The Simulation of the Movement of Fish Schools

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Many species of fish schools organize for short or longer periods of time without a leader. We searched for the behaviour patterns of the individual fish, which allow movement of such a school. On the basis of biological facts we constructed a number of behaviour models and tested them with computer simulations against biological reality.

Basic assumptions of our simulations are: (1) The motion of a fish is only influenced by the position and orientation of its nearest neighbours. (2) The new velocity and the turning angle of each fish (after a time step) are calculated by probability distributions taking into account random influences. (3) The movement of each model fish is based upon the same behaviour model, i.e. the modelled fish group swims without a leader.

The basic behaviour patterns are attraction, repulsion and parallel orientation. Our investigations show that it is very important how a fish mixes the influences of its neighbours. If a fish averages the influences of its neighbours, the model fish group shows the typical characteristics of a real fish school: strong cohesion and high degree of polarization. If a fish only responds to a single neighbour, the model creates a confused fish group.

1. Introduction

Fish schools are one of the most frequent social groups in the animal kingdom. In contrast to most mammal herds, many fish schools do not show a hierarchical structure (Breder, 1951, 1954, 1959; Radakov, 1973; Wilson, 1975; Aoki, 1980; Partridge, 1980, 1981). Herring and mackerel are typical species that form schools without "leaders".

Size, form and structure of schools are very different over time and among species. Even fish of the same species show a great diversity in schooling behaviour, often depending on the age of the school members. Nevertheless, many typical patterns of behaviour are described in the literature (Breder, 1959; Shaw, 1970; Nursall, 1972; Radakov, 1973; Wilson, 1975; Keenleyside, 1979; Pitcher & Wyche, 1983). While feeding or resting the fish assume a nearly random orientation. While the group is on the move, the fish show a highly parallel orientation. This parallel alignment changes in particular ways when the fish are attacked by predators (fountain effect, split effect, waves of agitation ...). These behaviour patterns demonstrate that a well-co-ordinated group-behaviour is possible without a domination of some individuals over others. But how is this achieved?

The schooling mechanism has been investigated in various approaches: descriptions of behavioural changes by limiting sensory clues, description of reactions to

moving or fixed objects and analyses of the individual movements within the school. The results showed that the most important senses for schooling are the eyes and the lateral line (Hunter, 1968; Shaw, 1970; Pitcher *et al.*, 1976; Köhler, 1979; Partridge & Pitcher, 1980; Blaxter *et al.*, 1981; Tembrock, 1983). Many investigators consider two basic behaviour patterns responsible for schooling: a biosocial attraction and a parallel orientation (review by Shaw, 1970). The behaviour interactions are not known in detail.

We hope that our work will make a significant contribution to the understanding of school organization. In this paper we will examine, with computer simulations, the influence of various behaviour patterns on the movement of leaderless, self-organized schools. Simulations of fish schools with different aims and models were reported by Inagaki *et al.* (1976), Radakov *et al.* (1978), Okubo (1980, 1986), Matuda & Sannomiya (1980, 1987), Aoki (1982, 1984), Sannomiya & Matuda (1984), Brinkman (1986).

We concentrate on school movements independent of external stimuli. This is a more difficult modelling problem in contrast to a movement influenced by external stimuli. External stimuli, such as visual, acoustic and olfactory stimuli, temperature, oxygen and salinity gradients, water velocity (currents) and electric fields, can simplify the school organization because they appoint a swimming direction to the fish (McFarland & Moss, 1967; Balchen, 1976). Nevertheless, schools showed a distinctly altered orientation capability on gradients in comparison with an individual fish (Kils, 1986).

Our aim is to formulate hypotheses of how the self-organization (co-ordination in the absence of leader and external stimuli) in fish schools may be managed. On the basis of biological facts, we design various behaviour models (response rules) for the individual fish. The models are tested with computer simulations for an entire group of fish in order to check if they produce a school behaviour. In this way we hope to find the behaviour patterns which are decisive for the formation of schools in reality.

2. Methods

At the beginning of the simulation, a certain number n of fish are set at random in a starting area. The orientations of the fish are also determined by chance. From time step to time step the new position, $x_i(t + \Delta t)$, and new orientation, $v_i^0(t + \Delta t)$, of each fish (i) in a two-dimensional space are calculated on the basis of the positions, $x_j(t)$, and orientations $v_j^0(t)$, of its neighbour fish (j) (for abbreviations see Appendix). How this is done in detail, is fixed by the chosen behaviour model. The behaviour models give the single fish instructions how to react in a respective situation. From the turning angle $\alpha_i(t)$, determined by the model, and the velocity $v_i(t + \Delta t)$, we calculate for each fish its new position $x_i(t + \Delta t)$ and orientation $v_i^0(t + \Delta t)$ (one time step later):

$$x_i(t + \Delta t) = x_i(t) + \Delta t \cdot v_i(t + \Delta t)$$

$$v_i^0(t + \Delta t) = \begin{bmatrix} \cos \alpha_i(t) & -\sin \alpha_i(t) \\ \sin \alpha_i(t) & \cos \alpha_i(t) \end{bmatrix} v_i^0(t) \tag{1}$$

$$v_i(t + \Delta t) = v_i(t + \Delta t) \cdot v_i(t + \Delta t).$$

If the fish group of the model shows the typical characteristics of real fish schools—the fish stay together (*cohesion*) and are highly parallel orientated (*polarization*)—for a large number of time steps, the corresponding behaviour model is selected as a possible candidate which may underlie real fish schools. The simulation approach allows us to narrow the circle of these candidates of behaviour patterns. We hope that this allows us to given suggestions for critical experiments.

We use simulations in two dimensions, 100 time steps long with eight fish. For each model we perform ten runs with different initial positions of the fish. At the beginning of our investigations we worked with 2000 time steps for one simulation, but we can demonstrate that 100 time steps are adequate to determine qualitative differences of our models.

3. Behaviour Models

In the literature, some suggestions can be found to model the movement of fish schools. Most of them are not useful for our problem because central assumptions are unrealistic. Some models did not take into account a parallel orientation behaviour (Breder, 1954; Inagaki *et al.*, 1976), others postulated that every fish knows the school velocity or the distance to the centre of mass of the school (Balchen, 1972, 1975; Brinkman, 1986; Forcardi, 1987). The model of Radakov *et al.* (1978) considered a situation where a fish always has the same neighbours. Empirical investigations exist (Hunter, 1966; Aoki, 1980; Partridge, 1981) where the positions in the school of the distinct fish change is the course of time. The models of Okubo (1986) and Matuda & Sannomiya (1980, 1987) are based on similar ideas as our models, but they use a physical force concept for modelling schools. We prefer the more biological model concept of Aoki (1982), whose essential points we revised for our studies.

All our behaviour models are composed of various model elements.

3.1. FUNDAMENTAL ASSUMPTIONS

First there are the *fundamental assumptions*, which are the same for all of our models:

(1) Every fish swims within the school according to the same behaviour model. This guarantees that the model fish group moves without a leader.

(2) The motion of the model fish group is not affected by external influences (no destination).

