Cellular Automaton Models for Fish Schools: Merging Social Behavior and Hydrodynamics

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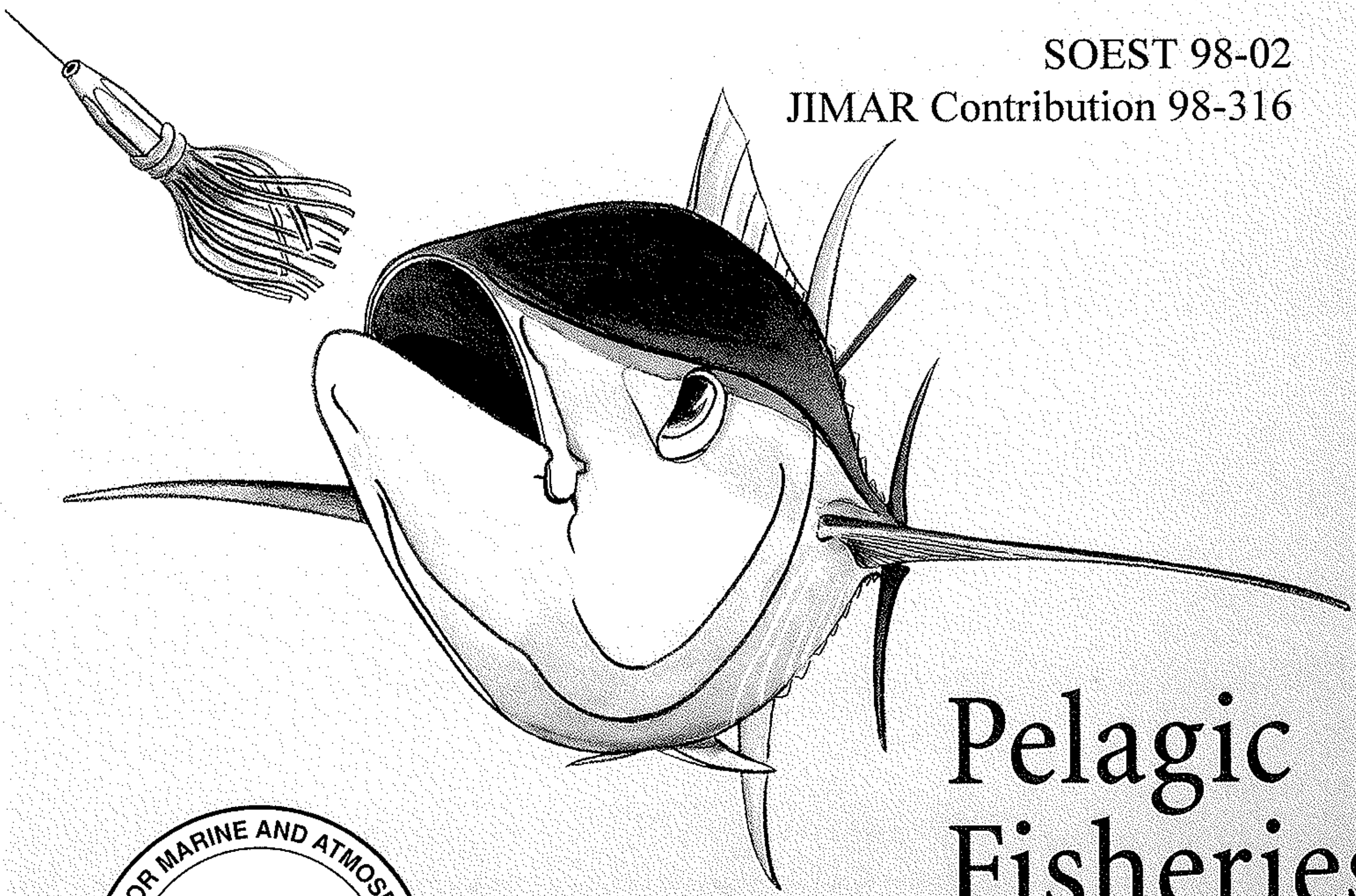

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Abstract

Schooling behavior in the context of animal aggregation is a challenging topic of economic importance for the estimation and conservation of stock sizes. An individual-based movement model will be developed, taking into account energetic advantages of schooling. This model is a cellular automaton with a hexagonal grid based on the geometry of a school where fish swim in a diamond-shape configuration in order to take advantage of the velocity induced by the tail strokes of preceding fish. Furthermore, knowing the induced velocity field makes it possible to consider the energetic needs of fish swimming in that school and to describe the breakup of schools as oxygen is depleted. This allows an estimate of maximum school size. The model presented here is a combination of a behavior and of a hydrodynamic schooling model.

1 Introduction

The investigation of fish schools as a phenomenon of complex structure and of self organization in animal life yields information that is of economical importance for fisheries worldwide. The fact that fishes school is essential for some fisheries, since fishing can be targeted on schools. Knowledge about school size, occurrence, and distribution can help to make decisions that enable us to efficiently harvest protein rich fish without exhausting the stock. Therefore, a better understanding of the formation of fish schools and their migration (*Sibert and Fournier*, 1994; *Sibert et al.*, 1995, 1996) is essential.

Increasing yields in fishery are misleading unless the relationship to catch intensity is presented. For example, during the period from 1939 to 1959 the annual catch of yellowfin tuna in the East Pacific increased from 56,250,000 kg to 85,500,000 kg, but the local amount decreased from 4050 kg/norm day to 2250 kg/norm day, where a norm day is defined by the size of the fleet and the total number of working hours. These data are even more misleading if the share of young fish in the catch is increasing, because only the survival of a pool of young fish can guarantee continued breeding in the fishery. What needs to be better understood is the size of the fish stock, which is not directly linked with the catch rates. Recent data show a stagnation rather than a decline in catch rates, but these data need to be read carefully, especially because the commonly used CPUE (catch per unit effort)[1] might increase due to improved technology, even as the fish stock decreases.

Catch numbers and samples of fishery do not provide much information as long as the size, distribution, and the migration routes of schools are not known. In this paper the emphasis is on the study of the size and distribution of schools.

We suggest a theoretical 2-dimensional model with normalized variables. This model can be used to simulate the formation of schools. The unit length in this model is the lateral average distance between two fish, and the unit time is the time a fish swimming at average speed needs to travel the unit length.

The application of this model to concrete situations will be the subject of a future study. In this paper we focus on the description of the theoretical model. The calculation of the maximum length of schools, assuming that oxygen is a limiting factor, is based on experimental data.

More than 4000 species of pelagic fish are schooling, among them the tuna, the herring and the mackerel. Large fish, such as the shark or the swordfish are *not* schooling, although some sharks temporarily form schools for mating. Within some species, such as *Micropterus*, a bass species, mature fish are solitary but

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[1] The definition of the CPUE depends on the catch strategy. It can be *numbers of fish per 100 hooks* for longliners, or *metric tonnes per day* for pole-and-line vessels (*Lawson*, 1994; 1996).

swim in a swarm when they are young. There are several reasons why fish school, and they differ in relative importance for different fish species.

