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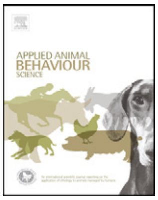

Simulations of the social organization of large schools of fish whose perception is obstructed

Hanspeter Kunz[a], Charlotte K. Hemelrijk[b,*]

[a] *Artificial Intelligence Laboratory, Department of Informatics, University of Zurich, Binzmühlestrasse 14, CH-8050 Zurich, Switzerland*
[b] *Theoretical Biology, Behavioural Ecology and Self-organisation, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

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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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[*] Corresponding author. Tel.: +31 50 3638084; fax: +31 50 3633400.
E-mail address: c.k.hemelrijk@rug.nl (C.K. Hemelrijk).

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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