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Abstract: In fish schools the density varies per location and often individuals are sorted according to familiarity and/or body size. Highdensity is considered advantageous for protection against predators and this sorting is believed to be advantageous not only toavoid predators but also for finding food. In this paper, we list a number of mechanisms and we study, with the help of anindividual-based model of schooling agents, which spatial patterns may result from them. In our model, schooling is regulated bythe following rules: avoiding those that are close by, aligning to those at intermediate distances, and moving towards othersfurther off. Regarding kinship/familiarity, we study patterns that come about when agents actively choose to be close to relatedagents (i.e., 'active sorting'). Regarding body size, we study what happens when agents merely differ in size but behave accordingto the usual schooling rules ('size difference model'), when agents choose to be close to those of similar size, and when smallagents avoid larger ones ('risk avoidance'). Several spatial configurations result: during 'active sorting' familiar agents grouptogether anywhere in the shoal, but agents of different size group concentrically, whereby the small agents occupy the center andthe large ones the periphery ('size difference model' and 'active sorting'). If small agents avoid the risk of being close to largeones, however, small agents end up at the periphery and large ones occupy the center ('risk avoidance'). Spatial configurationsare also influenced by the composition of the group, namely the percentage of agents of each type. Furthermore, schools areusually oblong and their density is always greatest near the front. We explain the way in which these patterns emerge and indicatehow results of our model may guide the study of spatial patterns in real animals.

Density distribution and size sorting in fish schools: an individual-based model

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In fish schools the density varies per location and often individuals are sorted according to familiarity and/or body size. High density is considered advantageous for protection against predators and this sorting is believed to be advantageous not only to avoid predators but also for finding food. In this paper, we list a number of mechanisms and we study, with the help of an individual-based model of schooling agents, which spatial patterns may result from them. In our model, schooling is regulated by the following rules: avoiding those that are close by, aligning to those at intermediate distances, and moving towards others further off. Regarding kinship/familiarity, we study patterns that come about when agents actively choose to be close to related agents (i.e., 'active sorting'). Regarding body size, we study what happens when agents merely differ in size but behave according to the usual schooling rules ('size difference model'), when agents choose to be close to those of similar size, and when small agents avoid larger ones ('risk avoidance'). Several spatial configurations result: during 'active sorting' familiar agents group together anywhere in the shoal, but agents of different size group concentrically, whereby the small agents occupy the center and the large ones the periphery ('size difference model' and 'active sorting'). If small agents avoid the risk of being close to large ones, however, small agents end up at the periphery and large ones occupy the center ('risk avoidance'). Spatial configurations are also influenced by the composition of the group, namely the percentage of agents of each type. Furthermore, schools are usually oblong and their density is always greatest near the front. We explain the way in which these patterns emerge and indicate how results of our model may guide the study of spatial patterns in real animals. *Key words:* assortment, density distribution, fish, self-organization, school form, spatial structure. *[Behav Ecol]*

In natural shoals of fish, the highest density is often at the front (Bumann et al., 1997) and schools are usually oblong (Pitcher, 1980). This is attributed to the tendency to seek protection against predators, as the front is regarded as the most dangerous part (Bumann et al., 1997). Furthermore, it appears that individuals are assorted by familiarity (e.g., Barber and Ruxton, 2000; Griffiths and Magurran, 1999) and body size (Hoare et al., 2000; Krause et al., 1996, 2000; Peukhuri et al., 1997; Svensson et al., 2000). Segregation by familiarity is thought to be beneficial because of cooperation against predators (Trivers, 1971) because it allows cohesion (Chivers et al., 1995), and it is also supposed to have foraging advantages. Segregation by size may be beneficial for two reasons: it may facilitate coordination of movement (Theodorakis, 1989), and it can have hydrodynamic advantages (Pitcher et al., 1985). Because fish of the same size are under the same selection pressure (Pitcher et al., 1986) and have the same needs, they may synchronize their behavior; and by clustering together they may reduce their visual conspicuousness, via reduction of the so-called 'oddity effect' (Landeau and Terborgh, 1986; Ranta et al., 1994).

Small individuals are either found at the periphery of the school (Krause, 1993a; Theodorakis, 1989) or in the center (Romey, 1997). There are descriptions of water insects in which small individuals remain in the center (Sih, 1980) and of fish in which they are at the periphery (Krause, 1993a). This may be related to different predator tactics; in insects predators often enter the swarm (Sivinski and Petersson, 1997), but in fish this is rare (Krause, 1994a).

Here, we do not want to give a functional explanation in terms of what is best for the fitness of different categories of individuals, but we try to connect a number of behavioral rules and body characteristics on the one hand to spatial patterns at a group level (i.e., 'macropatterns') on the other. This we do by means of an individual-oriented model of agents that school (called SchoolingWorld). We start from specific body characteristics and rules of behavior and are guided by the patterns that the model itself generates. We use the emergence of these patterns as hypotheses that may be investigated in real fish schools. This is a useful method, because complex patterns of behavior at a group level are more easily understood from the 'bottom up' than from the 'top down' (Braitenberg, 1984; Hemelrijk, 1996; Pfeifer and Scheier, 1999).

METHODS

Introduction to the model

Let us discuss mechanisms that may underlie spatial assortment by familiarity and size.

An 'active' preference to shoal with familiar individuals or with fish similar in size has been demonstrated in experiments several times: a single fish in a central compartment had the choice to swim close to a compartment containing fish of a similar or a different body size (Krause, 1994b; Krause and Godin, 1994; Ranta et al., 1992a, 1992b; Ward and Krause, 2001) and also close to a compartment with fish of different degrees of familiarity (e.g., see Griffiths and Magurran, 1999).