(3) Random influences are taken into account for the individual fish. Therefore, the position and the velocity of each fish were constructed as stochastic variables.

(4) The motion of each fish is only influenced by its nearest neighbours. This takes into account that vision and lateral line are considered to be the most important senses for school organization.

(5) We attempted to construct simple models possible. Only simple models promote a comprehension of the results. In other words, we are not interested in modelling every detail of the fish behaviour, but only the behaviours which are decisive for the school organization.

3.2. BASIC BEHAVIOUR PATTERNS

The basic behaviour patterns determine how a fish would act if it had only *one* neighbour fish.

From Aoki (1982) we distinguish four reactions according to different possible positions of the neighbour's: parallel orientation, repulsion, attraction and searching (Fig. 1).
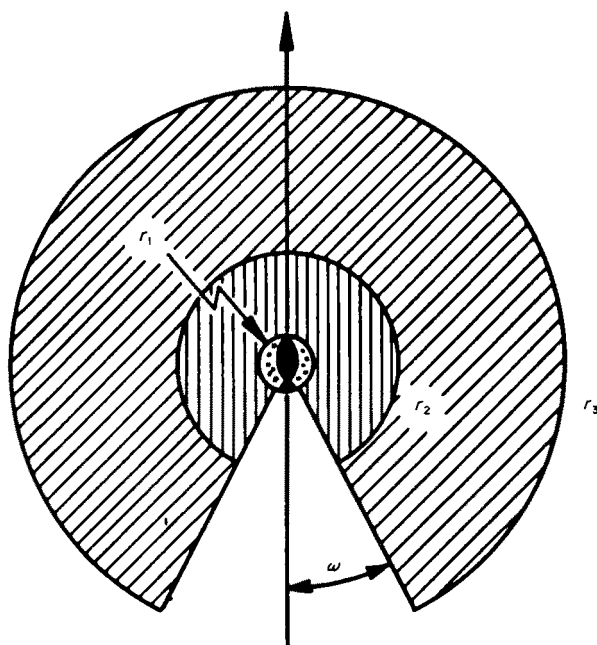

FIG. 1. Ranges of the basic behaviour patterns. The black fish reacts differently according to the range in which a neighbour is positioned: repulsion: ($r < r_1$ and not in the dead angle area, $r =$ distance between the black fish and its neighbour); parallel orientation: ($r_1 \leq r < r_2$ and not in the dead angle area); attraction: ($r_2 \leq r < r_3$ and not in the dead angle area); searching: ($r > r_3$ or in the dead angle area). The ranges are determined by the radius r_1, r_2, r_3 and the dead angle ω [the typical used values are ($r_1 = 0.5$ BL, $r_2 = 2$ BL, $r_3 = 5$ BL and $\omega = 30°$, BL, body length of a fish]. (▦), Parallel area; (▨), attraction area; (▤), repulsion area; (☐), searching area.

A schooling fish prefers to have its neighbours in distinct ranges. The mean distance to the nearest-neighbour (NND) varies among the species. Typical values are 0·3, −3 body lengths (BL) (Hunter, 1966; van Olst & Hunter, 1970; Symons, 1971; Pitcher, 1979; Aoki, 1980; Partridge, 1980; Partridge *et al.*, 1980; Pitcher & Wyche, 1983; Aoki *et al.*, 1986). In moving schools these typical distances are correlated with a high *parallel orientation* (Breder, 1959; Hunter, 1966; van Olst & Hunter, 1970; Nursall, 1973; Köhler, 1979; Klimley, 1980; Aoki *et al.*, 1986; Kils, 1986). Formulated as behaviour rule, we get: If the neighbour fish is in a certain preferred range (parallel orientation area, Fig. 1), the fish swims in the same direction as its

neighbour. Thus, the fish turns by the angle:

$$\beta_{ij} = \measuredangle \ (v_i^0, v_j^0)$$

(v_i^0, x_i^0 are the orientation and position of the fish, v_j^0, x_j are the orientation and position of its neighbour).

The three other basic behaviour patterns have the function to drive the fish mutually into their preferred (parallel orientation) range.

First we have the *repulsion behaviour*. Fish avoid collisions. Under a certain distance ("individual distance" Keenleyside, 1979), the parallel orientation of two schooling companions decreases rapidly (van Olst & Hunter, 1970). Often fish subsequently make 90° turns (Kils, 1986). For our simulations, we chose the following response rule: If the neighbour fish is too close (in the repulsion area, Fig. 1), the fish tries to avoid a collision. The fish turns by the angle:

$$\beta_{ij} = \min \ \{ \measuredangle (v_i^0, v_j^0) \pm 90° \}$$

The fish turns so that it swims perpendiculary away from the swiming direction of its neighbour. From the two possible orientations it prefers the one it reaches with a smaller turning angle.

Many authors describe biosocial *attraction* between fish of the same species (Breder, 1954; Keenleyside, 1955; Shaw, 1970). If a fish is too far away from the school it swims towards the school (Keenleyside, 1955). Formulated as model rule: If the neighbour fish (j) is too far away (in the attraction area, see Fig. 1), the fish swims in the direction of its neighbour.

$$\beta_{ij} = \measuredangle \ (v_i^0, x_j - x_i).$$

As the senses of fish are limited to certain distances (in contrast to Aoki, 1980) and by the body shadow (Keenleyside, 1955; Bone & Marshall, 1985; Hall *et al.*, 1986; Wardle, 1987) we introduced a *searching* behaviour in our model. If the neighbour fish is too far away or in the dead angle of the fish (in the dark area), the fish cannot perceive its neighbour and begins to search for a neighbour fish. Thus, the fish turns around by chance

$$\beta_{ij} = \text{chance } ([-180°, 180°]).$$

We see that a distinct turning angle β_{ij} can be attached to the influence of each neighbour fish. As a fish detects the position and orientation of its neighbour with some uncertainty, the fish does not turn exactly by the angle β_{ij}. In order to take into account these uncertainties and other random influences we construct a probability distribution $p(\alpha_i)$ for the realized turning angle with the angles β_{ij}. In the case of only *one* neighbour the probability distribution $p(\alpha_i)$ consists of a normal distribution with the mean β_{ij} [Fig. 2(b)]. With $p(\alpha_i)$ a random number is calculated which represents the turning angle α_i chosen by the fish

