are more oblong, because the higher density of larger schools forces individuals to avoid

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others more frequently. Since individuals avoid collisions by slowing down, former neighbours may subsequently move inwards and thus the school becomes more oblong. These predictions were subsequently confirmed in an empirical study (Hemelrijk et al., 2010), in which the 3-dimensional positions of individuals in schools were measured in schools of up to 60 mullets. Empirical results confirmed that larger schools were denser and more oblong (Hemelrijk et al., 2010).

Models of fish schooling have usually been based on three behavioural rules consisting of attraction to others further away, alignment with others at medium distance and avoidance of others that are close by (for a review, see Parrish and Viscido, 2005). They differ in a number of traits, such as in whether they are made in two or in three dimensions and in the number of interaction partners to which individuals react. Remarkably, the difference in dimensionality hardly affects results (Hemelrijk and Hildenbrandt, 2008; Hemelrijk and Kunz, 2005; Huth and Wissel, 1992, 1994; Kunz and Hemelrijk, 2003). However, how many and which neighbours an individual reacts to, matters clearly (Viscido et al., 2005). Most models employ a metric approach, where individuals interact with all neighbours that are located within a certain radius, i.e. a circular area around the focal individual excluding a blind field at its rear (Couzin et al., 2002; Niwa, 1994; Reuter and Breckling, 1994; Reynolds, 1987). Here, because the range of interaction is constant, the number of interaction partners increases with density of the school. Since larger schools are denser (Hemelrijk and Hildenbrandt, 2008; Hemelrijk and Kunz, 2005; Kunz and Hemelrijk, 2003; Reuter and Breckling, 1994), the number of interaction partners increases with school size. This becomes unrealistic in models of very large groups, in the sense that too many individuals interact (Viscido et al., 2002; Lemasson et al., 2009) and that group structure collapses (Mogilner et al., 2003). By reducing the range of interaction when local density increases, such a collapse has been avoided in the 3-dimensional model of large groups consisting of up to 2000 individuals by Hemelrijk and Hildenbrandt (2008). In other models, individuals are made to interact with a fixed number of their nearest neighbours, their so-called topological range (Aoki, 1982; Hildenbrandt et al., 2010; Huth and Wissel, 1992; Viscido et al., 2005, 2007), or with the first shell or layer of neighbours around it, as given by a Voronoi tessellation (Gregoire, 2003). Such restrictions are, however, unrealistic, because in reality neighbours are sometimes perceived over much larger distances in certain directions than in other directions.

The aim of the present paper is to study the consequences of a more realistic representation of interaction partners: individuals interact with all the neighbours they perceive, i.e. those that are not hidden behind others. We study the effect of such obstructed perception on local density and school shape (its asymmetry, the degree to which it is oblong and the convolutedness of its border) in relation to school size for groups of 10–10,000 individuals. Our earlier model (Kunz and Hemelrijk, 2003), henceforth referred to as the model with global perception, is taken as a control.

Table 1
Default parameters of the model. These were kept fixed over all experimental conditions.

Parameter	Symbol and value
Body length	$b = 0.2$ m
Cruise speed and s.d. (Gaussian noise)	$v_{crs} = 0.3$ m/s, $v_{sd} = 0.03$ m/s
'Default' rate of rotation	$\omega_{def} = 1/2\,\pi$ rad/s
Interaction radius	$r = 5.0$ m
Blind angle	$\gamma = 60$ degrees
Time step	$\Delta t = 0.2$ s

2. Methods

2.1. The model

Our model is an extension of our earlier model described in Kunz and Hemelrijk (2003). It is implemented in the programming language C and consists of a 2-dimensional world that is continuous and infinite. In each simulation step Δt all artificial fish are activated in random order. The individuals behave according to three responses, repulsion away from close by neighbours, alignment with individuals at intermediate distances, and attraction to neighbours at larger distances.

2.1.1. Position, speed and heading

At time t individual i is located at position $\vec{x}_i(t)$ and moves with a velocity $\vec{v}_i(t)$ during one simulation step Δt. Thus the location is updated as

$$\vec{x}_i(t) = \vec{x}_i(t - \Delta t) + \vec{v}_i(t)\Delta t$$

where $\vec{x}_i(t - \Delta t)$ is the position of individual i at the previous time step. The velocity $\vec{v}_i(t)$ comprises the heading $\alpha_i(t)$ and the speed $v_i(t)$

$$\vec{v}_i(t) = \begin{pmatrix} v_i(t)\cos\alpha_i(t) \\ v_i(t)\sin\alpha_i(t) \end{pmatrix}$$

of individual i. The speed $v_i(t)$ is set to v_{crs} (Table 1). It is subjected to Gaussian noise with a standard deviation of v_{sd}. Like in other models, it is independent of the behaviour of other individuals (Aoki, 1982; Couzin et al., 2002; Huth and Wissel, 1992, 1994). This seems to be a valid simplification, as similar results are found, irrespective whether the individuals adjust their speed to neighbours (Hemelrijk and Hildenbrandt, 2008) or not (Kunz and Hemelrijk, 2003)

The individuals' heading $\alpha_i(t)$ is updated each simulation step as follows:

$$\alpha_i(t) = \alpha_i(t - \Delta t) + \omega_i(t)\Delta t \pm \alpha_{sd}$$

where $\alpha_i(t - \Delta t)$ is the individual's heading in the previous time step and $\omega_i(t)$ its rate of turning or rotation, which depends on the interaction with neighbours. The heading $\alpha_i(t)$ is subject to Gaussian noise with a standard deviation of α_{sd}.