- *Protection*: Although the school in its entirety might be discovered more easily by a predator, swimming in a school reduces the probability for the individual to become a prey item. A single fish can "hide in the crowd." Additionally, a predator can be confused by school members escaping into different directions. This is the so-called "confusion factor."
- *Energy savings*: Swimming in its predecessor's wake results in hydrodynamical advantages for the fish (*Weihs*, 1973, 1974b, 1975; *Partridge et al.*, 1983).
- *Social aspects*: There are social advantages of schooling, such as a higher possibility of finding a partner. For example, the *Anthias squammipinnis* is a coral-reef fish living in schools with territories on the reef. Schools consist entirely of females except for one male. If the male is removed, one of the females changes sex in response to visual stimuli (*Barnes and Hughes*, 1988).
- *Foraging*: More eyes can find more prey items, but the food has to be shared. The latter might be a reason why large fish do not school. Schooling fish can more easily adjust their foraging behavior to changes in availability of food sources and patchiness of food items. The sampling ability is reduced in smaller groups of fish (*Pitcher and Magurran*, 1983).

The emphasis of this model is on the hydrodynamical aspects and the energy savings. Nevertheless, the model described here is flexible enough for considering other aspects such as social behavior, as will be explained further below.

There are four main patterns of schools:

1. Solitary fish.
2. Schools that are called "together but confused." These show a locally higher density of fish, but no common orientation.
3. Schools with a common orientation and swimming direction. Such schools occur for fish moving into a common direction, such as during migration. It is not yet known if schooling is a necessary condition for migration. Certain swimming configurations guarantee energetic advantages, and larger distances can be traveled with a given amount of energy. A diamond shape swimming formation is likely to be advantageous in terms of energy and can be observed in many schools (*Weihs*, 1973, 1974b, 1975).
4. Swarm balls. These provide protection against predators; if every fish tries to hide behind its neighbors, a ball is formed by the swarm, and the vulnerable surface is minimized.

This study focuses on schools of the third type, because such schools are expected to be found during migration, whereas swarm balls are usually a short-term event. They can be observed when a group of fish is disturbed by a potential predator.

In contrast to mammal herds, fish have no leader. The cooperation of a fish school as a complex phenomenon is the result of individuals carrying the same "program," i.e., having the same physiological properties for receiving information from the environment and the same behavior patterns for reacting to it. Therefore, cellular automata seem to be an appropriate method for modeling fish schools. This type of a mathematical

model is commonly used for describing the complex interaction of individual subunits. An arbitrary number of components (the cells) follows the same set of behavior rules and only reacts on cells in the local neighborhood (*Gerhardt and Schuster*, 1995). Cellular automata became famous through Conway's game of life and were systematically studied by Stephen Wolfram (*Demongeot et al.*, 1985; *Wolfram*, 1986, 1994).

Previously, fish schools have been modeled by partial differential equations and by means of Monte Carlo simulations (*Aoki*, 1980, 1982, 1984; *Breder*, 1951, 1954, 1959; *Huth and Wissel*, 1992). The large number of fish in a school suggests describing fish schools as an interacting particle system in the framework of Newtonian dynamics (*Niwa*, 1996). Cellular automata have been used for studying swarms, mainly mammal herds (*Gueron et al.*, 1996), insects (*Rauch et al.*, 1995), or bacteria (*Stevens*, 1990, 1991). In the case of insects or bacteria, a chemical substance is the medium of communication (pheromones or slime, respectively). Other means of communication might include pressure waves produced by the tail beats of swimming fish. This requires further studies of the lateral line and its perception area (*Bleckmann*, 1993). At the present stage of research, models suggesting energetic advantages as a driving force for schooling are not always coherent with laboratory studies of the average fish-to-fish distance (*Partridge and Pitcher*, 1979). This lack of coherence is due to differences in laboratory and natural environments and to idealistic assumptions in the theoretical models.

So far, models of fish schools have been evaluated by their ability to predict cohesion and polarization (*Huth and Wissel*, 1992). Modeling a high degree of cohesion is not necessarily equivalent to modeling a realistic fish school, since fish schools may break up because of oxygen depletion (*McFarland and Moss*, 1967), or solitary fish may not find a school if the school is too distant. In order to model the oxygen consumption of fish in a school, the energy costs of swimming in that school must be known. Therefore, we also consider hydrodynamics in our model, i.e., our model merges previous models of social behavior and of hydrodynamics. An initial number of fish does not necessarily have to form one school but can can build up several schools if oxygen is scarce or if searching strategies are of limited success.

2 The Model

Schooling models are based on the following basic assumptions:

1. Every fish in the school swims according to the same behavior. This guarantees that the model fish group moves without a leader.
2. The motion of each fish is only influenced by its nearest neighbors. Vision and lateral line are considered to be the most important senses for school organization.
3. Random influences are taken into account for the individual fish.

The first assumption is based on the main difference between mammal herds and fish schools. Because there is a leader, a mammal herd has a predefined direction of motion. Therefore, one can look at animals that do not belong to the herd as moving relatively to the herd. It is possible to introduce a coordinate system that moves with the herd. This is not the case for fish schools. Since there is no predefined moving direction, the movement of each fish has to be evaluated at each time step. We will return to this point when we discuss simultaneous automata versus a nonsimultaneous updating. (We decide to update each cell at each time step, because fish in a school move constantly and without a predefined direction.)

The second assumption is the rationale for modeling fish schools with cellular automata. Cellular automata are the appropriate tool to model complex phenomena that are based on local neighborhood rules only. It is still under investigation to what degree the vision, the lateral line, and the existence of an induced velocity field (due to the tail strokes of preceding fish) interact, complete or override each other when a fish approaches a school. For some species it is proven that poor light conditions can break up a school (*Breder*, 1951), yet apparently blind fish can join a school (*Pitcher et al.*, 1976).

The third assumption for schooling models—that random influences can be considered—is often presented as a probability distribution over possible swimming directions and velocities (*Huth and Wissel*, 1992). In our model, the cellular structure allows a discrete set of moving directions, only because a fish has to move into one of the neighbor cells. Stochastics are considered whenever one discrete swimming direction is chosen at random out of the set of possible directions. "Set of possible directions" means those directions that are in agreement with observed behavior.

Before we go into the details of our model, we briefly summarize the main features of a cellular automaton briefly and clarify the terms used.

Cellular automata are a class of models especially designed in order to describe interwoven activities of a number of subsytems. This is a simple approach for modeling a complex behavior: an arbitrary number of components, all behaving according to the same rules, interact. These rules consider the local neighborhood only. Each cellular automaton is defined through the following five properties (*Gerhardt and Schuster*, 1995; *Wolfram*, 1984):

1. **Cellular space** – The space is a discrete lattice of sites. The best known lattice is a two-dimensional rectangle, the "playground" of Conways's *game of life* (*Gardner*, 1983). In our case it will be a two-dimensional hexagonal grid. Such a grid is suitable in order to model a diamond shape swimming configuration, as it will be explained below.
2. **State space** – Each site takes a set of finite possible values. In our model each cell can be empty or can be occupied by one or more fish.
3. **Neighborhood** – The evolution of a site depends on local neighborhood rules only. Unlike on a rectangular grid, we do not have to differentiate between nearest neighbors and neighbors on the diagonal line. A cell in a hexagonal grid has six direct neighbors.
4. **State evolution** – The states of the cells evolve in discrete time steps. We fit these rules to the observed behavior of fish. A fish will move toward a school and, once within the school, preferably into cells that are not highly occupied.
5. **Boundary conditions** – We choose periodic boundary conditions in order to conserve the original number of fish.