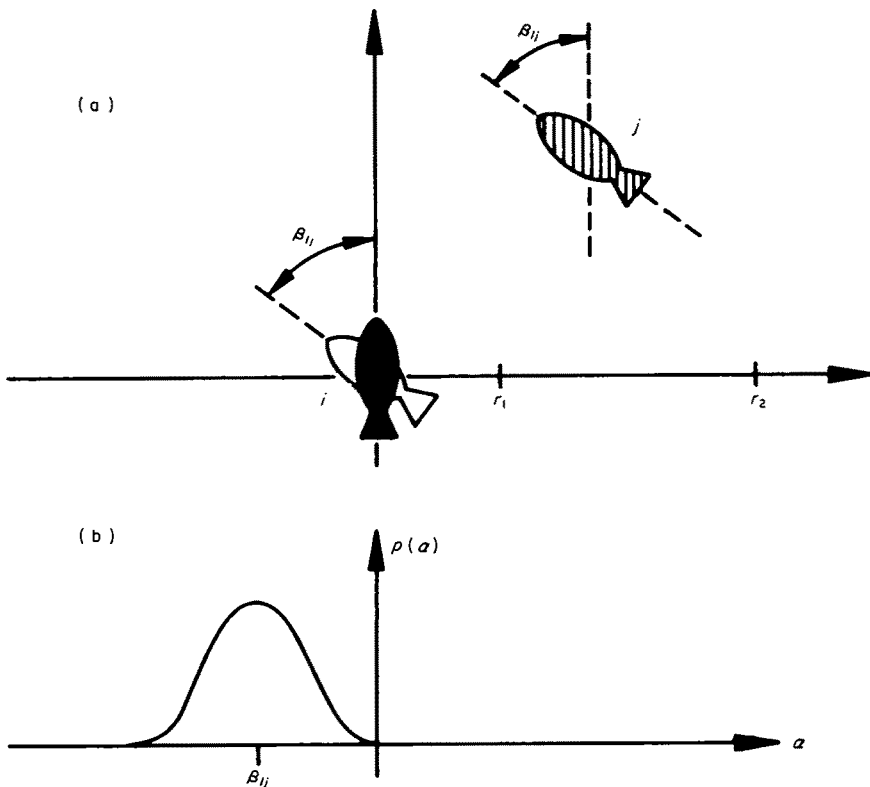$$\alpha_i = \text{chance } (p(\alpha_i)).$$

FIG. 2. Example for the parallel orientation: (a) The neighbour fish (hatched j) of the black fish (i) is positioned in the parallel orientation area of the black fish. The white fish shows the orientation of the black fish one time step later. Then it swims in about the same direction as its neighbour. (b) Probability distribution $p(\alpha)$ for the turning angle α of the black fish. The distribution consists of a normal distribution around the angle β_{ij}. The black fish is the ith fish, its neighbour the jth fish. With $p(\alpha)$ we calculate a random number which represents the turning angle chosen from the black fish.

The new velocity, v_i, of the fish is chosen independent of the other fish. This is done to simplify the model. The velocity v_i of every fish is calculated by chance with the typical distribution given by experiments, a Gamma distribution (Fig. 3; Aoki 1980, 1982).

$$v_i = \text{chance}\,(p(v))$$

$$p(v) = \frac{A^K}{T(K)} \cdot \exp\,(-Av) \cdot v^{K-1}.$$

[$\Gamma(K)$ Gamma function, v velocity, K, A parameters ($K=4$, $A=3\cdot3$)]. The distance moved is expressed in body lengths (BL). The average velocity of a fish is $1\cdot2$ BL sec^{-1}.

With the turning angle $\alpha_i(t)$ and new velocity $v_i(t+\Delta t)$ the new position $x_i(t+\Delta t)$ of the fish can be calculated by (1).
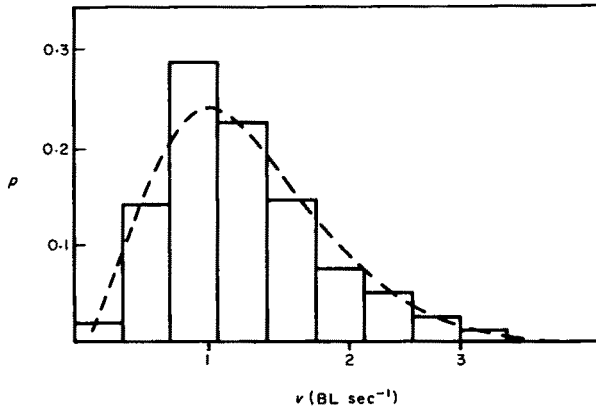
FIG. 3. Typical velocity frequency distribution in a fish school determined by experiments and fitted by a Gamma-distribution (histogram datas from experiments, parameters of the Gamma distribution $K = 4$, $A = 3 \cdot 3$, units in body length (BL). After Aoki (1980).

3.3. MIXTURE OF THE NEIGHBOUR INFLUENCES

The most important model element is the *mixture* element. It fixes, how a fish mixes the influences of *several* neighbours. As no biological knowledge concerning this point exists, we examined two concepts: decision (*D*-models) and averaging (*A*-models).

In Fig. 4 we demonstrate an example with two neighbours (striped). One neighbour swims to the left top corner, the other towards the right top corner. How does the black fish react?

In the *D-models* (with decision, Aoki, 1982) the fish decides to which neighbour fish it will adjust. Therefore, we construct a probability distribution for the turning angle α_i of the black fish, which is composed of two differently weighted normal distributions. The angle β_{ij} representing the influence of the jth neighbour determines the centre of the jth normal distribution (Fig. 4)

$$\beta_{ij}(\alpha_i) = \sum_{j=1}^{nb} \frac{1}{\text{S.D.} \sqrt{2\pi}} b(j) \exp -(\alpha_i - \beta_{ij})^2/2\text{s.D.}^2$$

[S.D. $= 15°$: standard deviation of the normal distributions, nb: number of neighbours taken into account, $b(j)$: weight factors].

In the maximum case, a fish takes four neighbours (nb ≤ 4) into account provided none are positioned in the dark area. If a fish perceives more than four neighbours, it selects four using certain priority rules. For example, it prefers those neighbours which are more positioned to the front of the fish (front priority), as suggested by investigations (van Olst & Hunter, 1970; Partridge, 1980; Partridge & Pitcher, 1980).

The chosen priority also determines the weight factors, $b(j)$, of the chosen neighbours. We renumber the neighbour fishes, so that

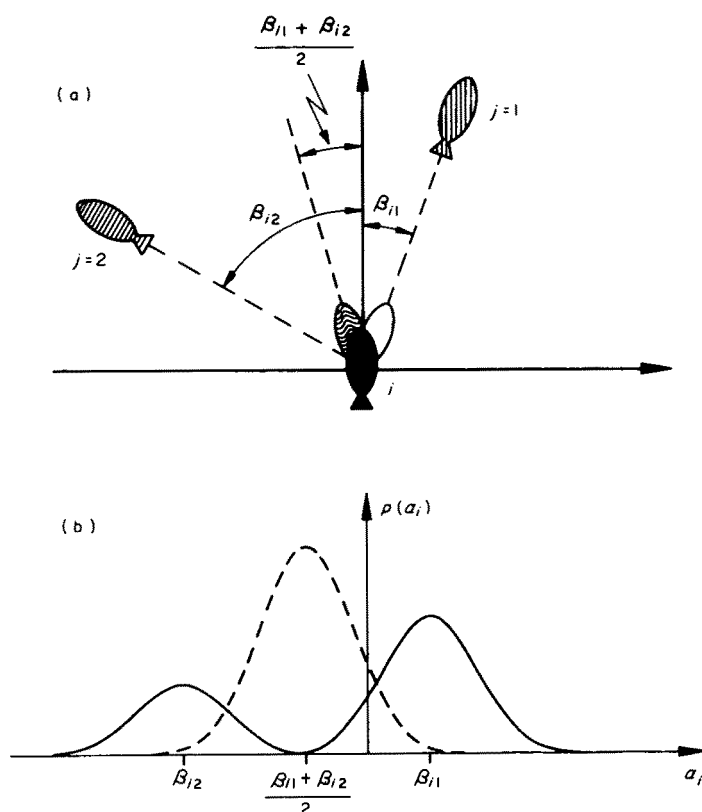$$\omega_1 < \omega_2 < \omega_3, \ldots,$$