2.1.2. Global and obstructed perception

We use our earlier model as a control (Kunz and Hemelrijk, 2003). In this model an individual i interacts with all neighbours located in it sensory field (Fig. 1a). In our new model, where perception is obstructed, the

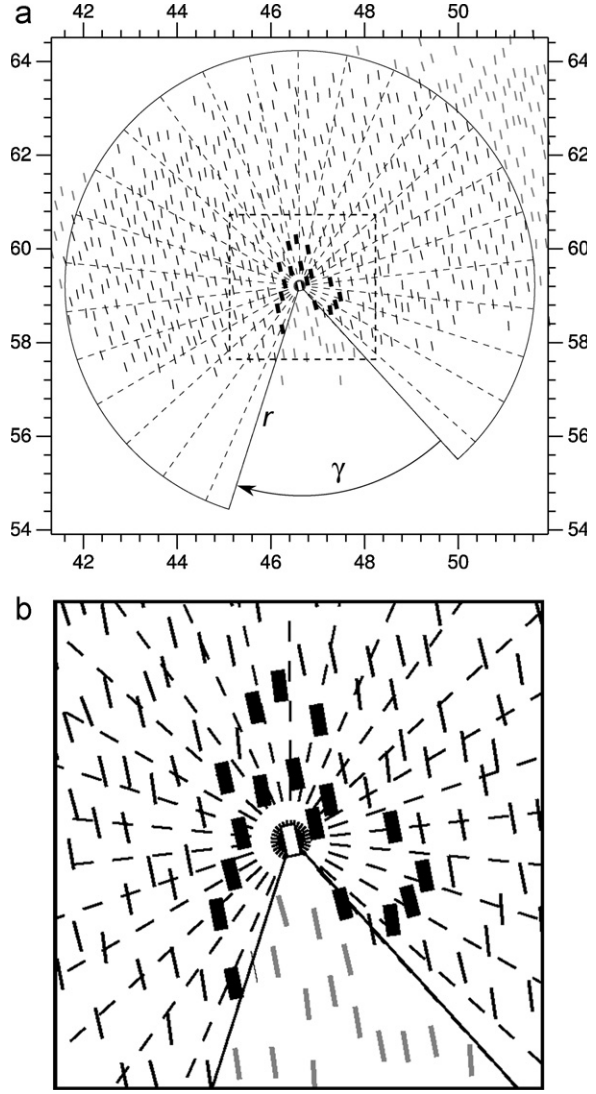

Fig. 1. The circular sensory field around an individual (white bar) with the blind angle γ at its back. For obstructed perception the interaction partners are indicated by fat black bars. Interaction partners for global perception are given by the (fat and thin) black bars. Neighbours outside the sensory field are painted grey.

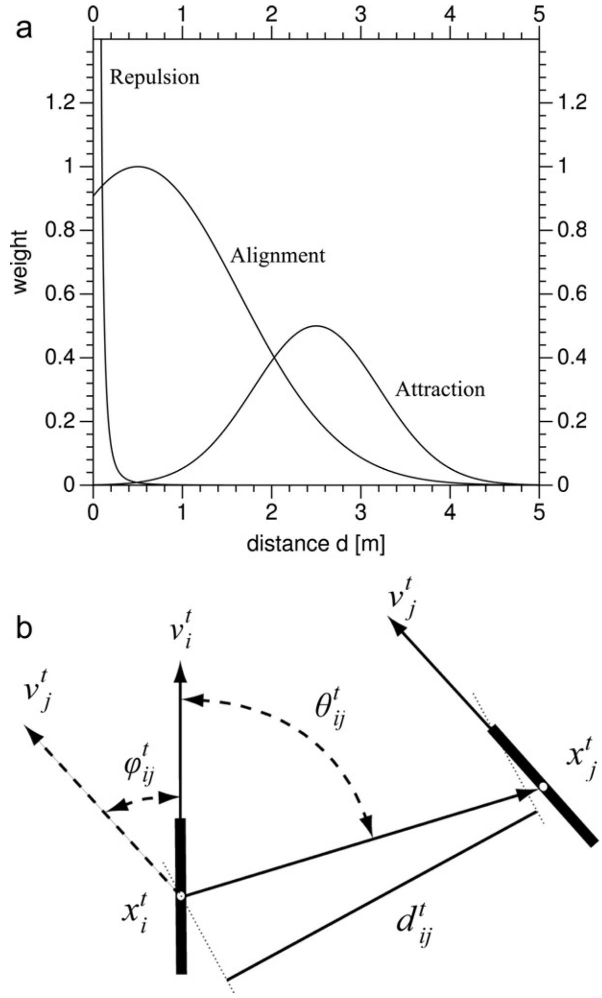

Fig. 2. (a) The weight factors for repulsion $w_r(d)$, attraction $w_a(d)$, and alignment $w_p(d)$ for obstructed perception (the weight factors for global perception are similar, see Kunz and Hemelrijk (2003)). d denotes the distance to the neighbour. (b) The location, headings, associated angles and vectors and bodies of two individuals i and j (black bars). Note that d_{ij} is measured between the center of agent i to the nearest point of agent j, but is shifted over the dotted lines for clarity in the figure.

interaction partners consist of all those individuals that are not masked by those closer to the focal individual. To find these, we divide the sensory field into sectors and assume that within each sector only the closest neighbour can be perceived (Fig. 1ab, fat bars). If this neighbour covers several sectors it is counted only once. Thus, increasing the number of sectors increases the number of different neighbours that may be visible simultaneously.