In the following we will describe our model for fish schools in referring to the properties of a cellular automata listed above.

2.1 The Cellular Space

Pictures of fish schools often show a striking organization of swimming positions, with fish swimming in rows shifted alternately to each other. That way the school shows a diamond shape swimming configuration. At

least qualitatively this can be explained by calculating the velocity field which is induced by the tail strokes of the swimming fish. For a detailed discussion of the following considerations we refer to the literature (*Weihs*, 1973, 1974b, 1975).

The induced velocity ((u, v) in the complex plane) can be derived from the complex potential w:

$$u - iv = \frac{dw}{dz}, \quad w = \Phi + i\Psi, \quad \nabla^2\Phi = \nabla^2\Psi = 0,$$

Φ is called the velocity function, and Ψ is called the stream function. They fulfill the Cauchy-Riemann differential equations.

Under the assumption of a low viscosity and high Reynolds numbers, we look at the vortices produced by the tail strokes as a *Karman vortex street* (i.e., the flow does separate).

Assuming a Karman vortex street, the complex potential of the vortex street can be calculated from the positions of the vortices in the complex plane:

$$w = -ik \sum_{n=0}^{\infty} \sum_{m=-\infty}^{\infty} [\log(z - A_1) + \log(z - A_2) - \log(z - A_3) - \log(z - A_4)].$$

Here m and n refer to the counting of the vortices and the $+$ and $-$ signs depend on the orientation of the vortices. The vortex strength k can be derived from the "thrust = drag" equation.

Gray (1968) verified experimentally that the Karman vortex street applies to the fish model.

The observed swimming positions then seem to be those that require less physical effort, i.e., those positions that are advantageous in terms of energy. The induced velocity field results in swimming positions that are more favorable and others that are less favorable in terms of energy. A fish can swim in the wake of its predecessor or against an induced current. Figures 1 and 2 illustrate the induced velocity field. The calculations underlying the figures show that preceding fish beating their tails in anti-phase produce a more favorable velocity field (without components perpendicular to the swimming direction) than fish swimming in phase. We do not claim that fish in a school deliberately move their tails in anti-phase. Such a behavior would be altruistic, because it favors the following fish. But we claim that sites where fish accidentally move their tails in anti-phase become more stabilized than sites with fish swimming in phase.

A calculation of the energetic minima suggests a diamond shape swimming configuration (*Weihs*, 1973, 1974b, 1975). Quantitatively, these calculations do not always fit the distances measured between fish in a school (*Partridge and Pitcher*, 1979), possibly because other factors such as social behavior and the perception area of the lateral line play important roles besides an optimal use of the available energy. Certainly, fish are also found in other positions than in the energetic minima. Other factors like predation and escape determine the swimming direction, and the induced velocity field is not stable, because of other objects drifting in the water. Qualitatively, a diamond-shape swimming configuration can often be observed, and we will take the induced velocity field as the natural grid for the cellular automata. That way hydrodynamics are taken into account in our model. In order to display simulations on a screen, we express the position of each cell in Cartesian coordinates $\{i, j\}$, where the sum of i and j is even, denoting the centers of the hexagons, see Figure 3.

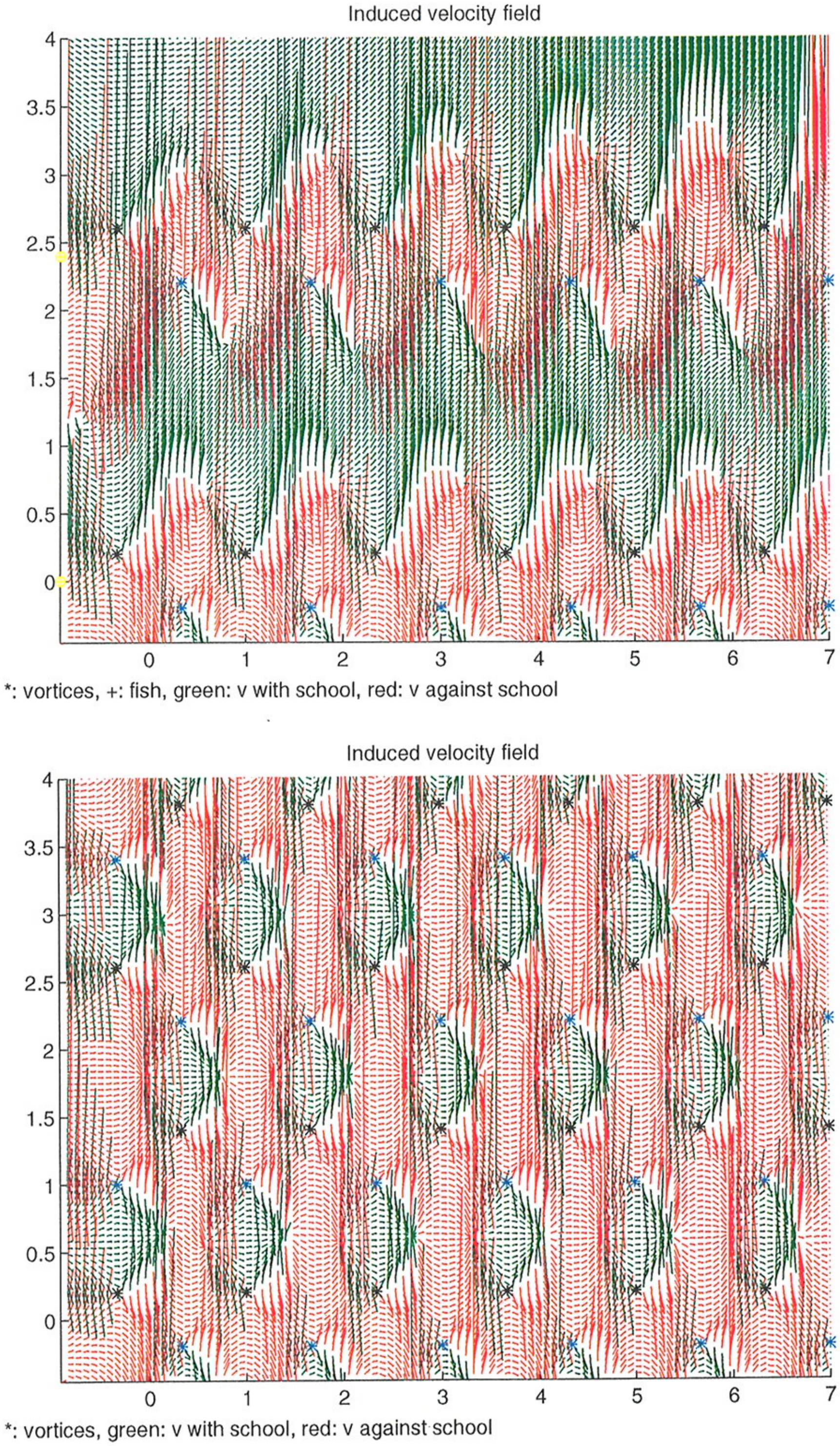

Figure 1: The induced velocity field of two fish (top) and four fish (bottom) swimming to the left with tail strokes in phase. The favorable swimming positions with the induced velocity vector into the swimming direction of the school marked in green show a velocity component perpendicular to the swimming position. This illustrates the diamond shape of the favorable swimming positions.