FIG. 4. Example for the decision and averaging models. (a) The black fish has two neighbours (hatched) in its parallel orientation area. The white fish illustrates a new swimming direction which the black fish probably chooses after the next time step if the decision model (D) is used. The fish with the undulated marking shows the probable new swiming direction for the averaging model (A). (b) Probability distribution $p(\alpha_i)$ for the turning angle α_i of the black fish. For the A-model probability distribution (dashed line) consists only of one normal distribution around the angle ($\beta_{i1} + \beta_{i2})/2$. The black fish averages the influences of its neighbours. It swims roughly in a direction located between its two neighbours. For the D-model the probability distribution (full line) consists only of two differently weighted normal distribution with standard deviations s.d. $= 15°$. The weight of the normal distribution of the right neighbour, which is positioned more in front of the black fish is double the weight of the other distribution (front priority, right neighbour $j=1$, left neighbour $j=2$, black fish = ith fish). In two of three cases the black fish swims roughly in direction of its right neighbour.

with

$$\omega_j = \measuredangle (v_i, x_j - x_i).$$

The "first" neighbour fish is accorded the greatest weight, the second, half the weight of the previous one, and so on:

$$b(j+1) = \tfrac{1}{2}b(j)$$

$$\sum_{j=1}^{nb} b(j) = 1.$$

For example, for four neighbours we get $b(1) = 8/15$, $b(2) = 4/15$, $b(3) = 2/15$, $b(4) = 1/15$.

According to various studies (Aoki, 1980; Klimley, 1980; Partridge *et al.*, 1980) we also investigated other priorities: side priority and distance priority. Using side priority we renumber the neighbours with respect to $\angle(v_\perp^0, x_i - x_j)$, where $v_\perp^0$ is perpendicular to the orientation v_i^0 of the fish. In the distance priority, the nearest neighbours are preferred.

Figure 4(b) illustrates the probability distribution $p(\alpha_i)$ for the turning angle α_i which belongs to the situation in Fig. 4(a). It can be estimated from $p(\alpha_i)$ that in two out of three cases the black fishes turns towards its right neighbour fish (front priority).

In the *A-model* (with *averaging*) the fish mixes the influences of its neighbours taking the arithmetic average of the influence angles, β_{ij}, of its neighbours. The probability distribution for the turning angle α_i is now

$$p(\alpha_i) = \frac{1}{\text{S.D.}\sqrt{2\pi}} \exp -(\alpha_i - \overline{\beta_{ij}})^2 / 2\text{S.D.}^2$$

with

$$\overline{\beta_{ij}} = \sum_{j=1}^{nb} \beta_{ij}/nb.$$

In this case only *one* normal distribution for the turning angle is centred around the mean angle $\overline{\beta_{ij}}$. For our example (Fig. 4) this means that the black fish swims in a direction which is close to

$$\overline{\beta_{ij}} = \frac{\beta_{i1} + \beta_{i2}}{2}.$$

4. Results and Discussion

4.1. STANDARD RUN

In the standard run, we chose the same parameters as Aoki (1982), for our results being comparable with his investigations ($r_1 = 0.5$ BL, $r_2 = 2$ BL, $r_3 = 5$ BL, $\omega = 30°$). Later we will discuss the influences of these parameters.

Figure 5 shows a sequence (six time steps in succession) from a typical simulation with the *A*-model and *D*-model (standard run). In the *D*-model [Fig. 5(a)], the modelled fish group did not advance very much. Every fish is orientated in a different direction. The fish group is called confused. This could be a feeding or resting school but not a moving school. In the simulation with the *A*-model [Fig. 5(b)], every fish swims approximately the same direction. The model fish group moves in a parallel fashion and advances well.