In relation to each interaction partner j the individual i tends to be repulsed $\omega^r_{ij}(t)$, be attracted $\omega^a_{ij}(t)$ and to align $\omega^p_{ij}(t)$. The total behavioural responses of individual i is the sum of the three actions averaged over all its interaction partners. Its rate of rotation is

$$\omega_i(t) = \frac{1}{|P_i(t)|} \sum_{j \in P_i(t)} \omega^r_{ij}(t) + \omega^a_{ij}(t) + \omega^p_{ij}(t)$$

where $P_i(t)$ denotes the set of all perceived neighbours (all within the interaction radius for global perception, or those not masked by closer ones for obstructed perception). In other words, individuals do not react to single neighbours independently. Instead, their behaviour is a weighted average of their reaction to all the neighbours perceived by them.

2.1.3. Repulsion, attraction and alignment

The strength of repulsion, attraction and alignment depend in a non-linear and continuous way on the distance d_{ij} between the individuals (inspired by Reuter and Breckling (1994)). The weight for repulsion $w_r(d_{ij})$ is highest for short distances, that for alignment $w_p(d_{ij})$ for intermediate and that for attraction $w_a(d_{ij})$ is highest for longer distances (Fig. 2a).

Repulsion implies that an individual i turns away from a nearby individual j with a rate of rotation (i.e. speed of turning) of

$$\omega_{ij}^{r}(t) = w_r(d_{ij}) \cdot \left\{ \begin{array}{ll} -\omega_{def} & \text{if}\,\theta_{ij}(t) > 0 \\ +\omega_{def} & \text{otherwise} \end{array} \right\}$$

where $w_r(d_{ij})$ is the distance dependent weight factor (Fig. 2a), ω_{def} is the 'default' rate of rotation of the individual (Table 1) and $\theta_{ij}(t)$ is the angle between the vector connecting individuals i and j and the heading of individual i (Fig. 2b). Note that the rate of turning $\omega_{ij}^{r}(t)$ caused by repulsion only depends on the sign of $\theta_{ij}(t)$, such that the individual i turns always away from j.

Attraction implies that individual i turns towards individual j with a rate of rotation of

$$\omega_{ij}^{a}(t) = w_a(d_{ij})\omega_{def}\theta_{ij}(t)$$

Note that, in contrast to repulsion, the rate of turning $\omega_{ij}^{a}(t)$ caused by attraction is proportional to $\theta_{ij}(t)$, thus individual i turns faster when the angle to individual j is larger. Therefore, when individual j is directly ahead, i does not turn at all.

Aligning implies that individual i matches its orientation to that of individual j by turning with a rate of rotation of

$$\omega_{ij}^{p}(t) = w_p(d_{ij})\omega_{def}\phi_{ij}(t)$$

where $\varphi_{ij}(t)$ is the difference in the headings of the two individuals (Fig. 2b). Thus, by turning proportionally to $\varphi_{ij}(t)$, individual i adjusts its heading to that of individual j.

We represent the body of the individual by lines of length b (Table 1). This influences the degree with which the individual blocks the perception of others (Fig. 2a). The distance d_{ij} between individual j and (the focal) individual i is measured as the distance between individual i's centre and the nearest point of individual j (Fig. 2b). Thus, it depends on the orientation of individual j.

2.2. Parameterization and initial conditions

Note that for ease of comparison the parameters (Table 1) are kept identical to those used in our former studies (Hemelrijk and Kunz, 2005; Kunz and Hemelrijk, 2003). The interaction radius r and the blind angle γ are similar to those used by Reuter and Breckling (1994). Body length l and cruise speed v_{crs} are chosen in a biologically meaningful way (Pitcher and Partridge, 1979). The weight factors for repulsion w_r, attraction w_a and alignment w_p are chosen such that for groups between 10 and 100 individuals the nearest neighbour distance corresponds to biological findings (Olst and Hunter, 1979; Partridge and Pitcher, 1980; Pitcher and Partridge, 1979) and are slightly adjusted for obstructed perception, such that groups of 50 individuals with 30 sectors resemble those with global perception. The 'default' turning rate ω_{def} and the variation in speed v_{sd} and heading α_{sd} we have tuned by hand in such a way that individuals are able to avoid others effectively but without introducing too erratic or jerky movements. The initial conditions are chosen such that a single school always forms. Individuals are positioned randomly in a circular area whose radius is chosen such that the initial density is approximately 10 individuals/m^2. They have random orientations chosen from a uniform distribution of angles within a sector of 90° and their velocity is set to the cruise speed v_{crs}.

Table 2
Model parameters that differed between experimental conditions.

Parameters	Global perception	Obstructed perception
Group size	10, 20, 30, 60, 100, 200, 300, 600, 1000	10, 20, 30, 60, 100, 200, 300, 600, 1000, 2000, 3000, 6000, 10,000
Number of perceptual sectors	–	10, 20, 30, 50

3. Experiments and measures

We study both models for a range of group sizes (Table 2). For global perception, the largest group size contained 1000 individuals because larger schools were unrealistically dense. We study the influence of the number of sectors if perception is obstructed (Table 2). For each parameter setting 5 replicas are performed. The simulations last for 5000 steps, which correspond to 1000 s (16.7 min). Unless indicated otherwise, measurements are done every 10 s and are averaged over the interval between 500 and 1000 s (to avoid transients at the beginning of the simulations).

Octave, a high-level language, intended for numerical computations, was used for data analysis.

As a global measure of the average density of individuals in a school we use the average distance to nearest neighbours.