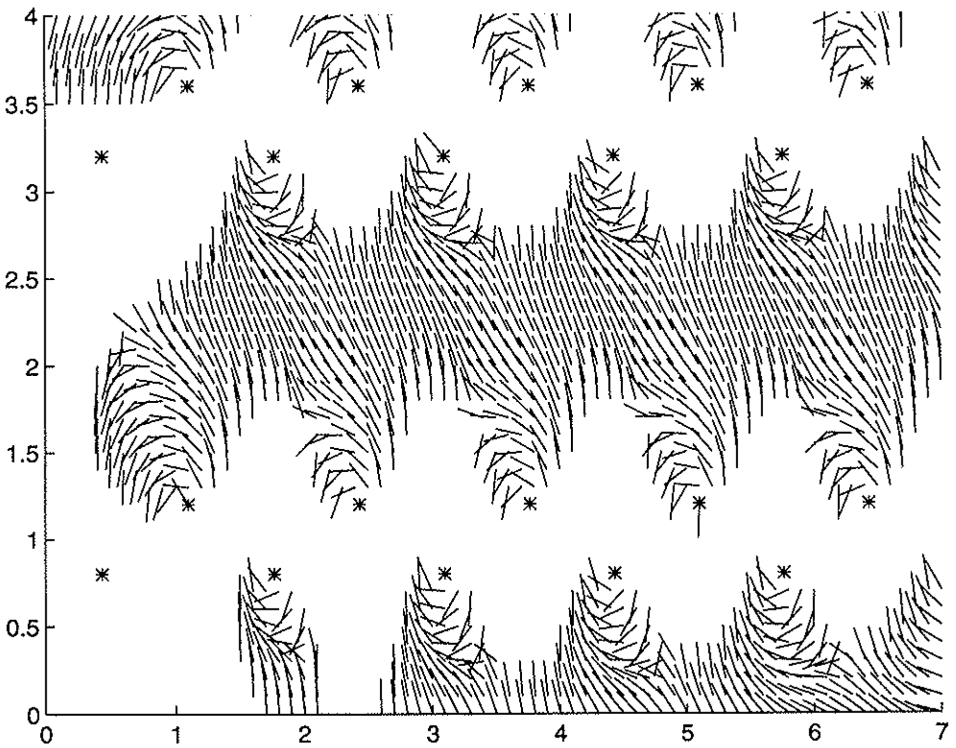

Figure 2: Same picture as Figure 1 (top) above with a magnification of the favorable swimming positions. Velocity vectors with a component against the swimming direction of the school are not printed for the sake of overall view. Two fish are swimming to the left with tail strokes in phase. The swimming positions with a velocity component into the swimming direction of the school also show a velocity component perpendicular to the swimming direction. The compensation of this component requires additional energy from the following fish.

2.2 The State Space

In the simplest version of our model, the state of each cell is a vector whose components are the swimming directions of each fish in that cell. Since there are only six possible swimming orientations (in the directions of the six neighbor cells), these components are a number from one to six. Zero indicates an empty cell.

$$s_{i,j} = \{o_1, o_2, ...\}, \quad o_k \in \{0, 1, 2, 3, 4, 5, 6\}, \quad i, j, k \in I\!N$$

Hence, the first component o_1 indicates if the cell is occupied and what the orientation of the first fish in this cell is. The vector components are consecutively filled up. If o_k is zero, all o_l with $l > k$ are zero, and there are $k - 1$ fish in the cell.

This type of a model is extremely flexible since additional components of the state variable can easily be introduced. In future versions of our model the state of a cell will be described with a tensor instead of a vector. The orientation vector is then one component of the state variable, other components possibly being the oxygen concentration and the velocity of the surrounding water:

$$s_{i,j} = \{o, C_{ox}, v\},$$

with $o = \{o_1, o_2, o_3, \ldots\}$, $C_{ox} \in I\!R$ and $v = \{v_x, v_y, v_z\}, v \in I\!R^3$.

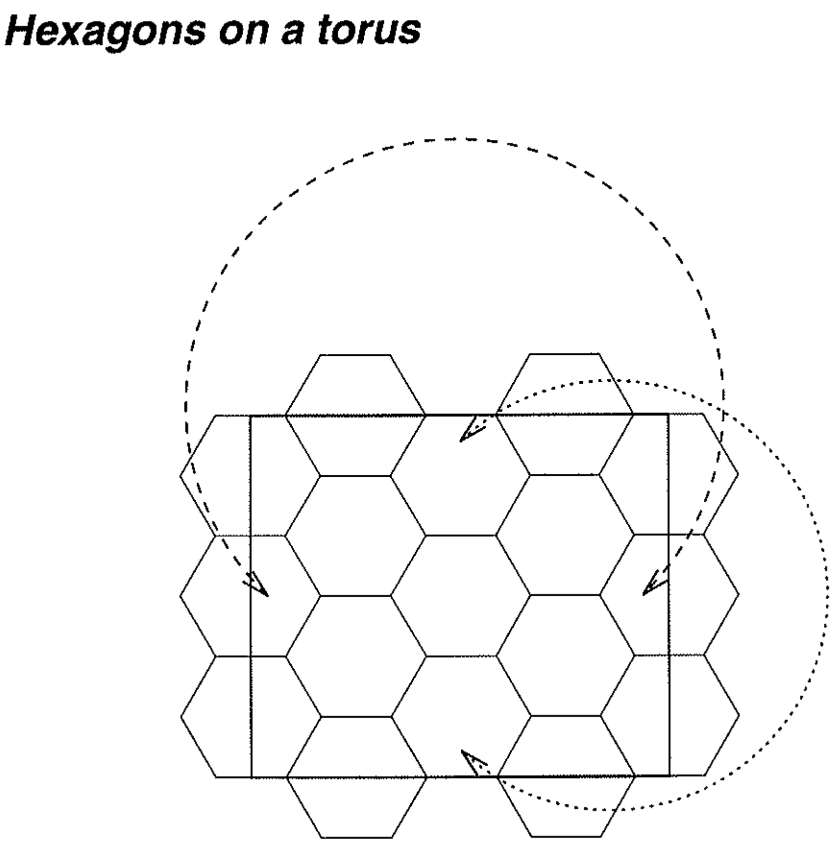

Figure 3: Boundary conditions leading to a torus. The centers of the hexagon cells can be expressed in Cartesian coordinates.