Furthermore, size assortment may be caused by differences in the swimming speed of fish of different sizes. Pitcher and Parrish (1993), however, say that this leads to complete separation of groups by size and, therefore, that it cannot explain size segregation in shoals. On the other hand, Couzin and Krause (2003) have shown in a model that individual

Table 1

Parameters of the agents

Parameter	Symbol and value
Time step	$\Delta t = 0.2$ s
Speed (average and SD)	$v_{avg} = 0.3$ m/s, $v_{sd} = 0.03$ m/s
SD of the heading	$\alpha_{sd} = \frac{\pi}{72}$ rad $\cong 2.5°$
Turning rate, 'default'	$\omega^{def} = \frac{1}{2}\pi$ rad/s
Blind field in the back	$\gamma = 60°$
Blind field for aligning region (front)	$\gamma' = 60°$
Line length	small: $b = 0.1$ m
	large: $b = 0.2$ m
Scaling factor of repulsion (Equation 8)	small: $a_r = 1.0$
	large: $a_r = 2.0$
Scaling factor of attraction (Equation 9)	$a_a = 1.0$
Scaling factor of aligning (Equation 10)	$a_p = 1.0$
Ranges of repulsion (Equation 8)	small: $r_r = 0.3$ m
	large: $r_r = 0.6$ m
Ranges of aligning (Equation 10)	small: $r_p = 1.0$ m
	large: $r_p = 2.0$ m
Range of attraction	$r_a = 5.0$ m
Eccentricity	small: $e = 2.0$
	large: $e = 4.0$
'Active sorting'	$c_r = 2$, $c_a = 2$, $c_p = 2$
'Risk avoidance'	$c_{riskAvoid} = 20$ (varied from $0-40$)

differences in swimming speed may lead to segregation of individuals in the same school, if the agents adjust their speed to that of their neighbors. In this paper, we study other mechanisms that may lead to segregation by size.

Size assortment in schools may also be the result of aggression as described for sardines, *Engraulis japonicus* (Kimura, 1934), the Atlantic herring (Schäfer, 1955), and cod (Brawn, 1961). This may reflect competition for food or for mates. The effect of competition on spatial structure has been illustrated by Hemelrijk (2000) in a model called DomWorld. She shows that among artificial agents that group and compete in a virtual world, both a dominance hierarchy and a spatial structure develop. In this spatial structure agents are assorted by dominance rank with high-ranking agents in the center and low-ranking ones at the periphery. Because social dominance is often associated with a larger size (Myrberg, 1972; Thines and Heuts, 1968), competition may also lead to assortment by size. We study this as a form of 'risk avoidance,' meaning that small agents avoid large ones in order to avoid aggression from large ones, as described by Pitcher et al. (1986).

As a 'control' we investigate what happens if agents differ merely in size (without size-related rules of active assortment and without rules of risk avoidance).

To understand the patterns of segregation to which these conditions lead, we extend our earlier model SchoolingWorld (Kunz and Hemelrijk, 2003) with characteristics of the agents (namely size and familiarity) and with behavioral rules for sorting and competition. This kind of model is useful because studies of complexity science have repeatedly shown that it is impossible to predict the consequences of individual behavioral rules at a group level without them (Camazine et al., 2001; Hemelrijk, 2002).

Our model SchoolingWorld has produced emergent (group-level) patterns that resemble those of schools of real fish (Kunz and Hemelrijk, 2003). It is inspired by models of Huth and Wissel (1992, 1994), Reuter and Breckling (1994), and Niwa (1994). In these models, schooling is a consequence

of the tendency to avoid other fish that are close by, to align to those at intermediate distances, and to move towards others that are further off (but within the range of vision).

In the models designed by others, agents are represented as points with their sensory regions as concentric circles around them (here indicated as 'point-agents'). In SchoolingWorld, we use a representation that is more realistic in two respects. First, the body is reflected as a line segment. Second, the sensory regions of repulsion and aligning are represented as ellipses (called 'elliptic-agents,' see Kunz and Hemelrijk, 2003), because they are situated (besides in the visual system) in the 'lateral line system' in real fish (Partridge and Pitcher, 1980). The lateral line consists of a series of hydrodynamic sensors along both sides of the body (Bleckman, 1993) that detect stimuli (e.g., changes in water pressure) close by. Therefore, ellipses reflect the operational area of the lateral line system more accurately than circles. We keep the region of attraction circular, however, because it is determined by vision (Partridge and Pitcher, 1980).

To represent familiarity, we divide agents into two classes, familiar and unfamiliar. Whether individuals distinguish between these categories on the basis of smell or of visual appearance does not matter for the model. To represent two different body sizes (large and small), we vary the length of the line segment and the size of the sensory regions of repulsion and aligning. For 'active sorting by size/familiarity' we increase the attraction and aligning tendency of the agents and diminish their tendency to avoid others of similar size/ familiarity compared to those of different size/familiarity. Note that 'active sorting by familiarity' is studied among agents of the same size. 'Risk avoidance' is implemented by supplying small agents with a strong tendency to avoid large agents. We compare collective patterns to those that result only from the effects of the difference in size (the 'size difference' model). Thus, any pattern that arises in the 'size difference' model emerges exclusively from body characteristics, whereas in the model of 'risk assortment by size' and 'active avoidance' patterns emerge from the combined effects of size and the additional behavioral rules.

We characterize collective patterns by the spatial variation in density and by the spatial distribution of the two classes of agents (size/familiarity), by their degree of segregation, by the surface, and by the form of the school as a whole.

The model

SchoolingWorld is implemented in the programming language C. In addition, Octave, a high-level language intended for numerical (matrix) computations (see www.octave.com), was used for data post-processing and Gnuplot, a command-driven interactive function-plotting program (see www.cs. uni.edu/Help/gnuplot), to generate various types of graphs.

Fish schools have been modeled in 2-D as well as in 3-D. Comparing a particular 2-D model (Huth and Wissel, 1992) to a 3-D one (Huth and Wissel, 1994), no additional phenomena are visible in the 3D-model. Therefore, we decided to implement our model, SchoolingWorld, in 2-D. The modeled artificial world is continuous and homogeneous. Time proceeds in discrete steps Δt. At each time step all agents are activated in random order.

