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# Models for tuna school formation

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## Abstract

Schooling behavior is a challenging topic in the context of animal aggregation. It is also 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. The latter considers 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 break up of schools due to oxygen depletion. This allows us to estimate maximum school sizes. © 1999 Elsevier Science Inc. All rights reserved.

*Keywords:* Fish school formation; Cellular automaton models; Behavioral model based simulations; Populations with spatial structure

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## 1. Introduction

The investigation of fish schools is interesting as a phenomenon of complex structure and of self organization in animal life. It is also of economic importance for fisheries worldwide. The fact that fish schools exist is essential for some fisheries, since fishing can be targeted on schools. The knowledge about school sizes, their occurrence and their distribution can help to make use of fish

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as protein rich food stuff without exhausting the stock. Therefore, a better understanding of the formation of fish schools and their migration [1–3] is essential.

Increasing yields in fishery are misleading as long as the catch intensity is increasing. During the period from 1939 to 1959 the annual catch of yellowfin tuna in the East Pacific increased from 56 250 000 to 85 500 000 kg, whereas the local amount decreased from 4050 to 2250 kg per 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 fatal if the share of young fish in the catch is increasing, because the young fish are guaranteeing the offspring. 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, because the commonly used CPUE (catch per unit effort) might increase due to improved technologies, even if the fish stock would be decreasing. The definition of the CPUE depends on the catch strategy. It can be *numbers of fish per 100 hooks* for long-liners, or *metric tonnes per day* for pole-and-line vessels [4,5].

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

We suggest a theoretical two-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 cross the unit length.

The application of this model to concrete situations will be 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. Within some species mature fish are solitaire, but swim in the swarm when they are young, such as *Micropterus*, a bass species. Some sharks, instead, form schools for mating. There are several reasons why fish are schooling. The relative importance of the reasons listed in the following is different for different fish species.

- *Protection*: although the school in its entirely form 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 [6–9].

- *Social aspects*: there are social advantages of schooling, such as a higher possibility to find 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 plus one male. If the male is removed, one of the females changes sex in response to visual stimuli [10].
- *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 [11].

The emphasis of this model is on behavior that possibly originates in energy saving strategies. In a phenomenological way we consider hydrodynamic aspects, as they can explain certain swimming configurations. Without developing our model on a hydrodynamic level, we use results of previous studies for the geometrical conception of our model. The model to be presented in the following is flexible enough for considering other aspects such as social behavior, as will be explained further below.

We consider four main patterns of schools. There are:

1. solitary fish,
2. schools that are called ‘together but confused’. They show a locally higher density of fish, but not common orientation,
3. 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 crossed with a given amount of energy. A diamond-shape swimming direction is likely to be advantageous in terms of energy and can be observed in many schools [7–9].
4. swarm balls guarantee protection against predators. If every fish tries to hide behind its neighbors, a ball is formed by the swarm. That way, the vulnerable surface is minimized.

This study focuses schools of the third type, because such schools are expected to be found during migration, whereas swarm balls are rather 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 on them. 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 [12]. Cellular automata became famous through Conway's game of life and were systematically studied by Stephen Wolfram [13–15].

Previously, fish schools have been modeled by partial differential equations and by means of Monte Carlo simulations [16–22]. The high number of fish in a school suggests to describe fish schools as an interacting particle system in the framework of Newtonian dynamics [23]. Cellular automata have been used for studying swarms, but mainly mammal herds [24], insects [25] or bacteria [26,27]. In the case of insects or bacteria a chemical substance is used as a medium of communication (pheromones or slime, respectively). It might be worthwhile to investigate pressure waves, produced by the tail beats of swimming fish, in a similar way as a means of communication [28], i.e. as an external field determining the swimming configuration. This requires further studies of the lateral line and its reception area. 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 [29]. This is due to differences in laboratory and natural environments and also due to idealistic assumptions in the theoretical models.

So far, models of fish schools were evaluated by their ability to predict cohesion and polarization [22]. Modeling a high degree of cohesion is not necessarily equivalent to modeling a realistic fish school, since fish schools may break up due to oxygen depletion [30] or solitary fish may not find a school if the school is too far. In order to model the oxygen consumption of fish in a school, the energy costs of swimming in that school must be known. An initial number of fish does not necessarily have to build up one school. Fish can build up several schools, if oxygen is scarce or if searching strategies are of limited success. In two sample calculations we will show how school size and oxygen depletion can be related.