2.3 The Neighborhood

Due to the hexagon shape of the cells, the neighborhood is extremely symmetrical. Each cell has six direct neighbors. Additionally, we consider an extended neighborhood. Within the direct neighborhood fish will adjust their swimming direction. Within the extended neighborhood, they will move towards each other (see Figure 4. The nearest neighbors form a concentric ring around the center cell under consideration. If the center cell has the coordinates $\{i, j\}$, the six nearest neighbors have the coordinates,

$$\{i, j+2\},\ \{i+1, j+1\},\ \{i+1, j-1\}\ \{i, j-2\}\ \{i-1, j-1\}\ \{i-1, j+1\},\ i, j \in I\!N$$

keeping in mind that a hexagonal grid expressed in Cartesian coordinates allows x, y-coordinates with even sums only.

The next concentric rings of cells consist of $12, 18, \ldots$ cells. The coordinates of these cells can easily be determined from Figure 4. In our terminology we speak about a neighborhood of radius r, where $r \in \{1, 2, 3, \ldots\}$. Even though the concentric rings of neighbor cells form hexagons rather than a circle, we refer to the term "radius" as the result of the division of the number of cells in such a ring by six. Hence, the direct neighbors belong to the neighborhood of radius one, the radius of the next ring is two, etc. We assume a dead angle area behind every fish, where that fish cannot realize neighbors.

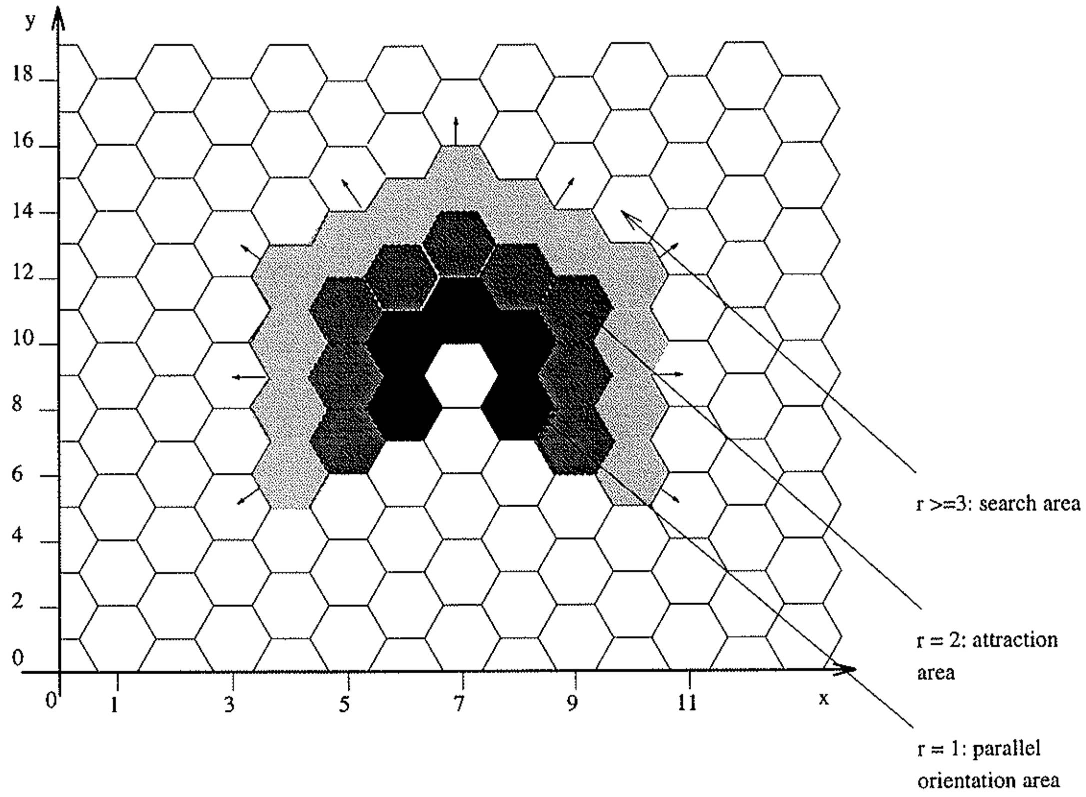

Figure 4: The neighborhood of a cell in a hexagon grid

2.4 The State Evolution

The rules for the state evolution are summarized in Figure 5 and are in accord with the general rules of schooling models mentioned in the introduction to this section.

In the following we explain the most simple set of rules for the state evaluation that is still reasonable in biological terms. More complicated rules are possible and desirable from a biological point of view, but the rules listed here for updating the automaton at each time step should be the basis for future model development.

The occupancy of each cell is checked at the beginning of the updating algorithm. If a cell is occupied by more than one fish, any additional fish will move towards the closest empty cell. That way the repulsion area of former schooling models is considered (*Huth and Wissel*, 1992). We assume that fish swimming too close to each other will disturb each other through their tail strokes.

The new moving direction (a number between one and six indicating one of the six neighbor cells) for all single fish in all occupied cells must then be determined. Parallel orientation has higher priority than searching. Therefore, for any occupied cell the orientation area is checked. If there are fish in the orientation area, the new moving direction of the fish under consideration is the rounded average of all swimming directions of all fish in the parallel orientation area, including the center fish. If the average is exactly between two possible swimming directions, either direction is chosen at random. If there are no fish in the orientation area, fish in the attraction area are checked, and the fish under consideration moves towards the closest fish. Only if there are no fish in the orientation area nor in the attraction area do the fish move at random, i.e., the