Position, speed, and heading

At the beginning of the simulation, a certain number of agents are put randomly in a starting area of 2.5×2.5 m and are given a random orientation, which was chosen between 0 and 90 degrees in order to obtain a single school. The initial
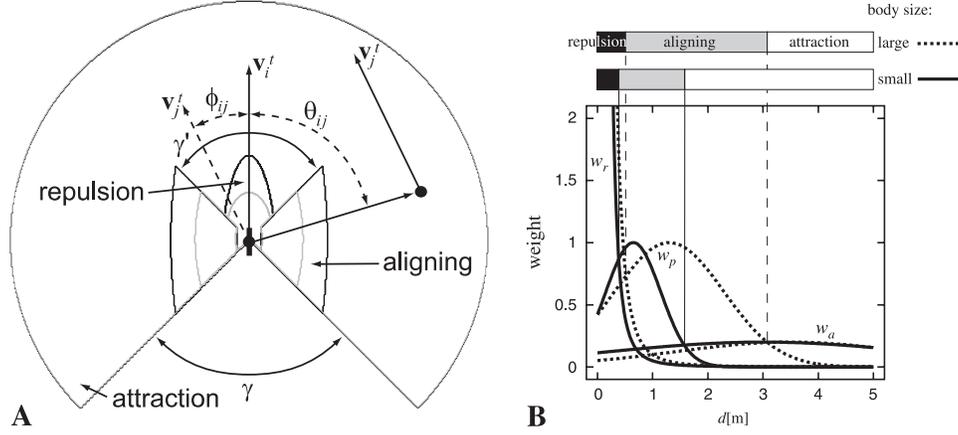
Figure 1
(A) The sensory regions of an agent. The agent is located at the center. The outermost circle represents the visual range, r_a. It contains three functional areas: of attraction, of aligning, and of repulsion (grey: regions of attraction and repulsion of small agents, black: the same of large ones). (B) Weight factors of repulsion, $w_r(d)$, attraction, $w_a(d)$, and aligning, $w_p(d)$, for small agents (solid lines) and large ones (dotted lines). d denotes the distance to the neighbor. Regions are classified into repulsion, aligning, and attraction by the largest of the three weight factors (top of figure). For further information, see text.

speed of the agents was set to v_{avg} (see Table 1). At time t agent i is located at position $\mathbf{x}_i^t$ and moves with a velocity $\mathbf{v}_i^t$ (speed and direction) during one simulation step Δt.

$$\mathbf{x}_i^t = \mathbf{x}_i^{t-\Delta t} + \mathbf{v}_i^t \, \Delta t \tag{1}$$

Similar to models by others (Aoki, 1982; Couzin et al., 2002; Huth and Wissel, 1992, 1994), the speed of agents v_i^t does not depend on that of other agents but is an independent stochastic variable. It is drawn from a Gaussian probability distribution $P(v_{avg}, v_{sd})$ at each time step.

The agent's heading direction, α_i^t, is updated every simulation step as follows:

$$\alpha_i^t = P(\underbrace{\alpha_i^{t-\Delta t} + \omega_i^t \, \Delta t}_{\alpha_{i,avg}^t}, \alpha_{sd}) \tag{2}$$

whereby $\alpha_i^{t-\Delta t}$ is the agent's heading in the previous time step and ω_i^t its rate of turning or rotation (which depends on other agents, see next section). α_i^t is drawn from a Gaussian distribution with a variable mean, $\alpha_{i,avg}^t$, and fixed SD, α_{sd}. The heading, α_i^t, and the speed, v_i^t, constitute the velocity

$$\mathbf{v}_i^t = \begin{pmatrix} v_i^t \cos \alpha_i^t \\ v_i^t \sin \alpha_i^t \end{pmatrix} \tag{3}$$

Repulsion, attraction, and aligning

The artificial fish have three behavioral responses: repulsion (between agents at short distances), aligning (at intermediate distances), and attraction (at greater distances) (Breeder, 1954; Huth and Wissel, 1992, 1994; Warburton and Lazarus, 1991).

Repulsion in nature is presumably determined by both the sensors of the lateral line and the visual system, and, therefore, we implement it as if it operates in an area immediately surrounding the agent, except for a 'blind area' at its back (Figure 1A). For aligning, the lateral line is most effective. Because it operates mainly at the sides, there are two 'blind areas' for aligning, one at the back and one at the front. Because attraction is determined by vision, there is only one 'blind area,' at the back.

During repulsion an agent i turns away from a nearby agent j with rate of rotation (i.e., speed of turning)

$$\omega_r = \begin{cases} -\omega^{def} & \text{if } \theta_{ij}^t > 0, \\ +\omega^{def} & \text{otherwise} \end{cases}, \tag{4}$$

where $\theta_{ij}^t = \angle(\mathbf{x}_j^t - \mathbf{x}_i^t, \mathbf{v}_i^t)$ (see Figure 1B) and ω^{def} is the 'standard' rate of rotation of the agents (see Table 1). Attraction implies that an agent i turns towards an agent j with a rate of rotation

$$\omega_a = \omega^{def} \theta_{ij}^t. \tag{5}$$

Note that, in contrast to repulsion, rate of turning ω_a caused by attraction is proportional to θ_{ij}^t. Aligning implies that agent i matches its orientation to that of agent j by turning with rate of rotation

$$\omega_p = \omega^{def} \phi_{ij}^t \tag{6}$$

where $\phi_{ij}^t = \angle(\mathbf{v}_j^t, \mathbf{v}_i^t)$ is the difference in the heading direction of the two agents (see Figure 1B). The actual behavioral reaction depends on the weights of repulsion (w_r), attraction (w_a), and aligning (w_p). These weights depend on the distance to the other agent (as in Reuter and Breckling, 1994), as follows:

$$d_{ij}^t = \|\mathbf{x}_j^t - \mathbf{x}_i^t\| \tag{7}$$

$$w_r(d) = \min\left(\frac{0.05 a_r}{d^3}, 10\right) \tag{8}$$

$$w_a(d) = 0.2 \, a_a e^{-\left(\frac{d - \frac{1}{2}(r_a + r_p)}{r_a - r_p}\right)^2} \tag{9}$$

$$w_p(d) = a_p e^{-\left(\frac{d - \frac{1}{2}(r_p + r_r)}{r_p - r_r}\right)^2} \tag{10}$$

The behavioral reaction is calculated as the weighed sum,

$$\omega_{ij}^t = w_r(d_{ij}^t)\omega_r + w_a(d_{ij}^t)\omega_a + w_p(d_{ij}^t)\omega_p \tag{11}$$