We measure shape in two ways: the degree to which a school is longer than wide (oblong) and asymmetrical. In order to measure the degree with which it is oblong, we enclose the school in the smallest rectangle oriented parallel to its direction of movement (Kunz and Hemelrijk, 2003) and measure oblongness as a ratio, i.e. of the length of the school in its direction of movement divided by its width. The asymmetry of the school shape (ignoring the movement direction) we compute as the ratio of length and width measured by means of a principle component analysis (PCA) of the positions of the individuals. Length is measured along the largest dimension of the school, which is given by the eigenvector associated with the largest eigenvalue of the co-variance matrix. The width is measured perpendicular to the length. This equals the aspect ratio used by Hildenbrandt et al. (2010). An asymmetry value of one corresponds to a roughly circular school whereas higher values indicate a more elliptic shape.

We characterize the convolutedness of the border of the school by calculating its convexity, i.e. the ratio of the group area divided by the area of the convex hull. Group

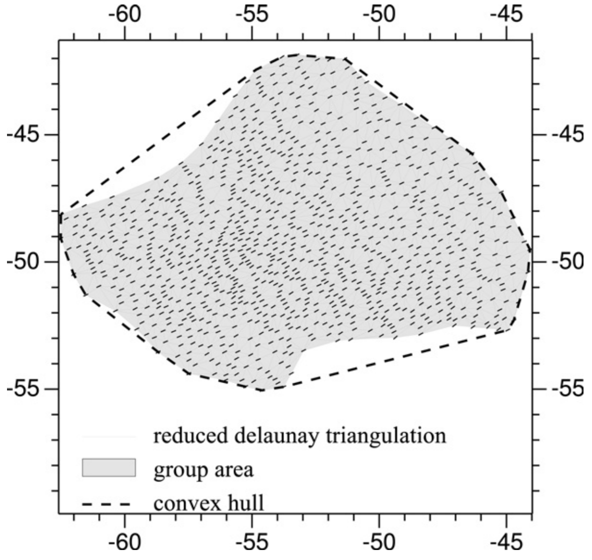

Fig. 3. A school of 1000 individuals (black bars). The grey triangles depict the Delaunay triangulation, whereby all triangles with an edge longer than 2 m have been omitted. The dashed perimeter illustrates the convex hull of the school.

area is measured as the area of the Delaunay triangulation where all triangles with an edge longer than 2 m are omitted (Fig. 3) to account for inward bounds. The maximal length of edges (2 m) is chosen as small as possible (for higher accuracy) but large enough to ensure that the Delaunay triangulation does not fragment the school. A convexity close to one indicates a roughly circular or elliptic school, whereas lower values reveal more irregular group shapes with inward bounds and appendages.

4. Results

Although it happens to a different degree for obstructed perception and the control, i.e. of global perception, with increasing group size nearest neighbour distance decreases (Fig. 4a), group area increases (Fig. 4b) and groups become more oblong (Fig. 5a).

However, compared to the control, in which nearest neighbour distance decreases strongly with group size (Fig. 4a) and becomes unrealistically small for groups larger than 1000 individuals, when perception is obstructed, nearest neighbour distance decreases with group size less (Fig. 4a), leading to more realistic group densities. Because density stabilizes for groups larger than 200 individuals, the surface area of the school increases linearly with school size (Fig. 4b). Further, with increasing size, group shape is more oblong and asymmetric (Fig. 5), more convoluted and thus less convex (Fig. 6a) and local density is more heterogeneous (compare Figs. 7 and 8): there are regions of higher density at the periphery as well as in the interior and occasionally there are holes. In large groups school shape (Fig. 6b) and local density (Fig. 7) is more variable over time than it is in small schools (Figs. 6b and 8ac) and in case perception is global (Figs. 6b and 8bd).

Small groups of up to 30 individuals resemble those in the control model with global perception: nearest neighbour distance decreases with group size (Fig. 4a) and group area (Fig. 4b) and oblongness increase with group size (Fig. 5a); group shape is convex and static over time (Fig. 6) and local density is highest in the interior of the school (Fig. 8).