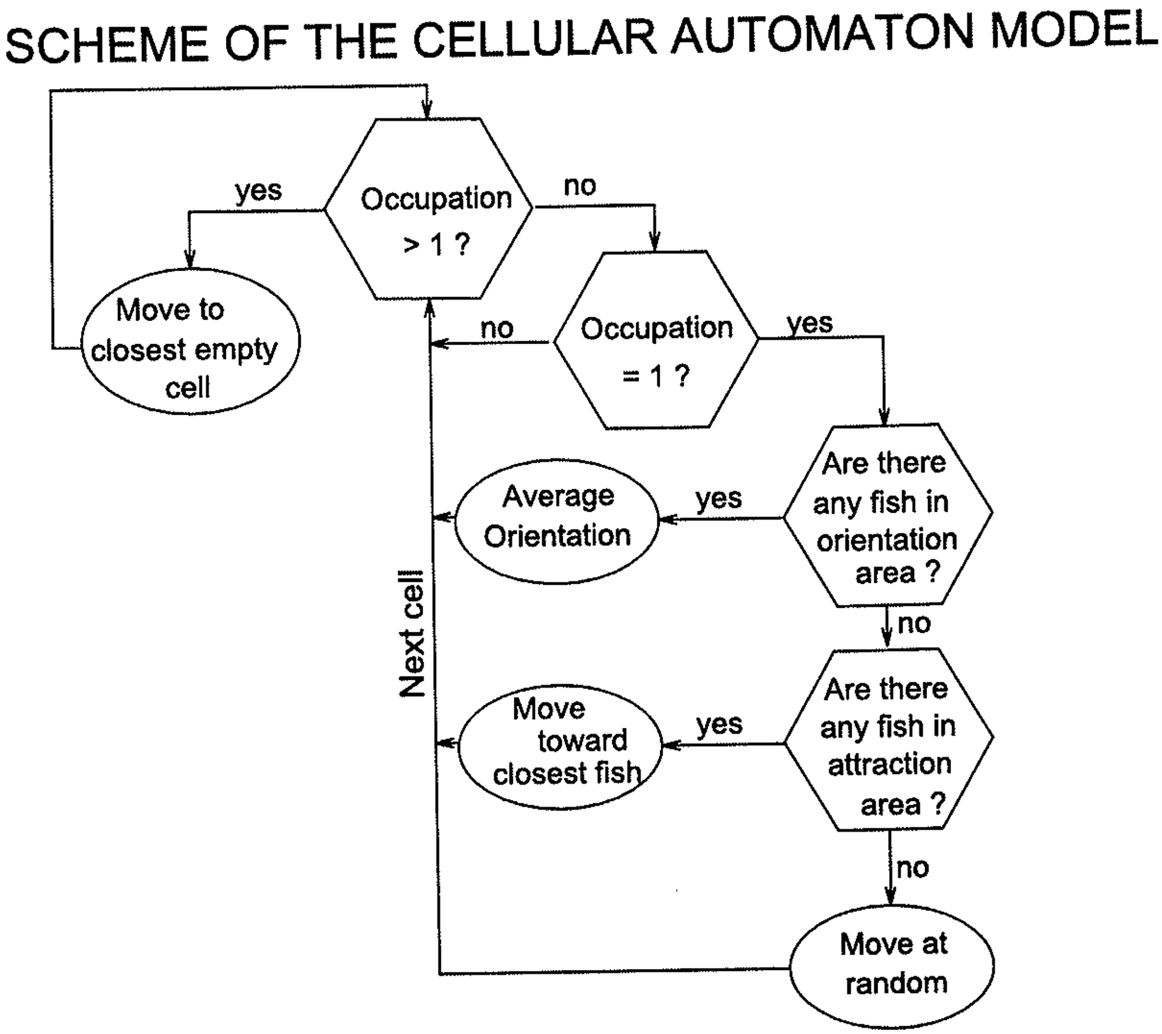

Figure 5: A scheme for the cellular automaton model

direction component of the state variable is a random number between one and six.

The orientation area and the attraction area are defined by their radius from a center in the cell of the fish under consideration. The term radius as it is used on our hexagonal grid is defined in the previous section. For the simulations, a radius of one or two is used for the orientation area and of two or three for the attraction area (see Figure 4).

As previously mentioned, this model is based on normalized parameters. In order to avoid a multiple occupation of cells, it is defined that a cell is equivalent to the repulsion area. If it is assumed that fish move from one cell to the next within one time step, it becomes clear that the length of a time unit is the quotient of the radius of the repulsion area divided by the average swimming speed of the school.

Strictly speaking, the state evolution of the cells rather than the fish is observed. Speaking in terms of cellular automata, the state vector of an occupied cell receives a direction component from the fish occupying that

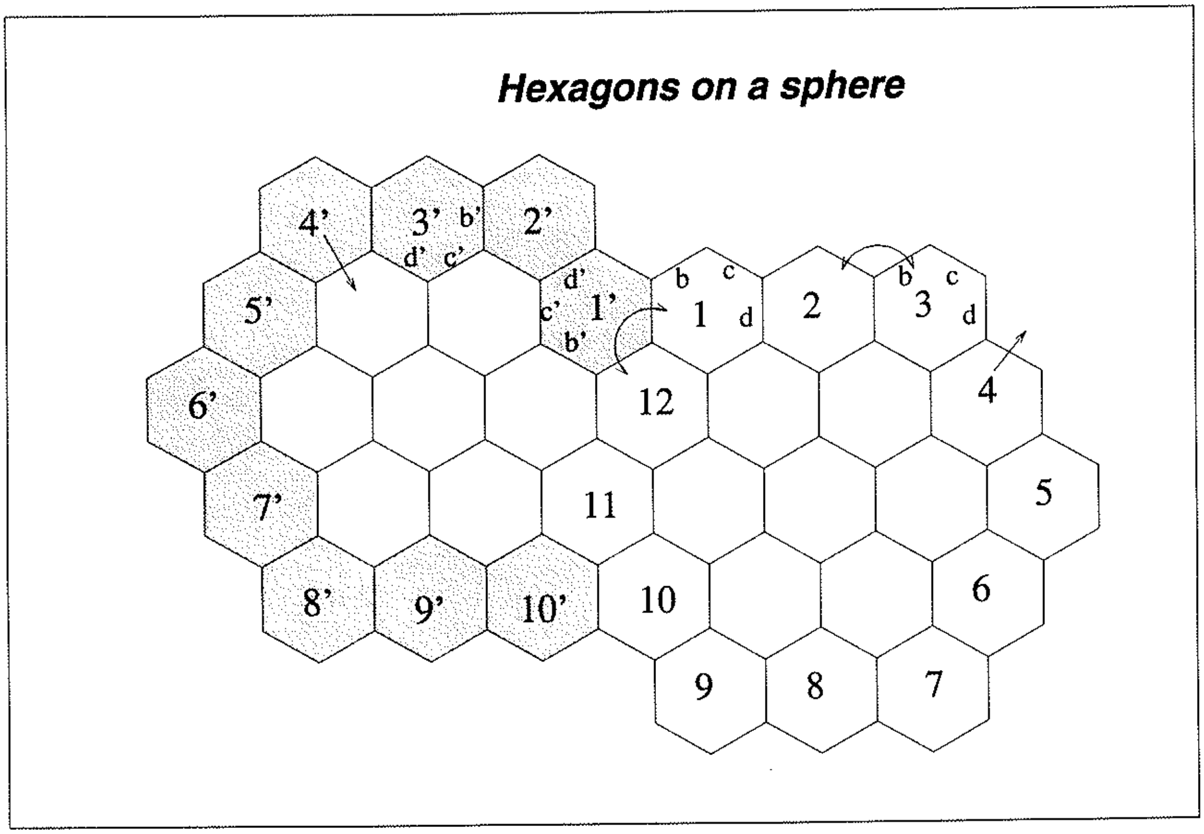

Figure 6: Closing a lattice of hexagons to a transformed sphere. The hexagons printed in gray form the equator line. They are twice plotted and can be identified through their numbers. Some hexagons along the equator line only have five neighbors, because they touch one of their neighbors with two edges. Because of these singularities we speak about a transformation and not about a homoeomorphism on the sphere.

cell. An unoccupied cell can switch to the state "occupied" if it has an occupied neighbor cell and if the direction component of the state vector of this occupied neighbor cell points into the empty cell.