The dependence of the weight factors on the distance to the interaction partner makes behavioral transitions continuous instead of discrete. Nevertheless, for convenience, we name
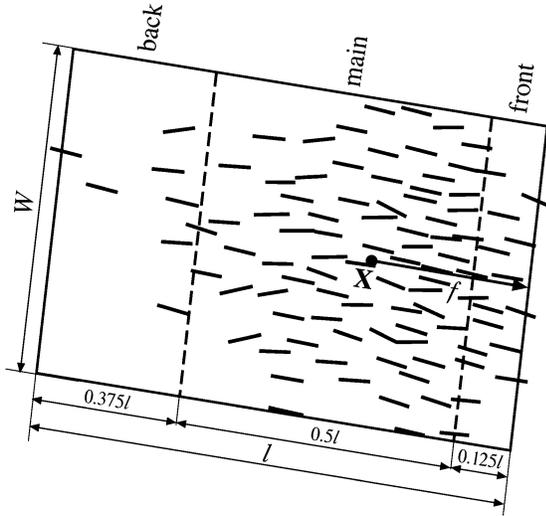
Figure 2
The method for obtaining measures of group width (w), length (l), and distance to front (f). The snapshot is randomly chosen and indicates the positions and orientations of agents in different parts of the school (front, main, and back).

the three behavioral regions (Figure 1) after the weight factor with the largest value.

When agent i perceives more than one agent j, its behavioral response (turning rate) is calculated as the average of its response to each neighbor separately.

Body representation

We represent both the size and the form of the agent's body in so-called 'elliptic' agents (Figure 1A); the body is represented by a line segment (with variable length, b, Table 1), and regions of repulsion and of aligning are elliptic, reflecting the operational area of the lateral line system (Healy and Prieston, 1973), whereas that of attraction is circular, reflecting the range of vision (for construction details see Kunz and Hemelrijk, 2003).

We represent the agent's size (large or small) by the length of the line b and by the size of the regions of repulsion and aligning (the size of the region of attraction is kept independent of body size because it reflects the area of vision). In line with the findings by Olst and Hunter (1970) that inter-individual distance increases with body size, but less so than proportionally to body length, we increase the size of the repulsion and aligning regions accordingly (by scaling a_r, r_r, and r_p; Figure 1, Table 1, Equations 8–10). Furthermore, because the increase in length of larger fish is greater than its increase in width, we made the asymmetry of the elliptic regions of large agents greater than that of small ones (see 'eccentricity,' e, Table 1). Note that by using a line (instead of a point) to represent the agent's body, it occupies space and others often perceive it as being slightly closer than if it is represented as a point (Kunz and Hemelrijk, 2003).

'Active sorting' and 'risk avoidance'

In the case of 'active sorting' we lower the tendency to avoid agents of similar size (or familiar agents) and increase the tendency to avoid others of different size (or that are unfamiliar), by dividing/multiplying the scaling factor of repulsion, a_r, by a constant, c_r (see Table 1). In addition, the strength of aligning and attraction among fish of the same size (or that are familiar) is increased, whereas it is reduced

among individuals of different size (or that are unfamiliar). We implemented this by multiplying/dividing the scaling factor of aligning, a_p, by a constant, c_p, and that of attraction, a_a, by a constant, c_a.

'Risk avoidance' is asymmetric. The tendency of small agents to avoid large ones is increased, but the tendency of large ones to avoid small ones is not changed. This is realized by the scaling factor of repulsion, a_r. During an encounter of a small fish with a large one, it is multiplied by a constant, $c_{riskAvoid}$. This can be interpreted as the avoidance of a potential danger by small fish.

Data and measures

We study each model (familiarity assortment, size difference, risk avoidance, and active assortment) for different percentages of each type (small and large) of agent (0%, 25%, 50%, 100%). Groups always consisted of 100 agents. We performed 25 runs for each combination.

For each simulation step the following statistics are calculated. As an indication of the expanse of the group (compare 'expanse' by Huth and Wissel, 1992), we use the average distance of all agents to the center of the school, c^t:

$$c^t = \frac{1}{N} \sum_i \|\mathbf{X}^t - \mathbf{x}_i^t\|, \quad \mathbf{X}^t = \frac{1}{N} \sum_i \mathbf{x}_i^t$$

where $\mathbf{X}^t$ denotes the center of the school (center of gravity, calculated as the average x- and y-values over all agents). N indicates the number of agents.

The so-called 'normalized center distance of large agents' characterizes the spatial configuration of small and large agents in the school. It is the average distance of the large agents to the center of gravity, c_l, divided by the average distance of all agents to the center of gravity, c^t:

$$c_l^t = \frac{1}{c^t} \frac{1}{N_l} \sum_i \|\mathbf{X}^t - \mathbf{x}_i^t\|$$

N_l denotes the number of large agents. If c_l^t is greater than one, large agents are more likely to be found at the periphery, whereas if it is less than one, they tend to occupy more central positions.

To quantify the coordination of the heading directions of the agents, we measure the deviation of each agent's orientation to the average heading, α_{avg}^t, of the group. This is usually referred to as 'polarization,' p^t (Huth and Wissel, 1992), but we call it 'confusion,' because higher values indicate greater disorder (Kunz and Hemelrijk, 2003). It is calculated as the square root of the mean quadratic deviation angle:

$$p^t = \sqrt{\frac{1}{N} \sum_i (\alpha_{avg}^t - \alpha_i^t)^2}, \quad \alpha_{avg}^t = \frac{1}{N} \sum_i \alpha_{ij}^t$$

To quantify the form of the school, we enclose the complete school by the smallest rectangle oriented parallel to the direction of movement of the group (Figure 2) and we calculate the degree to which a group is oblong, by dividing group width (orthogonal to the swimming direction) by group length (the longest group size in the direction of swimming).

To indicate the degree of centrality of the position of the center of gravity, $\mathbf{X}^t$, we divide the distance of the center of gravity to the front by the total length of the group.