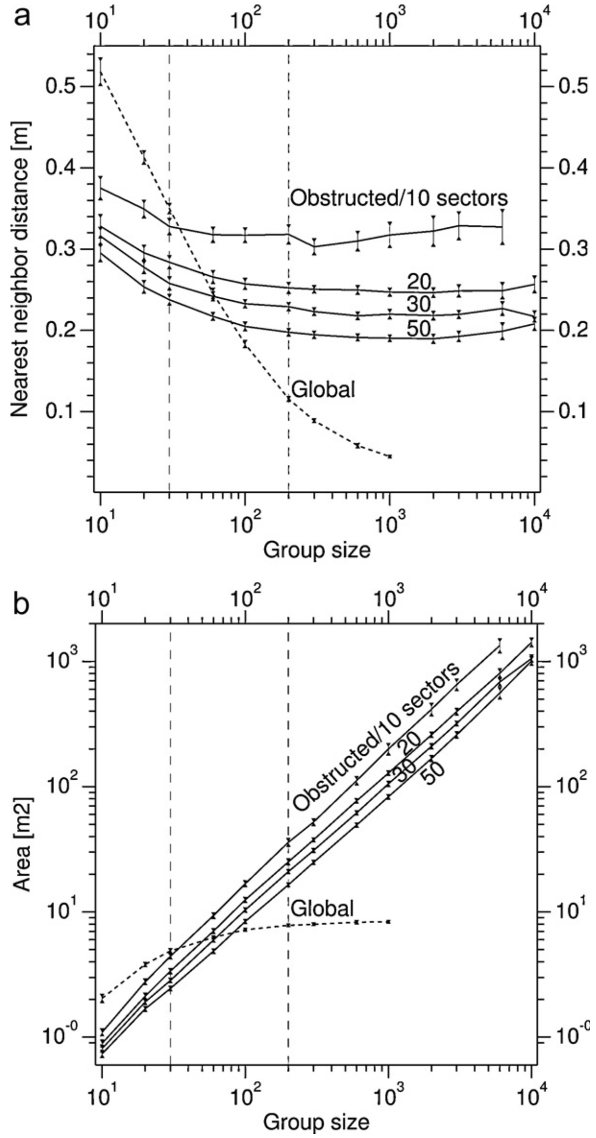

Fig. 4. Average nearest neighbour distance (a) and group area (b) for obstructed and global perception (control model). The weight factors (see Section 2) are chosen such that nearest neighbour distance is similar for groups of 50 individuals under global and obstructed perception (30 sectors). Therefore, for smaller groups nearest neighbour distance is larger when perception is obstructed. For global perception, schools of more than 1000 individuals become unrealistically dense and when perception is obstructed groups of 10,000 individuals occasionally fragment for 10 sectors; results are thus shown only for smaller groups. Note that (a) has a half- and (b) a full-logarithmic scale.

Although we did not perform a detailed sensitivity analysis, changing the weight factors for the behavioural responses affects our model in a way similar to that reported by Couzin et al. (2002). Increasing the strength or range of repulsion makes groups sparser, increasing

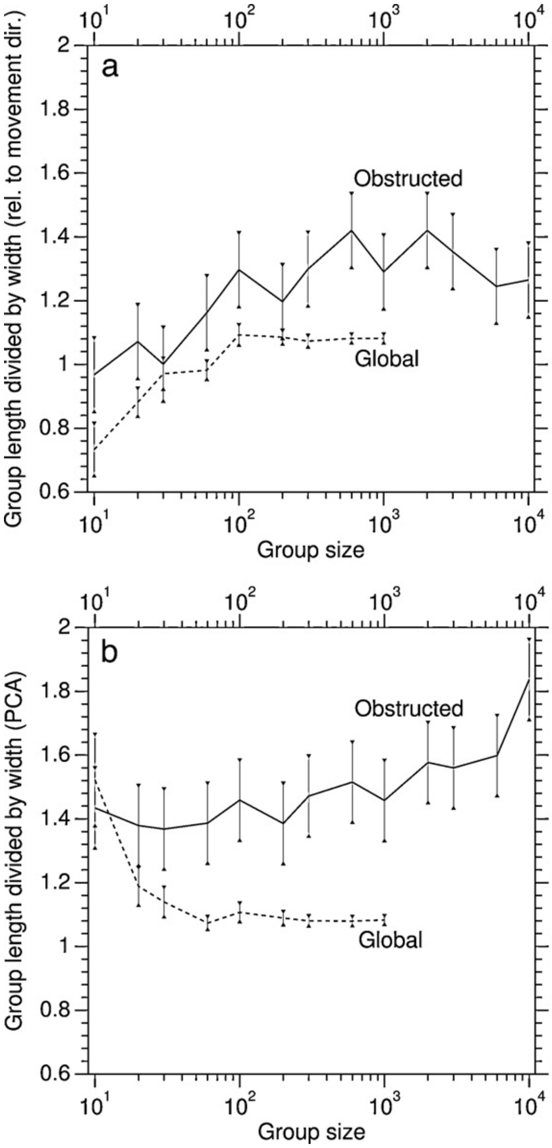

Fig. 5. Group shape (measured as length divided by width) relative to the direction of movement, called oblongness (a), and shape measured by the ratio of the longest dimension divided by the one orthogonal to it (independent of the movement direction), called asymmetry (b). As the influence of the number of sectors appears unimportant and because variability is high, the plots for obstructed perception are lumped together for all numbers of sectors (10, 20, 30 and 50). Obstructed = obstructed perception, Global = global perception in control model.

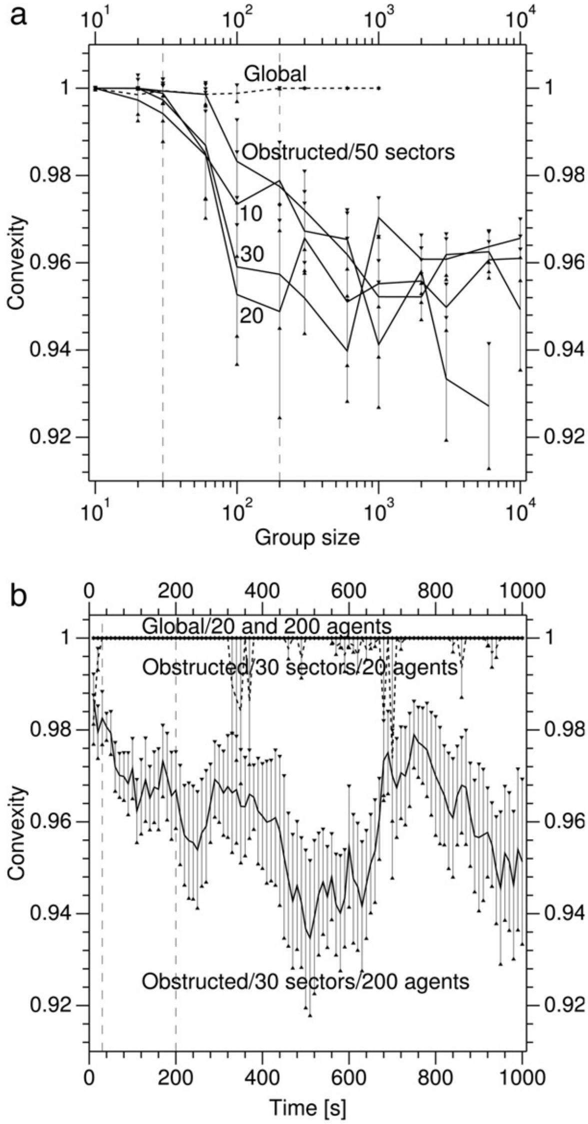

Fig. 6. Convexity of group shape (group area divided by the area of the convex hull) vs. group size (a) and over time (b) for groups of 20 and 200 individuals. Note that the plots for global perception (control model) and groups of 20 individuals with obstructed perception are almost identical (b).

the strength of attraction or its range increases density. Increasing the range of alignment leads to milling, i.e. the groups form a ring. Very strong repulsion or very weak attraction leads to fragmentation of the group, very weak alignment makes the group unordered, so that it becomes stationary.