2.5 The Boundary Conditions

Periodic boundary conditions are chosen in order to conserve the initial number of fish. As already mentioned, the location of the hexagon cells is expressed in Cartesian coordinates. Thus, periodic boundary conditions yield a torus. The high symmetry of the hexagons enables closure of the space into a transformed sphere (see Figure 6). However, the display of a grid that consists of the proper amount of hexagons that can be closed to a transformed sphere, is not very clear. Therefore, the classical boundary conditions that lead to a torus are used (Figure 3). In any case, the boundary conditions should not have a major influence on the simulation results.

3 Results

3.1 Simulations

For the sake of an overall view we present simulations with a relatively small number of fish in generalized coordinates. The calculation of the maximum possible length of a school is based on experimental data.

With the cellular automaton described in the previous section we simulate the behavior of a number of fish initially distributed at random. Also the initial swimming directions are determined at random out of the six possible swimming directions (on a hexagonal grid). The code is written in C++ and on request available from the author. For each simulation the initial value of the random generator was written down in order to allow a reproduction of the obtained results at a later time. The state of the cellular automaton was at each time step stored in data files, and the entire state evolution can be displayed with a matlab program (*Wolfram*, 1988). For this publication we show the initial and final step of a sample evolution (see Figure 7).

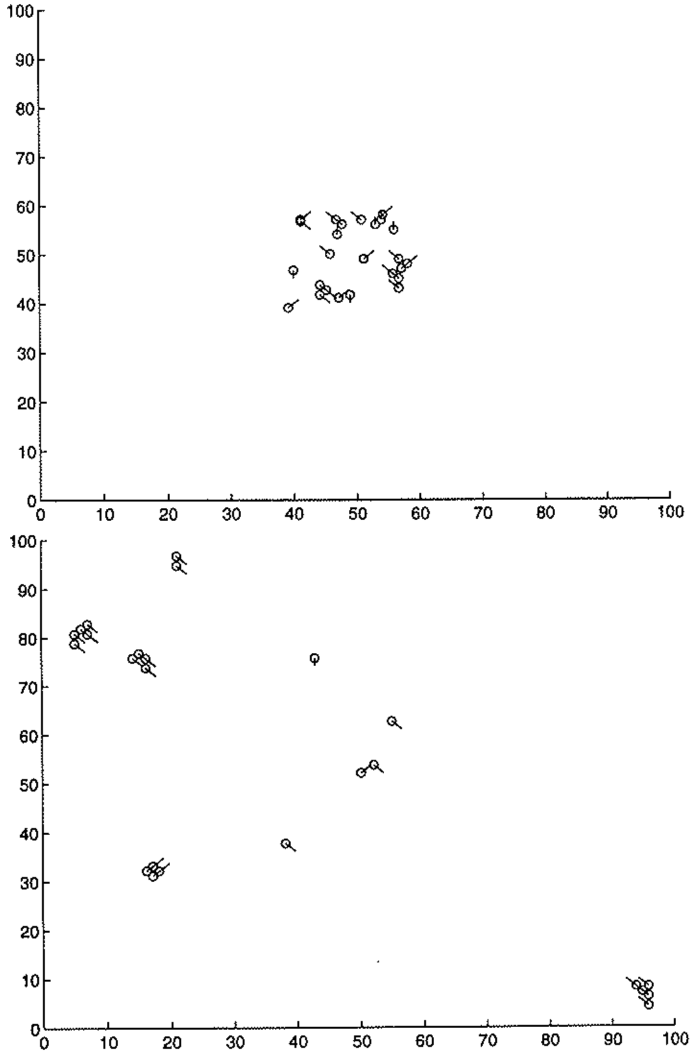

Figure 7: Initial distribution of 25 fish and the formation of schools after 40 time steps.

For the statistical analysis, the number and size of schools is recorded as well as the polarization of each school. It is a matter of definition how dense an aggregation of fish has to be in order to be considered as a school. Therefore, we counted schools for an evaluation radius of one, two, or three. With an evaluation radius of one, fish are considered to belong to the same school only if they occupy nearest neighbor cells. With an evaluation radius of two, one empty cell may be between fish of the same school, and with an evaluation radius of three there may be a gap of two empty cells. Table 1 shows the statistical analysis for the final formation in Figure 7 for the measure radius one and two. With the measure radius two, a conglomeration of two not-parallel oriented fish, as they can be found in Figure 7 in the center of the second picture, is still considered as a school. We calculate the average size of a school by dividing the total number of fish by the number of schools (single fish are considered as schools of size one). The mean swimming direction of each school is determined through the vector sum of the swimming velocities of all fish divided by the number of fish in the school under consideration. For the standard deviation of the school size we evaluate

$$\sigma_n = \sqrt{\sum_i (n - n_i)^2/n}, \qquad i = 1, \ldots, s,$$

where s is the number of schools, n_i the size of school i, and n the average school size.

Equivalently, we determine the standard deviation of the mean swimming direction for each school:

$$\sigma_{\bar{\alpha}_i} = \sqrt{\sum_i (\bar{\alpha}_i - \alpha_{i,j})^2/n_i}, \qquad j = 1, \ldots, n_i,$$

where $\bar{\alpha}_i$ is the mean swimming direction of school i and $\alpha_{i,j}$ the swimming direction of a single fish in that school (*Huth and Wissel*, 1992). A perfect polarization is reached if $\sigma_{\bar{\alpha}_i} = 0$.

All results show a perfect polarization, i.e., no or only little derivation from the swimming direction. This is not surprising, since we discretized the possible swimming directions to only six. Therefore, the resolution of possible swimming directions is not higher than sixty degrees (360/6). This is acceptable, because the emphasis of this study is the investigation of school sizes. Furthermore, schools with strongly coherent swimming directions can indeed be observed. This holds even more in the time average, as schools would fall apart otherwise.

The results on the school size instead depend on the model assumptions. All simulations show schools as well as solitary swimming fish after a sufficient amount of time steps. Not only the radius of the attraction area, but also the radius of the orientation area affects the size of the school: if fish start to swim into the same direction, even if they are not nearest neighbors, they are more likely to become the nucleus of a school.

3.2 The Length of Fish Schools

In the following we calculate the maximum length of fish schools, assuming that oxygen is the limiting factor. Toward the rear of a school, oxygen can be depleted by the oxygen consumption of fish in the front of the school. Oxygen reductions of about thirty percent are reported for schools of mullet. If fish in the end of the school actively roil the water surface, the school is close to breakup (*McFarland and Moss*, 1967).

In order to calculate the oxygen consumption throughout a school, we need to know the oxygen need of fish swimming in a single line. The oxygen requirement depends on the swimming speed of the fish.

The *gross metabolic rate* (GMR in [W/t]) is a function of speed, water temperature, light, age, season, etc. Typical values (*Bushnell and Brill*, 1991, 1992; *Bushnell et al.*, 1990) are

Table 1: Statistical results for simulation of 25 fish in measure radius 1 and measure radius 2.