To detect variation in turning rate depending on location, we calculate the average agent turning rate (i.e., the absolute rate of change of the agent's heading direction) in the front, main, and back section of the group separately (Figure 2).
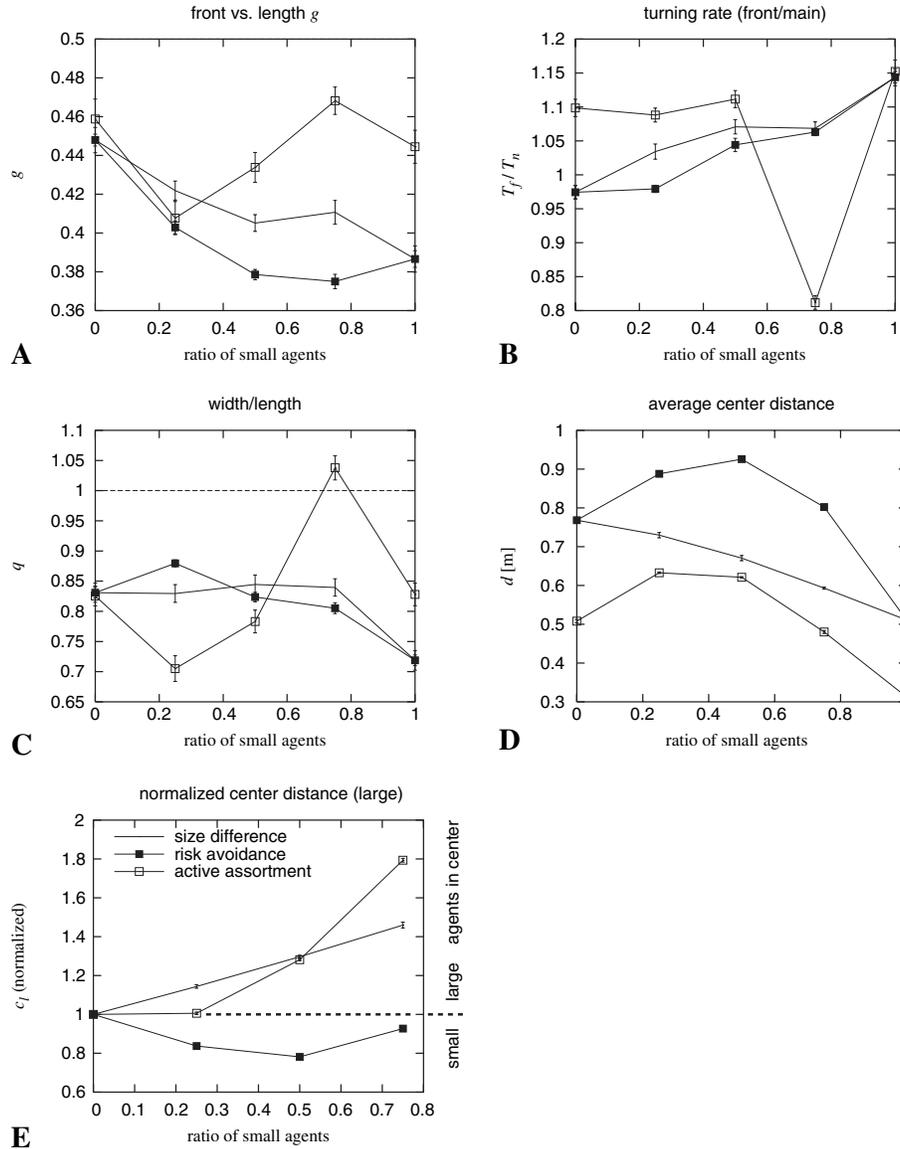
Figure 3
Averages and SE of various measurements for models of 'body size', 'active assessment', and 'risk avoidance' and for different percentages of small agents. (A) Location of the center of gravity. (B) Turning rate among agents at the front divided by that among agents in the middle of the school. (C) Degree to which groups are oblong. (D) Average distance to center. (E) Normalized average center distance of large agents.

Group speed v_g^t is measured as the speed of the center of gravity, X^t, of the group.

Per run these measures were averaged over time steps 2000–3000 (omitting the transitory period). Averages and their SEs over 25 runs are plotted in Figures 3 and 4. We discuss only results that are clearly significant, which can be judged from the large differences between the average values and the small sizes of the SEs. Furthermore, we confine ourselves to runs in which agents aggregate in a single school (as happened in 98.9% of the runs) that is polarized and coordinated (Shaw, 1970), because in real fish size assortment is mainly found in such schools (Krause, 1994b; Krause and Tegeder, 1994).

RESULTS

Density and form of schools

For all behavioral mechanisms and group compositions, the density of the agents is higher at the frontal part of the school.

This is measured by the relative position of the center of the school (i.e., distance of the center of gravity to the front divided by the total length of the school is smaller than 0.5; see Figure 3A). This is due to several causes: at the very front individuals align and are attracted to neighbors at their sides only (there are no or only few neighbors ahead). Consequently, the turning rate of agents is higher at the front than in the main part of the school (Figure 3B). This slows down the forward movement of frontal agents (as they zigzag instead of moving straight) and a 'jam' develops near the front.

The form of the school is usually oblong (group width divided by length being smaller than one; see Figure 3C), because individuals approach each other from the side only (by turning towards each other) and not from the back (because they cannot speed up). An exception is that during 'active sorting' in a school with many small agents (75%), the group is slightly wider than long (Figure 3C). This is caused by
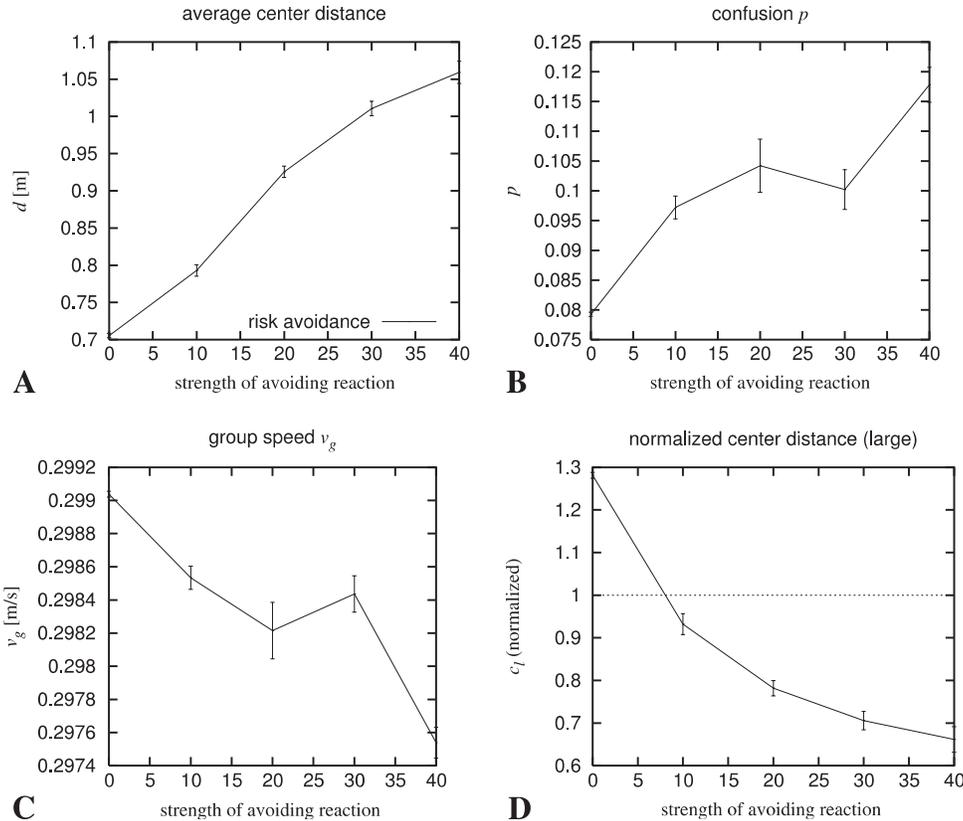
Figure 4
Degree of 'risk avoidance' of (A) group surface, (B) confusion, (C) velocity of the group, and (D) (normalized) center distance of large agents (average and SE). Groups contain an equal number of small and large agents.