5. Discussion

We developed a new model of schooling, where the interactions among individuals are represented more naturally, in the sense that individuals interact only with those neighbours that they can perceive because, as suggested by Breder (1954) and Huth and Wissel (1994), these neighbours are not masked by closer ones.

The differences in nearest neighbour distance, group shape and density between the model with obstructed perception and the control with global perception can be explained by the lower number of interaction partners if perception is obstructed. Here, the relative number of interaction partners (i.e. number of interaction partners divided by group size) decreases with school size, it decreases from 60% in groups of 10 individuals to below 0.2% in groups of 10,000 individuals, but in the control it is always about 80%. Thus interactions are more local. For groups larger than

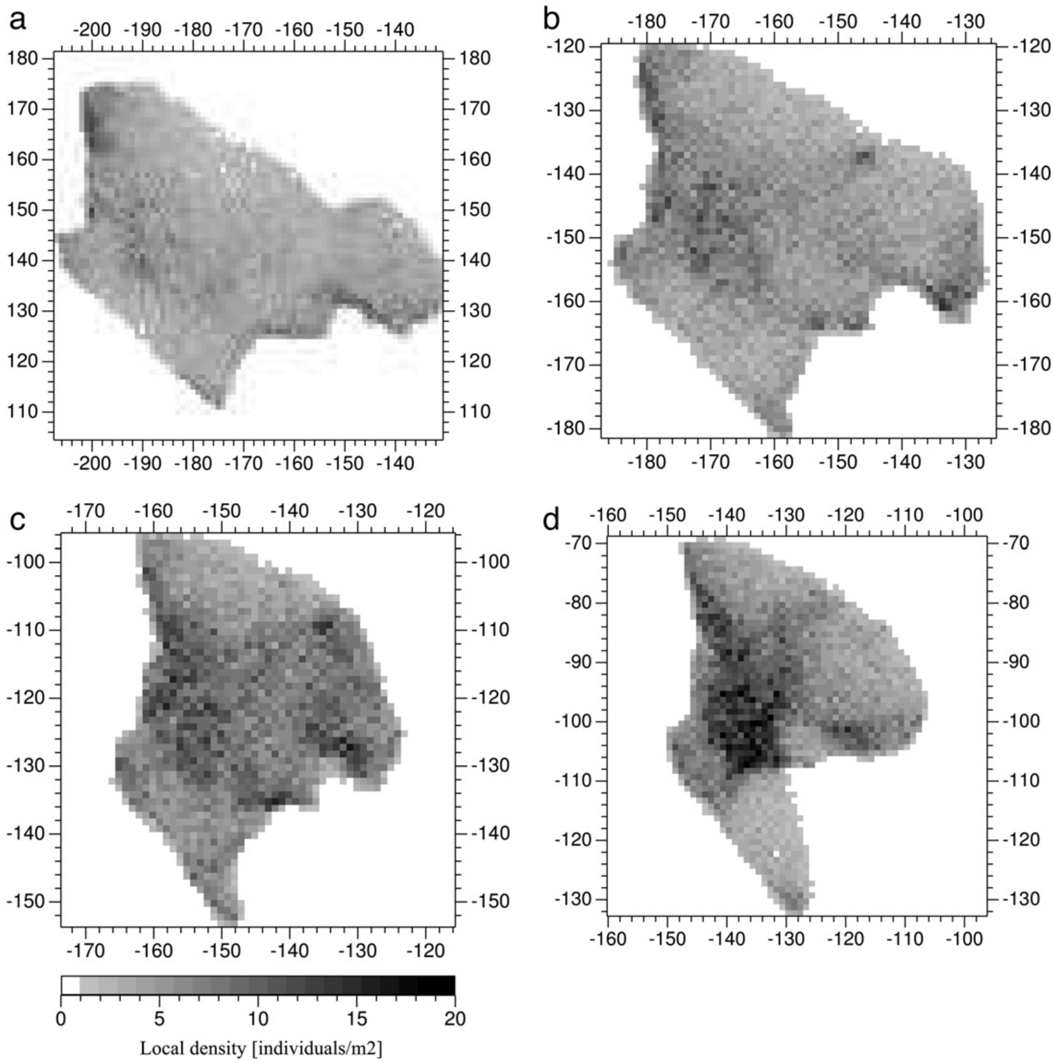

Fig. 7. Snapshots of a group of 10,000 individuals at different time steps. Local density is colour coded, and ranges from 0 to 20 individuals/m^2.

approximately 200 individuals, the number of interaction partners becomes independent of group size, because it is at its maximum (between 4 and 11, depending on the number of perceptual sectors) and therefore, nearest neighbour distance stabilizes (Fig. 4a). For groups of increasing size the shape of schools is more asymmetric (Fig. 5b), more convoluted (Fig. 6a) and more variable over time (Fig. 6b), because local interaction does not coordinate the group globally, such that subgroups may move in different directions. This causes the formation of 'appendages' and 'inward bounds' and regions of high or low density (Fig. 7).