For comparison with the motion of a real school [Fig. 6(b); Partridge, 1981], the same sequence of the *A*-model school is represented in Fig. 6(a) in a different form. We see that the simulated school looks like the real school.
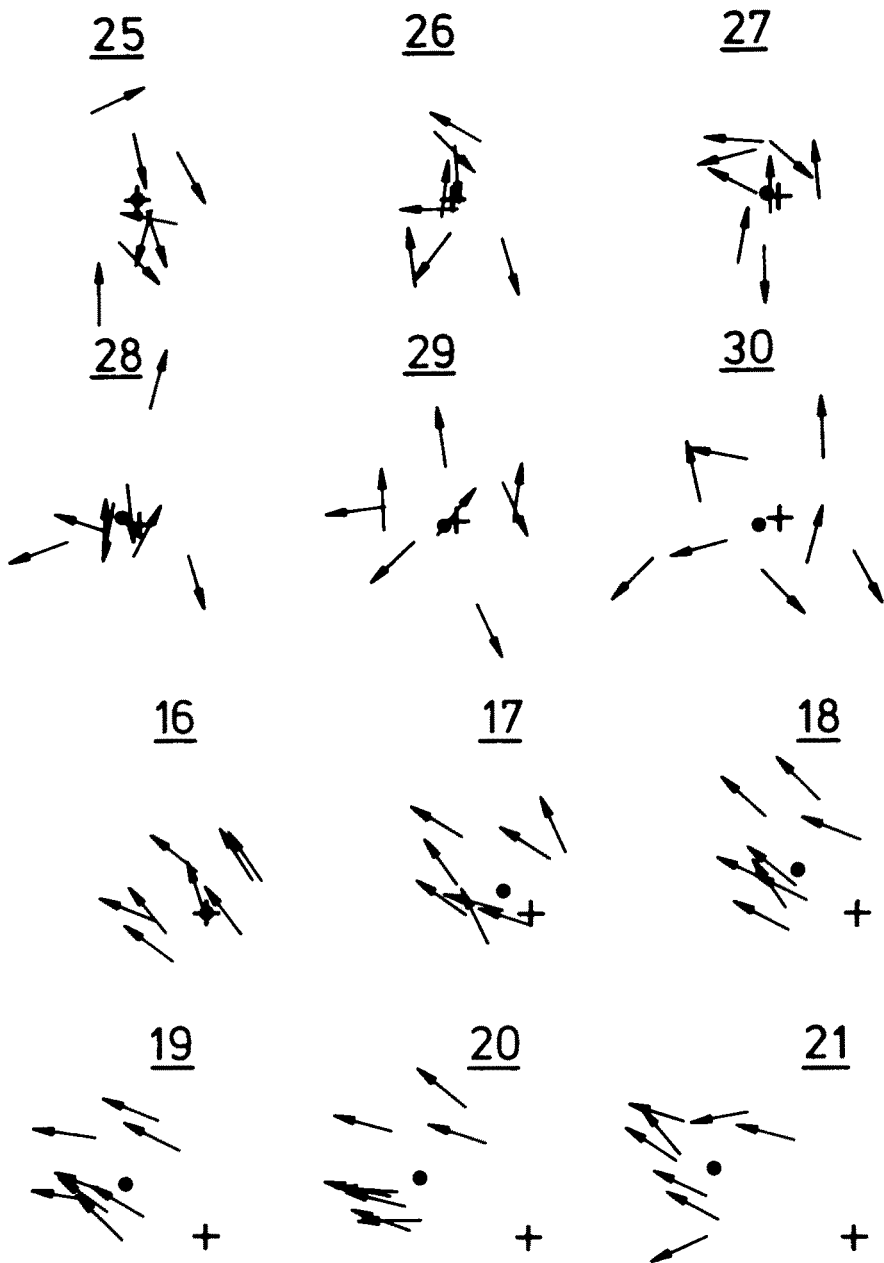
FIG. 5. (a) Sequence from a typical simulation run with the decision model. The arrows represent the fish. Time steps 25-30 are shown. The black dot marks the current centre of mass of the school. The cross marks the position of the centre of mass at the first illustrated time step. The polarization p of the school is 57°, 74°, 70°, 80°, 80°, 77° (see text for explanation). (b) Sequence from a typical simulation run with the averaging model (time steps 16-21), same presentation as in Fig. 5(a). The polarization p of the school is 12°, 16°, 10°, 9°, 8°, 17° respectively.
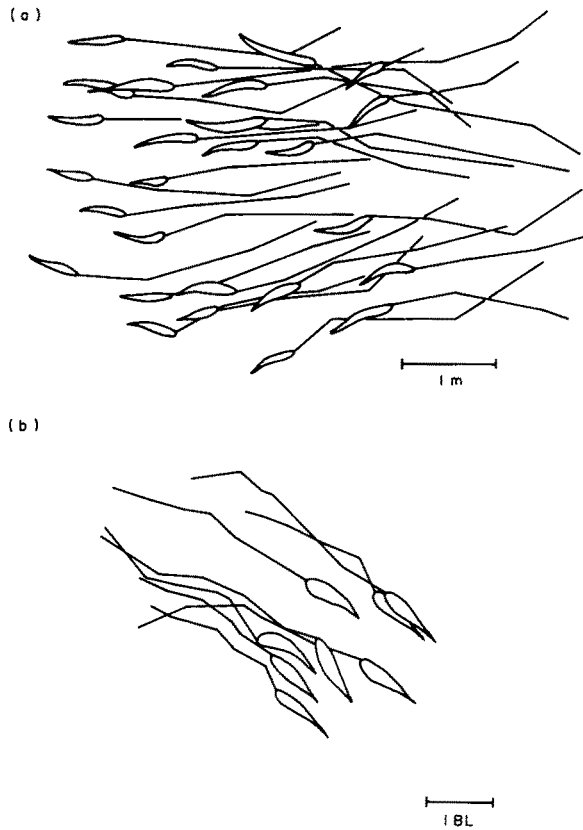
FIG. 6. Paths of the members of a fish school. (a) After experiments by Partridge (1981). The fish were traced by videotape and the positions of the fish are plotted every 1·4 sec. (b) Fish school of our simulations (*A* model). The positions of the fish are plotted every 0·5 sec. (BL body length).

The path of the centre of mass (of the same simulations illustrated in Fig. 5) is shown in Fig. 7. The path of the *D*-model (full line) is very twisty. The fish group changes its direction very often. On the other hand the fish group of the *A*-model (dashed line) keeps the direction for many time steps. Thus, the fish group covers a great distance. The bends in the path arise from short confusion periods.

4.2. POLARIZATION *p* AND EXPANSE *a*

In addition we searched for variables which quantify the typical characteristics of fish schools. Our investigations have shown that two variables are useful: *the expanse and the polarization*.

The *polarization*, *p*, is defined as the arithmetic average of the angle deviation of each fish to the mean swimming direction of the fish group, *sv*: (mean derivation
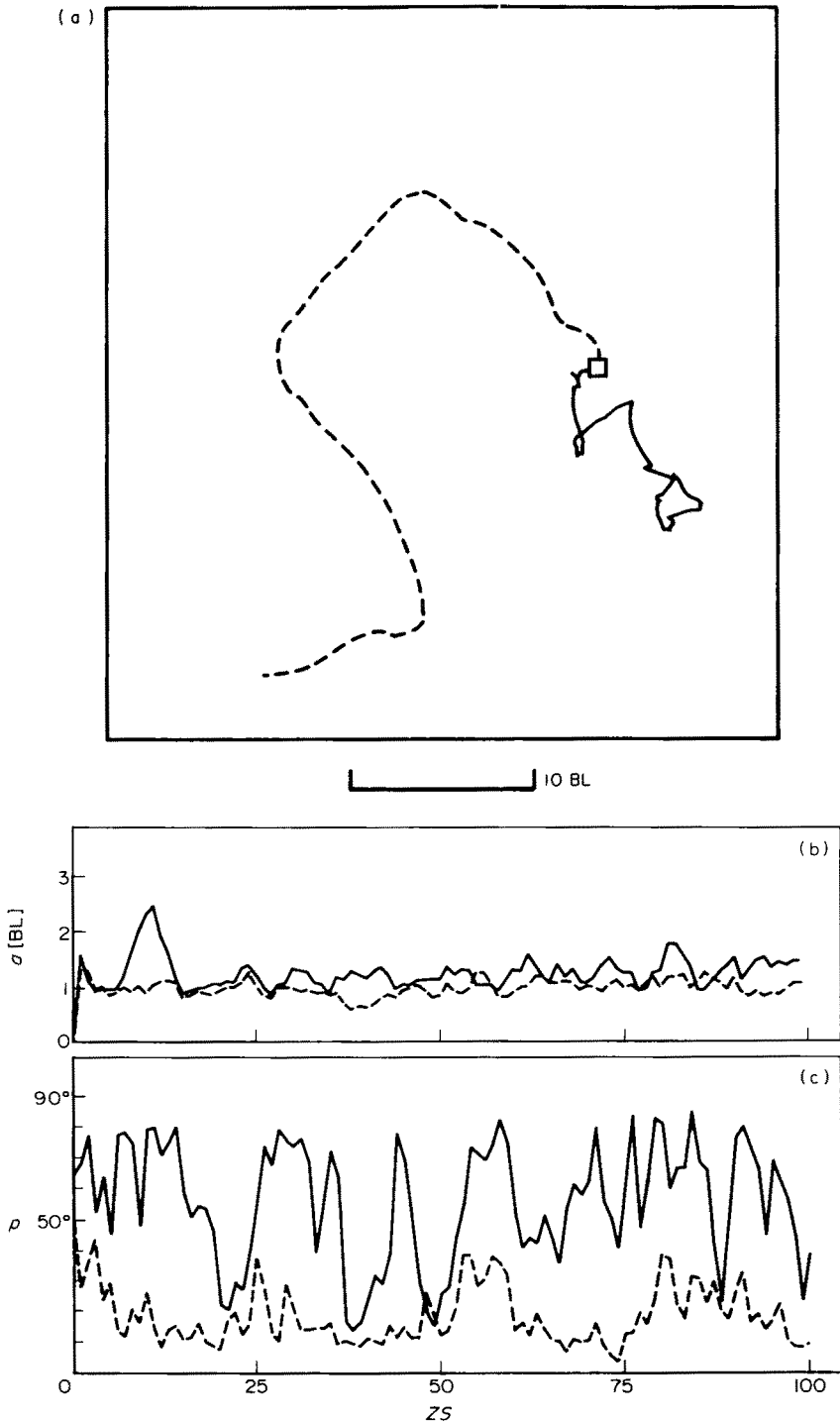
FIG. 7. Different presentation of the results of two typical simulation runs with the decision model (full line) and averaging model (dotted line) respectively (compare Fig. 5). (a) Path of the centre of mass of the school. The initial point is marked by the little box. The duration of the simulation is 100 time steps. (b) Corresponding expanse α (in BL = body length) vs. time steps (ZS). (c) Corresponding polarization p vs. time steps (ZS).