In previous Monte Carlo simulations, positions and swimming angles were continuous variables. They can be evaluated for each fish at each time step by means of probability distributions, whose maxima are determined by the states of the neighbor fish [16–18,22]. Efforts have to be made to determine the neighbor fish at each time step, which forbids dealing with too large numbers of individuals. It has been suggested to make a choice of representative individuals for simulating large schools [31].

Our basic assumptions (see below) on fish behavior are equivalent to those made in the studies mentioned above, but we model in a discrete state space with a discrete set of swimming positions and angles. This reduces the numerical effort, and, instead, we are able to present simulations with a larger and therefore more realistic number of fish. We do not consider our approach as an oversimplification, as pictures of fish schools show a striking order of well defined swimming positions, and as hydrodynamical considerations suggest such an order as well.

## 2. The model

Schooling models are based on the following basic assumptions [17,22]:

1. Every fish in the school swims according to the same behavior model. The model fish group moves without a leader, even though temporary leaders seem to appear in the simulations.
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 item points out 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 leader of 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 – either at each time step or in a random sequence.

Due to the second point it stands to reason to model 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 which 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 bad light conditions can break up a school [21], yet apparently blind fish can join a school as well [32].

The third requirement for schooling models – the consideration of random influences – is often solved by a probability distribution over possible swimming directions and velocities [22]. 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: if a fish averages the swimming directions of its neighbors, a swimming direction not pointing a neighbor cell might result. In such a case one of the neighbor cells closest to that swimming direction is chosen at random.

Before we go into the details of our model, we will summarize the main features of a cellular automaton briefly. This we do for clarifying the used terms.

Cellular automata are a class of models especially designed in order to describe interwoven activities of a number of subsystems. 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 [12,33]:

1. *Cellular space* – a discrete lattice of sites. The best known lattice is a two-dimensional rectangle, the ‘playground’ of Conway’s *game of life* [34]. In our case it will be a two-dimensional hexagon 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 towards a school, and once within the school preferably into cells which 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 cellular automata listed above.

### 2.1. The cellular space

Pictures of fish schools often show a striking organization of swimming positions. Fish swimming in rows shifted alternately to each other. That way fish show 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 [7–9].

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

$$u - iv = \frac{dw}{dz}, \quad w = \Phi + i\Psi, \quad \nabla^2 \Phi = \nabla^2 \Psi = 0, \quad (2.1)$$

$\Phi$  is called the velocity function, and  $\Psi$  is called the stream function. They fulfill the Cauchy–Riemann-differential-equations.

Under the assumption of a low velocity 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

$$w(z) = -ik \sum_{n=0}^{\infty} \sum_{m=-\infty}^{\infty} [\log(z - A_1(m, n)) + \log(z - A_2(m, n)) - \log(z - A_3(m, n)) - \log(z - A_4(m, n))]. \quad (2.2)$$

Here  $z$  is a point in the complex plane, and  $A_j(m, n)$  are the positions of the vortices, where  $m$  refers to the counting of vortices stemming from neighbor fish, and  $n$  refers to the counting within a single vortex street of vortices shed by one single fish. The  $+ -$  signs are depending on the orientation of the vortices. The vortex strength  $k$  can be derived from the ‘thrust = drag’ equation. For more details see Ref. [7].

Gray 1968 verified experimentally that the Karman vortex street applies to the fish model [35]. The observed swimming positions then seem to be positions which require less physical effort, i.e. these positions are advantageous in terms of energy. Due to the induced velocity field, there are swimming positions which are more favorable and others which are less favorable in terms of energy. A fish can swim in the wake of its predecessor or against an induced current. In deriving  $w(z)$  (Eq. (2.2)) with respect to  $z$  the induced velocity field can be calculated. It is illustrated in Figs. 1–3. The calculations underlying the figures show that preceding fish beating their tail 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 situations where fish accidentally move their tail in anti-phase rather become stabilized than situations with fish swimming in phase.

A calculation of the energetic minima suggests a diamond-shape swimming configuration [7–9]. Quantitatively, these calculations do not always fit the distances measured between fish in a school [29]. Possibly, because other factors such as social behavior and the reception 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 escaping 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 base the grid for the cellular automata on the induced velocity field. 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,  $s$  (Fig. 7).