the clustering of a subgroup of large agents at each side of the school (Figure 5IIIC).

Groups are most compact (as measured by the average distance of all agents to the center) during 'active size assortment' and least compact during 'risk avoidance' (Figure 3D). This is because 'risk avoidance' causes small agents to maintain a larger distance to large ones and, therefore, the group spreads out. Increasing 'risk avoidance' (from $c_{riskAvoid}$ equals 0 to 40) enlarges the surface or expanse of the group (measured by the average center distance), decreases its coordination (increases confusion), and, therefore, slows it down because of more frequent zigzag movements (Figure 4A, B, and C, respectively).

Segregation by familiarity and by size

Assortment according to familiarity among agents of the same size leads to subgroups of familiar agents that may occur at any location in the group (Figure 5I). Segregation is clearer if one class of agents is in the minority (25%). This arises because cluster formation by attraction among only a few agents tends to lead to a single cluster only. More agents (50%) can form several clusters (Figure 5IB).

Assortment according to size is, in contrast to assortment according to familiarity, a concentric configuration. In the models of 'active sorting' and 'size differences' large agents occupy the periphery and small ones the center (Figure 5II,III), and this pattern is reversed in that of 'risk avoidance' (Figure 5IV and 5V).

Remarkably, also in the model of 'size difference' that lacks a preference for similar agents, spatial assortment is found. This is a consequence of the difference in size between agents,

which drives large agents to the periphery, because their larger repulsion regions cause them to avoid small ones at a greater distance than vice versa (Figure 5II).

In contrast to 'active assortment by familiarity,' 'active assortment by size' leads to a concentric spatial configuration of agents of both sizes. This arises from the additional effect of size difference. Note that during 'active assortment by size' the segregation is stronger than in the 'size difference' only model, because it is supported by a preference to keep agents of similar size in close proximity (compare Figure 5III and II).

'Risk avoidance,' in contrast, counteracts the effects of 'size difference,' because by strongly avoiding large agents, small agents avoid large neighbors earlier than vice versa, and consequently the small ones are driven to the periphery. Thus, the spatial configuration may reverse (Figure 5IV). Obviously, whether or not this spatial reversal actually occurs during 'risk avoidance' depends on the relative strength of risk avoidance (represented by $c_{riskAvoid}$). The stronger it is, the clearer the reversed spatial configuration with small agents at the periphery and large ones in the center becomes (Figure 5V). The center distance of large agents thus becomes increasingly smaller than one while increasing 'risk avoidance' ($c_{riskAvoid}$ from 0 to 40; see Figure 4A). Lower values (less than one) indicate that large agents are closer to the center and small ones to the periphery (as shown for the highest degree of risk avoidance [$c_{riskAvoid} = 40$] in Figure 5V for different group compositions). Due to the small body size, and thus closer proximity of small agents, more than 50% of small agents are needed to surround the large ones completely (Figure 5V).