angle, Hunter, 1966)

$$p(t) = \sphericalangle \, \overline{(sv, v_i^0(t))}$$

with

$$sv(t) = \sum_{i=1}^{n} v_i^0(t).$$

The mean swimming direction $sv(t)$ of the fish group is calculated by adding the orientation vectors v_i^0 of each fish. The polarization p quantifies the intensity of the parallel orientation of the fish group. The polarization has values between 0° and 90°. For $p = 0°$ the fish group is optimally parallel (polarized), for $p = 90°$ it is maximally confused (compare Fig. 5).

Van Olst & Hunter measured that schools with a high parallel orientation have polarization values between 10° and 20° (1970). Similar results can be derived from other investigations (Hunter, 1966; Köhler, 1979; Aoki, 1980; Klimley, 1980; Pitcher & Wyche, 1983).

Figure 7(c) illustrates the polarization time sequences for the two typical simulation runs. The D-model (full line) shows most of the time p values at about 50° and higher. The fish group is in a state of permanent confusion. In the A-model (dashed line), the p values lie low (about 20°). This means that the fish group remains highly polarized nearly all of the time (as shown in Fig. 5). The p values of about 40° for short periods can be associated with the bends in the path of the fish group's centre of mass.

The *expanse*, a, is defined as the average of the distances quadratic from every fish to the fish group's centre of mass. This variable quantifies the spatial size (the compactness, the cohesion) of the fish group

$$a(t) = \sqrt{\overline{[x_i(t) - s(t)]^2}}$$

[$s(t)$ centre of mass of the fish group].

If the fish group (eight fish) stays together, the typical expanse a has values of about 1 BL. If the fish group disperses or divides into subgroups the expanse increases to a value of 4 BL or more (compare Fig. 5).

In the literature, we find different variables which quantify the compactness of the school. Very often, the mean distance to the nearest neighbour was measured (see section 3). Expanse a and NND are correlated. Expanse values of 1-2 BL corresponds to NND of 0·5-1·3 BL (cf. Fig. 8).

Figure 7(b) shows time sequences of the expanse for the two typical simulation runs discussed above. The expanse a for the D-model (full line) lies slightly above the values of the A-model (dashed line). Nevertheless both models keep their fish group together ($a \approx 1$ BL).

4.3. COMPARISON OF D- AND A-MODELS

Figure 8 gives an overview of our most important results. Here the mean (over ten simulations with 100 time steps) of the polarization, p, and expanse, a, are

shown for the D-model, the A-model and several variations. The original model with decision (D) is the worst. The biggest problem is the repulsion mechanism which confuses the model fish group again and again. By adding a maximal angle ($D2$), which the turning angle of a fish cannot exceed in one time step, or by the elimination ($D1$) of the repulsion mechanism ($r_1 = 0$) we can improve the models with the decision concept, although, the models (N, M) with averaging (A-models) are always better. Here the addition of a maximal turning angle has a negative effect ($N2$, $M2$). In contrast, the elimination of the repulsion area ($N1$, $M1$) scarcely produces better results. The repulsion mechanism does not disturb the polarized swimming of the fish group. The change in the priority in the models with averaging does bring about an essential change in results (compare M with N). Summing up the models with averaging (M, N) produce a model fish group showing the characteristics of a real moving fish school [high polarization (low p), strong cohesion, (low a and NND)]. In the case of simulations with 20 and 30 fish the same characteristics are also found.

It would be of interest to know why the averaging models are better than the models with decision. Figure 9, which shows an example with three fish, gives a first
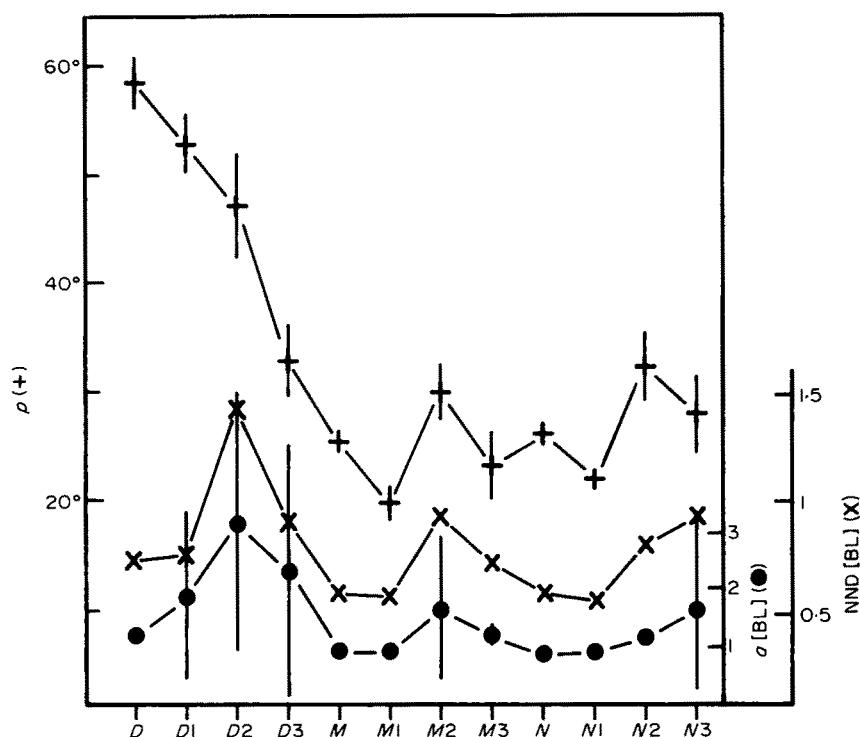