The results are qualitatively similar for different numbers of sectors (Figs. 4 and 6a). However, nearest neighbour distance and group area are smaller for a higher number of sectors (Fig. 4ab) because of the associated higher number of interaction partners and thus the stronger attraction. This higher density at a higher number of influential neighbours confirms the findings in related models by others (Huth and Wissel, 1992; Viscido et al., 2005).

Small groups in our model resemble those in metric models (in which individuals interact with all neighbours within the radius of interaction), but large groups in it resemble those in topological models (in which individuals interact with a fixed number of nearest neighbours). In small groups of up to approximately 30 individuals, the effect of masking is weak and the individuals interact with almost the entire group (the number of interaction partners ranges between 20% and 60% of the whole group). Therefore, results are qualitatively similar to those of metric models: nearest neighbour distance decreases with increasing group size (Hemelrijk and Hildenbrandt, 2008; Kunz and Hemelrijk, 2003; Reuter and Breckling, 1994), and larger groups are increasingly oblong (Hemelrijk and Hildenbrandt, 2008; Hemelrijk and Kunz, 2005). Note, that the model by Hemelrijk and Hildenbrandt (2008) is only partly metric, because the radius of interaction decreases with increasing local density. Thus, it is keeping the number of interaction partners at around 15 and is thus almost topological for groups larger than 15 individuals.

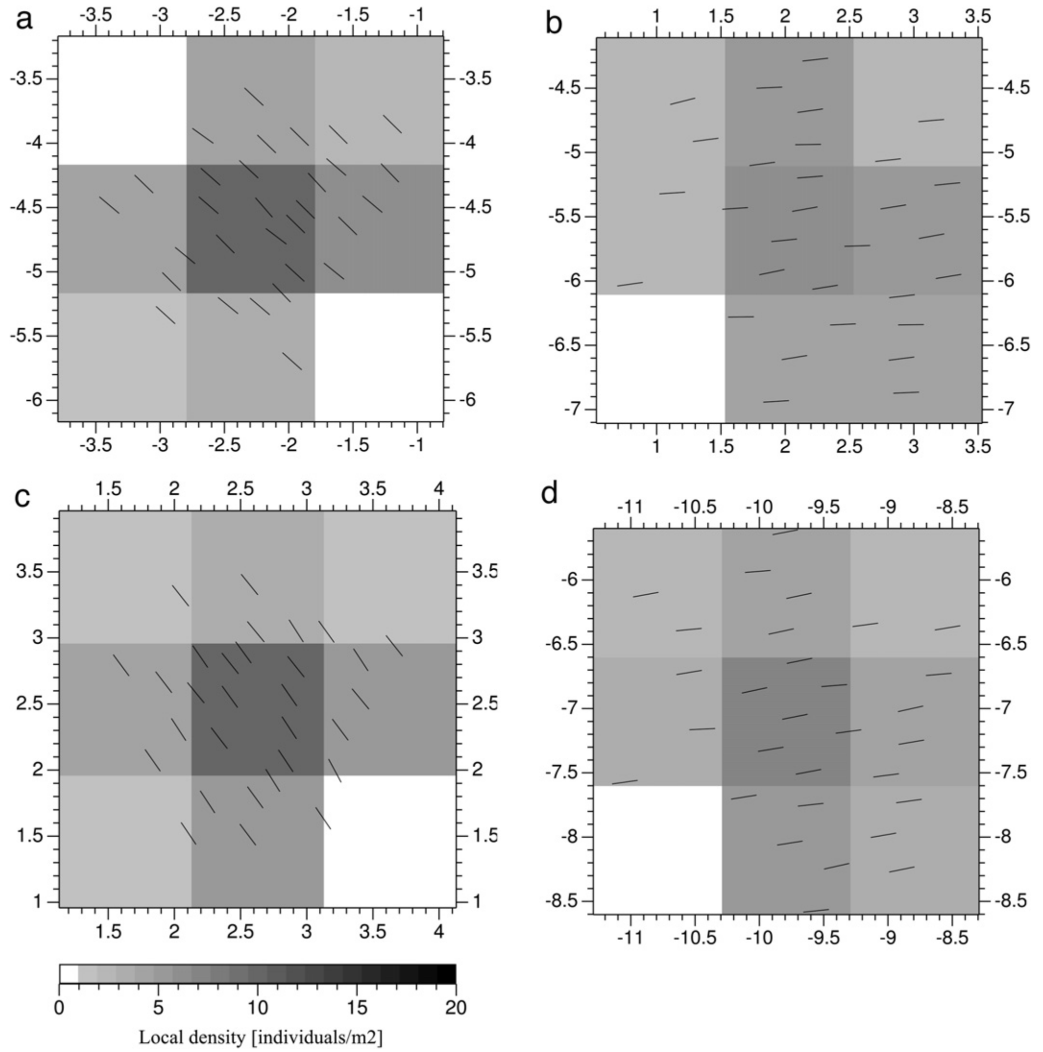

Fig. 8. Snapshots of two groups of 30 individuals after 700 and 900 s with obstructed (ac) and global perception (bd), respectively. Local density is colour coded, and ranges from 0 to 10 individuals/m^2. As the weight factors are chosen such that nearest neighbour distance is similar for groups of 50 individuals with obstructed and global perception (Fig. 4a), density in groups of 30 individuals under obstructed perception is lower than it is under global perception (control model).