School #	School size	Mean swimming direction	Standard deviation
measure radius = 1			
1	5	-60	0
2	4	-120	0
3	1	-60	0
4	4	-60	0
5	1	0	0
6	2	-60	0
7	1	-60	0
8	5	120	0
9	1	-60	0
10	1	-120	0
	average school size: 2.5		
	standard deviation: 3.4		
measure radius = 2			
1	5	-60	0
2	4	-120	0
3	2	-90	30
4	4	-60	0
5	1	0	0
6	2	-60	0
7	1	-60	0
8	5	120	0
9	1	-60	0
	average school size: 2.8		
	standard deviation: 2.9		

6.84 J/s for a 2.8 kg yellowfin tuna swimming with 1.3 bl/s,
7.63 J/s for a 1.8 kg skipjack swimming with 2.2 bl/s,

where "bl" denotes body lengths.

The required energy can be recalculated in oxygen need, using the *oxycaloric equivalent* E_{O_2} (energy/V_{O_2}). For muscular work it is

14.1 J/mg O_2 or 20.1 J/ml O_2.

We compare the oxygen need to the oxygen available in sea water. The oxygen concentration in sea water of 20°C is $C_{ox} = 5.3$ ml O_2/l water. The appropriate temperature for tuna is higher than that—about 27°C—possibly resulting in a lower oxygen concentration.

The oxygen available for a fish in a school is

$$O_{av} = u_{eff} \times A \times C_{ox},$$

where u_{eff} is the *effective* speed and A is the capture cross section of a single fish. The *effective* speed can be higher than the speed that determines the metabolism ($u_{metabol}$) if the fish performs energy saving strategies.

The oxygen need for n fish in a consecutive row is

$$O_{need} = n \times \mathrm{GMR}(u_{metabol})/E_{O_2}.$$

Oxygen is entirely depleted if

$$n_{max} = \frac{u_{eff}\, A\, C_{ox}}{\mathrm{GMR}(u_{metabol})\,/\,E_{O_2}}$$

We calculate an upper limit of the school length. Of course, the school will break up before the oxygen of the surrounding water is entirely depleted. On the other hand, we neglect a refreshment of oxygen due to the mixture with water from the larger environment of the school.

In the following we show two examples for two tuna species, using the physiological data from the beginning of this section. Assuming an average body length of 53.7 cm for a school of yellowfin tuna, the previous considerations yield a school of 108 fish swimming in a consecutive row, or a school length of 58 m. Assuming a school of skipjack with an average body length of 47.2 cm, the previous considerations result in 145 fish or a school length of 68 m. The striking unity of body size of fish within the same school has been reported and is not an additional assumption in the previous calculations.

The oxygen need can be reduced when fish swim with energy saving strategies. As mentioned throughout this study, swimming in advantageous positions is an energy saving strategy. Every second row of fish needs only 50% of the normally at that speed required energy, because it swims with the water stream. Therefore, the entire school length can increase by 4/3.

Another energy saving strategy is burst and coast swimming (*Weihs*, 1974a; *Videler and Weihs*, 1982). A fish can reach the same effective speed and reduce the required energy by 40 to 80%. That way the school length can increase by a factor of 1.25 to 2.5.

4 Discussion

The objective of the work suggested here is to model realistic school sizes. This is decisive for estimation of stock sizes.

As a technique, we suggest a cellular automaton model, since the phenomenon of schooling is apparently based on the same behavior pattern for each member of the school. We succeeded in simulating the evolution of several schools distributed in space. Previous studies modeled the formation of one large school only.

Previous studies have shown that so-called averaging models lead to better results than decision models (*Huth and Wissel*, 1992). In averaging models, each fish averages the behavior of its neighbor fish; in decision models each fish chooses at random a "leader" fish in its environment. We relate the better results of the averaging model to the hydrodynamic conditions of a school. The induced velocity field is a superposition of wakes produced by all fish in that school. No fish can choose to swim in the wakes of one other neighbor fish only.

We combine behavior and hydrodynamic models for fish schools. We consider hydrodynamic advantages in introducing a hexagonal grid, where the cells to be occupied are already in the favorable positions.

So far, our model is two-dimensional only, assuming that the major interaction of fish happens in the plane of their swimming direction. This is very convenient from a mathematical point of view, because it is very elegant to derive the velocity field in the complex plane from the complex potential. It has to be investigated how fish swimming above each other influence each other and if the mathematical assumptions made here are justified. Because of the technical problems, there are only a few studies and video recordings of large fish schools in the deep sea (*Aoki et al.*, 1986). Schools of larger fish such as tuna can hardly be studied in basins, since lab conditions alter the natural environment too much. Changing the swimming direction constantly due to the limitations of a basin requires additional energy from the fish.

The introduction of a natural geometry, such as a hexagonal grid, simplifies the consideration of hydrodynamic aspects and restricts our model at the same time to a certain class of fish schools. Fish schools of an entirely different structure such as swarm balls or unorganized fish aggregations cannot be considered. Our model applies mainly to such fish that school for the sake of energy savings. Tuna is supposed to belong to that group, because the energetic requirements on tuna fish are outstanding and extreme (*Brill*, 1994, 1996). Since tuna fish are not able to actively pump water over their gills, they need to swim to maintain an adequate oxygen supply. At the same time, swimming increases the metabolism and therefore the oxygen need (*Bushnell and Brill*, 1991, 1992; *Bushnell et al.*, 1990).

In a later version of the model it would be interesting to introduce a "reason-for-schooling-factor." In such a model, foraging, protection, energy savings, and reproductive advantages would be numerically weighted according to the fish species under consideration. Depending on these weights the simulation of the schools would result in structures such as swarm balls, diamond shapes, or soldier lines (*Partridge et al.*, 1983).

The vector structure of the state variables allows an arbitrary number of components. Therefore, the model can be easily extended, taking into account further aspects such as prey density, distance to possible predators, and the chemical composition of the surrounding water.

As already mentioned, cellular automata can be updated either simultaneously or in an asynchronous way. For one-dimensional automata it has been shown that the fact of a simultaneous updating by itself can cause structures which have nothing to do with the underlying problem (*Ingerson and Buvel*, 1984). It is not yet clear if this holds for two-dimensional automata. We consider simultaneous updating appropriate, because fish in a school continuously swim. It would not be realistic to simulate a single fish moving while all other fish are "waiting." This is different from mammal herds, which from time to time stop for the purpose of feeding. We do not claim that every fish decides at the same moment where to swim next, but that the evaluation steps of the cellular automaton are momentary displays of an ongoing action. Nevertheless, it remains interesting to investigate cellular automata with a set of behavior rules for school formation with the evaluation of one cell at a time.

Last but not least, searching strategies deserve further interest. Which search strategies result in an easier aggregation of initially solitary fish? What is the optimal distance to be crossed, before a fish that does not succeed in finding a school needs to change its swimming direction?

With the model suggested here we hope to introduce a new model type that merges former behavior and hydrodynamical models. We hope that the questions that arose in this context, such as search strategies, size and polarization of schools, can also give direction for further experimental studies.

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