FIG. 8. Mean polarization p, nearest neighbour distance NND, and expanse a for 12 different model variations, calculated from ten simulations with 100 time steps in each case (bars = s.d.). Abbreviations: D decision with front priority, M averaging with front priority, N averaging with side priority; variations: 1 without repulsion area ($r_1 = 0$), 2 with maximal turning angle (45°), 3 without repulsion area and with maximal turning angle (45°). See text for discussion.
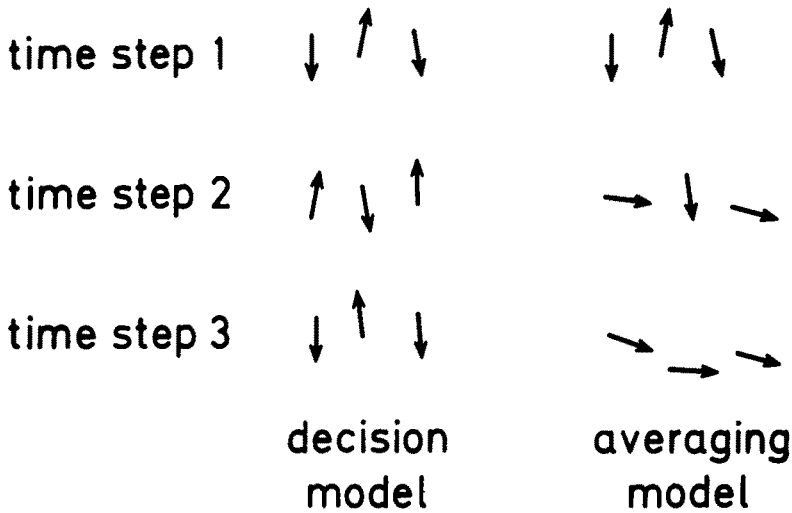
FIG. 9. Attempt of an explanation of the operation of the decision and averaging concept. See text for explanation.
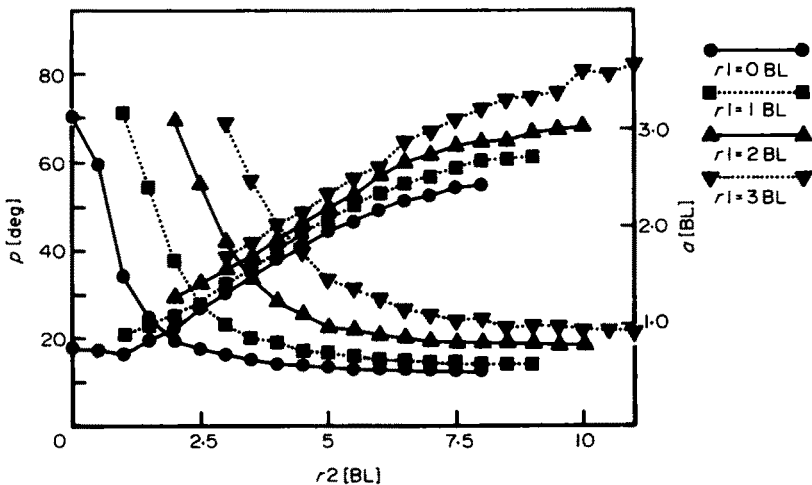

FIG. 10. Polarization p and expanse a vs. the size of the parallel orientation area r_2, for four different sizes of the repulsion area r_1. Each point represents the mean value from 10×100 time steps simulations with eight fish (all other parameters like in the the standard run). The enlargement of the parallel area r_2 lead to schools with a higher parallel orientation (low p values) but lower cohesion (high a values). Therefore the value of r_2 is of great importance of the results of the simulations. The increase of the repulsion area (r_1) decrease relatively little the parallel orientation and cohesion of the school.

hint. We assume that all the fish lie mutually in their parallel orientation areas and every fish reacts to its nearest neighbour. At the beginning the two outer fish are orientated downward, the fish in the middle upward. In the next time step the fish in the middle turns downward. It has reacted to the outer fish. The outer fish are influenced by the fish in the middle and turn upward. This continues as long as no perturbation destroys this "balance". With the same initial situation, the averaging model produces a totally different evolution. The two outer fish average the direction of the respective two other fish and turn to the right (the fish in the middle is not only orientated upwards but also a little to the right). The fish in the middle average the two outer fish and turn downward. Now the fish group has already improved its polarization.
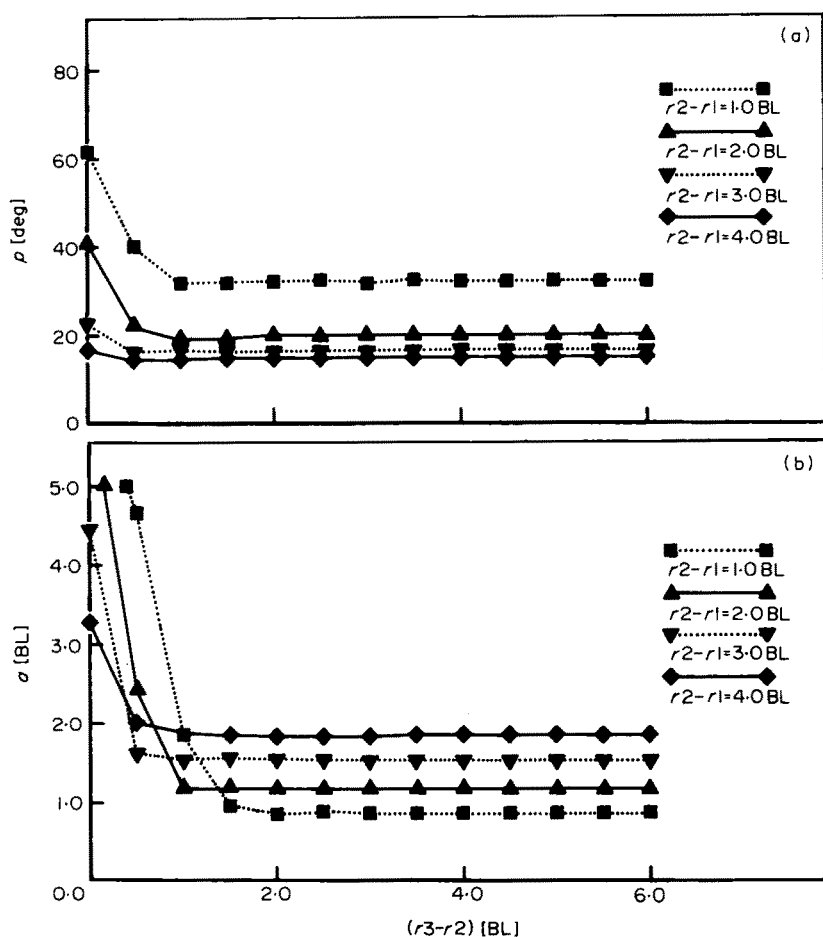

FIG. 11. Polarization p and expanse a vs. the size of the attraction area r_3-r_2, for four different sizes of the parallel orientation area. (All other parameters like in the standard run.) Values of $r_3 \geq r_2 + 1$ BL produces nearly the same results.