There are two deviations from these spatial patterns. When large agents are at the periphery, they sometimes are lacking
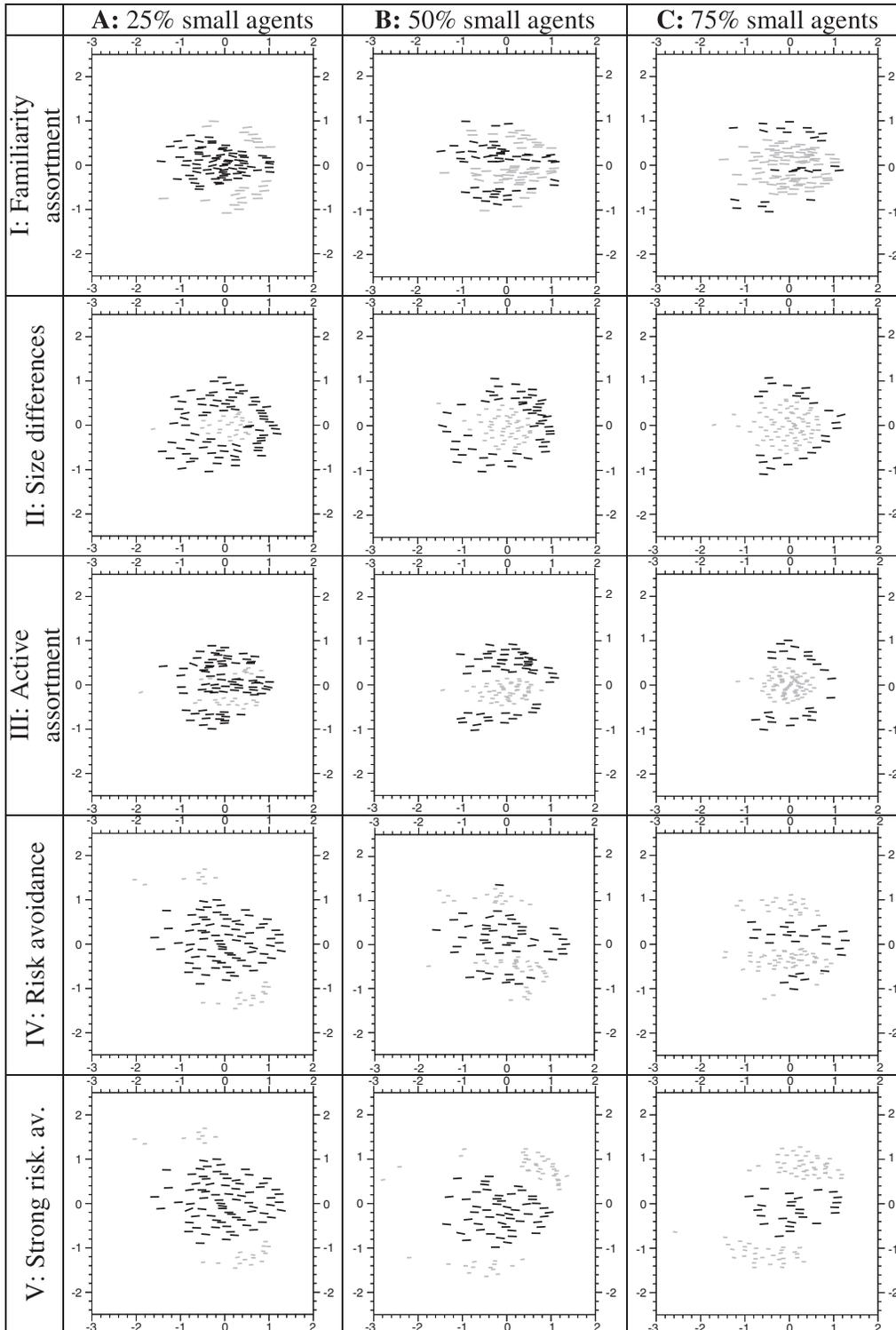
Figure 5
End configuration of single runs (randomly chosen) of different models with different percentages of small agents. Light grey: small agents, dark: large agents. (V) Strength of risk avoidance is doubled (40). For further explanation see text.

at the back (Figure 5IIC,IIIB,IIIC) and when small agents are on the outside (during 'risk avoidance'), segregation is weak (Figure 5IVB,IVC).

Large agents are lacking at the back because they move to the side to avoid having small ones directly ahead of them. In the 'size differences' model, this happens mainly when the number of large agents is small (Figure 5IIC), but during 'active sorting' it also takes place when large agents and small ones are equal in number (Figure 5IIIB,IIIC), because large agents are attracted by other large ones to the periphery, in addition to just avoiding small ones ahead of them.

Furthermore, segregation is weak if the percentage of agents that have a more extensive tendency to avoid others is large. Thus, during 'active sorting,' if large agents are numerous (and small agents are few, 25%), they will form several clusters, because they easily find each other. These clusters are stable because large agents that are at their borders avoid small ones and thus move back into the cluster. Thus, these clusters remain stuck among small agents, preventing further segregation (i.e., joining of clusters).

Thus, during 'risk avoidance' segregation is weak for medium and high percentages of small agents due to similar cluster formation because small agents get stuck among large ones (Figure 5IVB,IVC). In contrast, when the percentage of small agents is low, they have little opportunity to cluster together (because they seldom meet each other) and thus are driven to the periphery (Figure 5IVA).

The typical spatial configurations, with large agents at the periphery (in the cases of 'size difference' and 'active sorting') and small agents at the periphery (in the case of 'risk avoidance'), differ significantly from each other, as can be seen from the (normalized) center distance, c_l, of large agents shown in Figure 3E. Note that values less than one indicate that large agents are in the center, and those greater than one indicate that large agents are at the periphery.

In the cases of 'size difference' and 'active sorting,' where the small agents occupy the center, the average center distance of large agents increases with the percentage of small ones: a larger number of small agents naturally take up a larger area. Thus, the large agents, which are located peripherally, are further from the center (see Figure 3E). Note that during 'active sorting' at a low percentage of 25% small agents, the average normalized center distance of large agents, c_l, equals approximately one, and thus small agents are not clearly in the center because they get stuck among large ones as mentioned above (see Figure 5IIIA).

Conversely, in the case of 'risk avoidance,' where the large agents are found in the center, a small number of large agents occupies a smaller surface, and this decreases the average distance to the center of larger agents, c_l. At 25% large agents (75% of small ones), there is an increase in the center distance of large agents despite their low number, because clusters of small agents, as mentioned above, may be caught in-between large agents and thus may stay in the center (see Figure 5IVC).

DISCUSSION

SchoolingWorld generates a wide range of spatial patterns. For instance, the center of the school (center of gravity) is located in the front half of the school and schools are oblong; sorting according to familiarity causes familiar agents to cluster at any place in the group; agents of different size sort themselves concentrically, with large agents in the center and small ones at the periphery or vice versa.

Density and form of schools

In the model, the density in the school is highest near the front: the center of gravity is always located in the front half. This arises by self-organization as follows.

Because agents at the front see no group members ahead of them, they are attracted only by those at either side. Therefore, their movement direction varies continuously (their turning rate is high), which causes them to slow their forward movement. Note that even though we provide agents with a fixed velocity (with random 'noise,' as is the case in the other models, Aoki, 1982; Couzin et al., 2002; Huth and Wissel, 1992, 1994), the front agents still appear to be 'slowing down' because of their zigzag movement. This leads to a 'jam' near the front.

Schools are usually oblong. In an earlier model (Kunz and Hemelrijk, 2003) we found that this oblong form also occurs in schools of agents of one size and that it becomes more marked with a higher number of agents. This arises in the model from the combination of aligning behavior and the overall attraction of the agents to the center of the group. This attraction causes the agents to turn towards the center and consequently reduces the width of the group. Because the agents move forward at a 'constant' speed, the ones that lag behind cannot accelerate, and therefore the length of the group remains constant.

Remarkably, a similar slowing-down and 'jamming' has been found by Deneubourg et al. (1989) in a model that closely resembles the swarming behavior of army ants. Exactly the same characteristics (of frontal density and oblong groups) have also been found in shoals of roach (*Rutilus rutilus*) by Bumann et al. (1997).