In groups with more than 200 individuals, most neighbours are hidden behind closer ones, and the number of interaction partners becomes independent of group size like in models with a fixed number of interaction partners (i.e. topological interaction-range). Consequently, the results resemble those of topological models of schools of fish and of flocks of birds: nearest neighbour distance depends not on group size when group size is significantly larger than the number of interaction partners (Hildenbrandt et al., 2010; Viscido et al., 2005). A higher number of interaction partners (i.e. due to a higher number of visual sectors in our model) leads to a shorter nearest neighbour distance (conforming to Huth and Wissel, 1992; Viscido et al., 2005; Warburton and Lazarus, 1991).

Apart from these similarities, our model of obstructed perception differs from metric (with fixed interaction ranges) and topological models (with a fixed number of interaction partners) in two important ways: First, the number of interaction partners and the range of interaction varies according to the details of the actor's perception of others (depending on local density, body size and number of sectors). Second, in our model individuals perceive others over larger distances in the directions where the density of neighbours is lower and over shorter distances in the direction where density is higher. This is the case for real animals too, particularly if they are located at the border of a group. The necessity to incorporate this in schooling models was already pointed out by Huth and Wissel (1994). In our model with obstructed perception, individuals at the border of a school are more likely to interact with individuals in a neighbouring school (Fig. 9) than if interaction is topological or metric with a short interaction range (Hemelrijk and Hildenbrandt, 2008). How such differences in choosing interaction partners influence the formation and maintenance of groups of different sizes, we will investigate in future models.

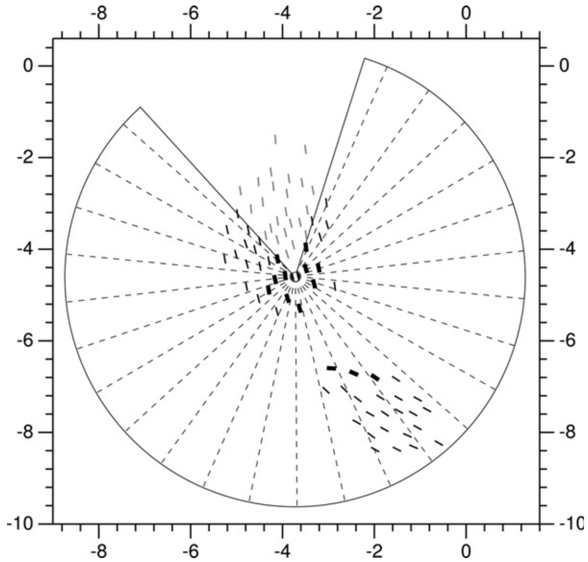

Fig. 9. Illustration of the interaction partners (fat black bars) of an individual (white bar) with obstructed perception. As it is close to the border it interacts with distant individuals that are part of another group.

Results of our model resemble the following empirical data: In small schools of up to 60 individuals of various species (mullets, minnows, herring, saithe, cod, three-spined sticklebacks and rudd) density increases with group size (Hemelrijk et al., 2010; Partridge, 1980; Partridge et al., 1980; Keenleyside, 1955). For schools up to 2.2 million individuals (herring, sprat and saithe) the average inter-individual distance varies greatly within and between schools (up to a factor of 100) but does not seem related to school size (Misund, 1993); dense areas and regions of almost empty space are found frequently in schools of a few hundred juvenile roach and perch (Guillard et al., 2006) and in schools of many thousands of sardines (Freon et al., 1992; Gerlotto and Paramo, 2003). Similarly, in starling flocks ranging between 500 and 2500 individuals average density varies considerably across flocks (by a factor of 3) but is not associated with the number of birds; regions of high density may occur at any location, also at the border of the group (Ballerini et al., 2008).

School shape is found to be oblong for small schools of up to 30 herring, saithe and cod (Partridge et al., 1980), 60 mullets (Hemelrijk et al., 2010), a few hundred juvenile roach and perch (Bumann et al., 1997; Guillard et al., 2006), a few hundreds of roach and several thousands of minnow (Pitcher, 1980) and many thousands of herring (Axelsen et al., 2001) and sardines (Gerlotto and Paramo, 2003). Furthermore, group shape becomes increasingly irregular for schools of many thousands of herring (Axelsen et al., 2001), sardines (Gerlotto and Paramo, 2003) and anchovy (Squire, 1978) and also changes dramatically over time for herring (Pitcher et al., 1996) and anchovy (Squire, 1978).

Our model of obstructed perception is, to our knowledge, the first one that can explain the characteristics found in large schools of fish, such as the occurrence of complex and changing school shape and the high variability of the inter-individual distances. Remarkably, despite the disturbances generated by the shape-changes, schools in the model still do not split up.

Note that our model is conceptual. It has not been tuned to match a specific species. Its comparison to empirical data was qualitative only. Furthermore, for the sake of simplicity our model is two-dimensional. Extension of our model to three dimensions would make individuals interact with a greater number of neighbours. Since our results of different numbers of sectors (and thus interacting neighbours) are qualitatively similar, we expect results of a 3-dimensional model to resemble those of a 2-dimensional one.

For future research it is of interest to analyse the resemblance of our model to empirical data quantitatively, especially for large schools of more than 200 individuals because for such large groups the influence of obstruction of perception is strong. For example, it could be studied, whether the dynamics of shape and the spatial distribution of individuals resemble those found in nature (e.g. Misund, 1993) or if our model is capable to explain the number and size of vacuoles found in schools of real fish (e.g. Gerlotto and Paramo, 2003).

In conclusion, by confining the interaction only to those neighbours that can be perceived, instead of including all neighbours within the interaction radius, the model generates patterns of schooling that are more realistic particularly for large schools. As to the question whether in large groups special coping mechanisms are needed (the topic of this issue), we conclude that in models of self-organized schools, it suffices that perception is obstructed in order to generate patterns that characterize those of very large groups.

Conflict of interest

None.

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