In the next time step, the two outer fish average over the other fish again and they turn toward the right bottom corner. The fish in the middle reacts to the two outer fish and turns to the right. Now the fish group is highly polarized. We see that the averaging concept produces an order in the school. Although this example rests on a special situation, we believe that it indicates a decisive cause for the different results in the decision and averaging concepts.

4.4. THE INFLUENCE OF THE PARAMETERS

For one of the best models (A-model with front priority, M in Fig. 8) we investigated the influences of the model parameters.

The enlargement of the parallel area (r_2-r_1) leads to schools with a higher parallel orientation but a lower cohesion (see Fig. 10). High polarized schools need a big parallel area. The increase of the repulsion area (r_1) decrease the parallel orientation and reduces the school cohesion scarcely.

The attraction area (r_3) influences the results only in a small range. We found that values of $r_3 \geq r_2 + 1$ BL produce nearly the same results. This suggests that attraction is already fully effective with a "radius" $r_3 - r_2 \approx 1$ BL (Fig. 11).

The variation in the number of neighbours from which a fish is influenced is shown in Fig. 12. Here we see, that the knowledge of the orientation and position of three neighbours is nearly equal to the knowledge of all fish.

Figure 13 compares our model with experimental results from van Olst & Hunter (1970) on the basis of the polarization and the NND. Nearly all experimental data
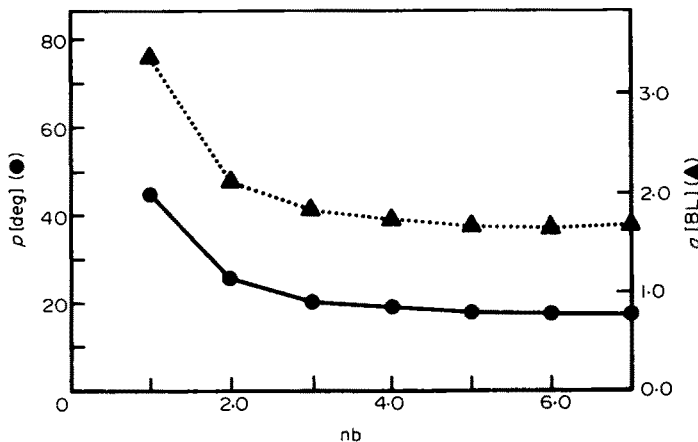

FIG. 12. Polarization p and a vs. the number of neighbour nb from which a fish is influenced (with $r_1 = 0.5$ BL, $r_2 = 4$ BL, $r_3 = 7$ BL, other parameters like in the standard run). The more neighbours a fish take into account the better the parallel orientation (low p) and cohesion (low a) of the school. Values of nb $< = 3$ nearly produce the same results. In other words: the knowledge of the orientations and positions of three neighbours is nearly equivalent to the knowledge of all fish. This demonstrates the economic advantage of a co-operative behaviour.
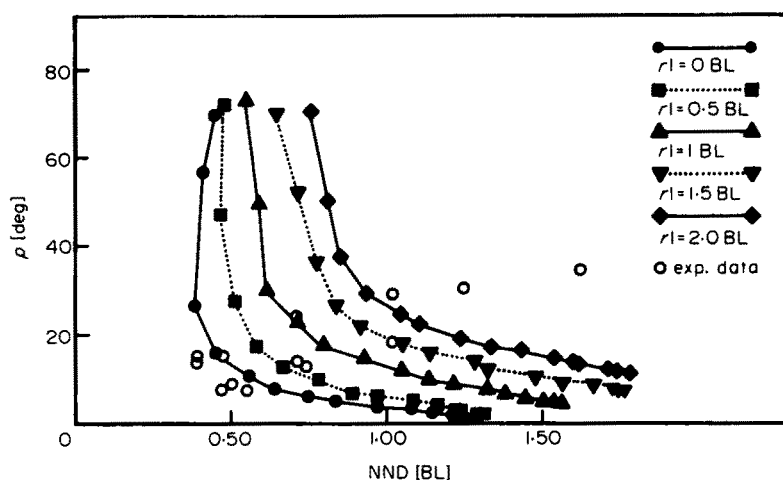
FIG. 13. Comparison of the results of our model with experimental data for the polarization (*p*) and nearest neighbour distance (NND). Each black point represents the result of 10 × 100 time step simulations (for special parameters) in form of a mean *p* and mean NND value. Within a curve we varied (from top to bottom) the size of the parallel orientation area ($r_2-r_1 = 0-13$ BL, in 0.5 BL steps, compare with Fig. 10). The different curves represent different sizes of the repulsion area ($r_1 = 0-2$ BL, compare with Fig. 10) (s.d. = 0°, all other parameters like the standard run). The experimental data were measured from van Olst & Hunter (1970) for schools of jack mackerel, pacific mackerel, northern anchovy and jackmelt (with different ages). Nearly all experimental data can be reproduced by our model. The differences between the species/ages are expressed in our mode by different range parameters, in other words by different sense capabilities.

can be reproduced by our model. The model expresses the differences between species by different range parameters r_1 and r_2. These range parameters represent the sense capabilities of the fish. This suggests that different school polarizations and school sizes between the species result from different sense capabilities.

4.5. OUTLOOK

In this paper we have shown that our *A*-models are able to reproduce the typical characteristics of normal moving schools. In the next step, it would be interesting to compare the internal structure of our model school with experimental results. We would certainly have to improve our model, in particular we would have to work on an adaptation of velocities between neighbours. So far we have limited ourselves to cases where external influences are absent. Having found a model which describes this situation in a realistic way, we may use it as a basis to describe other effects on schools (disturbances, predators or other environmental factors).

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APPENDIX

Abbreviations

i	number of a fish
j	number of the neighbour of a fish
t	time
$x_i(t)$	position vector of the ith fish at time t
$v_i(t)$	$= dx_i(t)/dt$ velocity vector of the ith fish at time t
$v_i(t)$	$= |v(t)|$ absolute value of the velocity vector of the ith fish at time t
$v_i^0(t)$	$= v_i(t)/|v_i(t)|$ orientation vector of the ith fish at time t
$\alpha_i(t)$	turning angle of ith fish between the time t and Δt
$\beta_{ij}(t)$	angle which represents the influence of jth neighbour of the ith fish at time t
$\measuredangle (a, b)$	angle between the two vectors a and b
$v_\perp$	vector perpendicular to v
Chance $(p(d))$	function which represents the creation of a random number with a probability distribution
Chance $([a, b])$	function which represents the creation of a random number out of the interval $[a, b]$
BL	body length of the fish
p	polarization

a   expansion
NND   nearest neighbour distance

Parameter Values (Standard Run)

Δt	0·5 sec	duration of a time step
n	8	number of fish in a fish school
r_1	0·5 BL	radii and angles which characterize the basic behaviour areas
r_2	2 BL	(Fig. 1)
r_3	5 BL	
ω	30°	
nb	4	maximal number of neighbours which can influence a fish
S.D.	15°	standard deviation of the normal distributions which represent the influences of the neighbours
il	4·5 BL	length of the edges of the quadratic start area