Using models for minimization of predation and corresponding experimental procedures on creek chub (*Semotilus actromaculatus*), these authors conclude that both traits are beneficial to minimize predation risk. Bumann et al. (1997), however, do not provide a theory to explain how fish come to form such characteristic schools. SchoolingWorld does suggest an explanation: an oblong group-shape with the highest density at the front automatically results from the behavioral rules of repulsion, aligning, and attraction. It is of interest to verify the origin of the high density at the front in schools of real fish by analyzing whether the turning rate is higher at the front than in the main part of the school.

Spatial segregation by familiarity and size

Segregation by familiarity (in the absence of size differences) is clearer if one class of agents is in the minority. This arises because in this case there are fewer agents to be attracted to and, therefore, clusters become fewer, but larger. A similar result has been found by Schelling (1971) in his model of racial segregation, in which two types of agents require at least a minimum percentage of agents of the same type close by, otherwise they leave the subgroup. Stronger clustering of individuals whose type is in the minority is adaptive in nature, because fish of the minority type run a higher risk of predation, as Theodorakis (1989) has shown in his experiments in which odd-sized fish were eaten more often by large mouth brass, *Micropterus salmonides*. SchoolingWorld and Schelling's (1971) model show that such stronger clustering may arise as an emergent phenomenon.

In the 'size difference' model (in which agents merely differ in body size), size sorting is spatial and emerges purely from the larger repulsion region of large agents. This provides us with yet another reason why large agents may be at the outside of the group: their large size.

Our results are supported by those of related models used by Romey (1996) and Couzin et al. (2002); in shoals in which the repulsion area of the agents differed, agents with smaller repulsion areas appeared to end up in the center. (Note that here we also varied the size of the line segment and the aligning area.)

The mechanism of 'active assortment by size' strengthens segregation according to body size via self-reinforcing effects. The larger the cluster of identical agents, the stronger the attraction of other agents of the same size. Similar effects are found for clustering of all kinds of objects and organisms (Camazine et al., 2001; Schelling, 1969). However, the pattern of small agents in the center is disturbed when the percentages of large and small agents differ; if large agents

are in the majority (75%), clusters of large agents tend to get stuck among small ones. If large agents are rare, they cluster together at the side, because they avoid small ones ahead of them.

Furthermore, the degree of segregation during 'risk avoidance' is higher when small agents are few, because then large agents are in the center surrounded by separate clusters of small ones. If, however, small agents are numerous, they find each other more easily and end up in clusters that are trapped among large agents. The degree of segregation depends on the strength of the tendency of 'risk avoidance,' since it is counteracted by effects due to differences in size; large agents move to the periphery because their repulsion area is larger, but 'risk avoidance' reverses the situation if small agents have an even stronger tendency to avoid large ones than vice versa. In DomWorld (Hemelrijk, 1998, 2000), in contrast, such counteracting forces are absent during the process of dominance assortment, because here all agents have identical sensory regions. Agents differ only in their capacity to win or lose fights. Subordinates that lose more often flee more frequently and, therefore, automatically end up at the periphery of the group.

Spatial segregation in real fish

Of course, our model is no more than a minimal representation of what happens in real fish. In real fish body size varies continuously and real fish of different body size differ in many more aspects than we have studied here. For instance, they may differ in their tail-beat and swimming speed. These two traits may augment assortment even further than is the case in our 'size difference' model. Also, our model does not represent food and feeding behavior, and the distribution of food, of course, influences the distribution of individuals. If food is clumped, large individuals that are hungry will drive smaller ones to the periphery. If food is distributed randomly, most food is obtained at the periphery of the group.

Both spatial distributions found in the model, with large agents at the periphery or in the center of the group, are found in nature. The spatial configuration with small individuals in the center has only rarely been described, but it has been found in water insects (male whirligig beetles, Romey, 1997; water insects, Sih, 1980). It is unclear, however, whether this configuration is consistent in water insects. The converse pattern with large fish in the center is described for a larger number of species of fish, both under 'undisturbed' captive conditions (for the hammerhead shark, *Sphyrna lewini,* Klimley, 1985; for the bluntnose, *Pimephalus notatus,* and stoneroller minnows, *Campostoma anomalum,* Theodorakis, 1989) and under experimental conditions (Krause and Tegeder, 1994; minnows, *Phoxinus phoxinus,* Pitcher et al., 1986). In relation to SchoolingWorld, it is of interest to know whether and for which species large individuals are missing from the back when large individuals are at the periphery. When large individuals are in the center, it is of particular interest to note whether clusters of small fish are caught among the large ones for certain compositions of large and small individuals but not for others, as SchoolingWorld suggests.

How do these opposite spatial configurations of large and small agents relate to the risk of predation and the competition for food? When, in nature, in schools of certain species, large individuals are continuously in the center, this may be explained by permanent strong cohesion as a consequence of both predator-avoidance and food distribution. If the large ones are in the center only during feeding, this may indicate feeding competition, if food sources are clumped (possibly in hammerhead sharks, Klimley, 1985; in minnow,

Theodorakis, 1989). If this spatial configuration is found only during predator threat (chub, *Leuciscus cephalus,* Krause, 1993b), this pattern seems to result primarily from increased cohesion for protection against predators.

The configuration with large ones at the outside would reflect a situation where the group is compact (in loose groups this assortment is lacking) due to predation avoidance and where competition (for whatever it may be) is weak.

Which of the three rules (the 'active sorting,' the 'risk avoidance,' or the 'size difference' model) protects best against predators, does, of course, depend on the strategy of the predator (whether s/he attacks at the center or at the periphery), but this has not been investigated here.

Conclusion

The two objects of this study are the connection between individual behavior and the collective patterns of (1) density distribution in the schools and school form and of (2) segregation according to familiarity and size. This approach can be extended by adding other features that can lead to spatial segregation, such as age (e.g., in ants, Sendova-Franks and Franks, 1995), sex (e.g., Ruckstuhl and Neuhaus, 2002), motivation (such as hunger, Krause, 1993b), parasites (Krause and Godin, 1996), and ecological factors. Possibly, this kind of model may also be made to apply to swarms of other taxa, such as insects. As it is, we hope that our results may inspire empirical scientists to study spatial patterns in schools of real fish and relate their findings to the results of our model.

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