In general, cellular automata are criticized if they show patterns that possibly reflect nothing more than the underlying grid, and efforts – such as randomizing the grid – are made to avoid such situations, since they are due to numerical reasons without reflecting the biological reality [36]. Here, instead, the grid is chosen deliberately and consciously, as we intend to implement the anisotropy due to the wakes into our model.

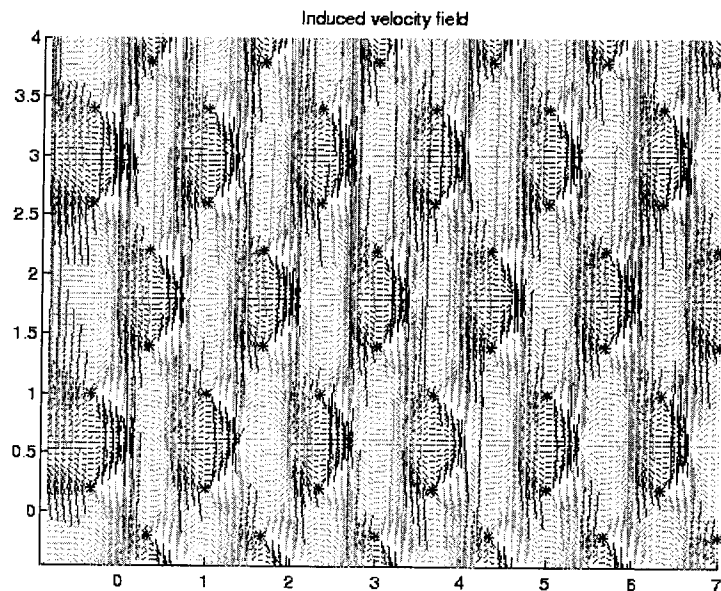


Fig. 1. The velocity field left behind by four fish swimming to the left (calculated with the derivation of the complex potential with respect to the complex variable, see Eq. (2.2)). The vortices left behind by the fish swimming to the left are marked with an asterisk. Vector arrows are not plotted for the sake of overall view, and directions are indicated by color shadings instead. Velocity vectors with a component into the swimming direction of the school are plotted in a darker grey. In the positions plotted in a lighter grey the induced velocity field is directed against the swimming direction of the preceding fish. Focusing the darker areas shows that the favorable positions form a diamond structure.

## 2.2. The state space

In the simplest version of our model the state of each cell is a vector whose nonzero 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 between one and six. Zero indicates an empty cell, and the number of nonzero elements indicates the number of fish in that cell.

$$s_{i,j} = \{o_1, o_2, \dots\}, \quad o_k \in \{0, 1, 2, 3, 4, 5, 6\}, \quad i, j, k \in \mathbb{N}. \quad (2.3)$$

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.



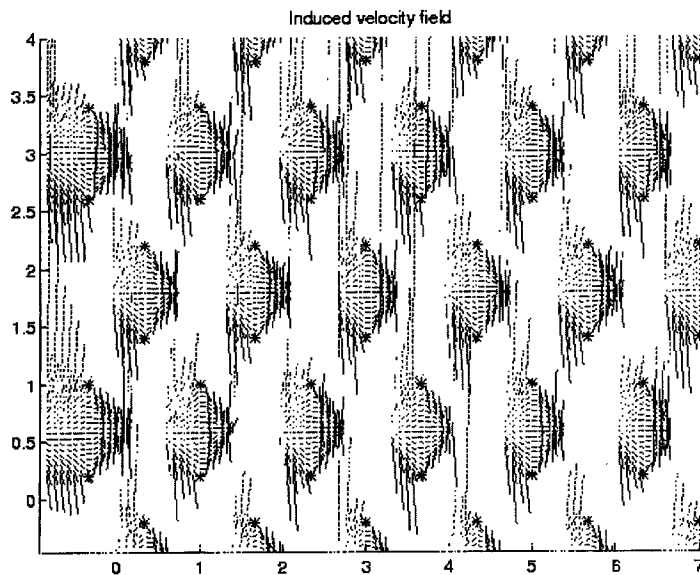


Fig. 2. Same picture as before. Velocity vectors with a component against the swimming direction of the school are not plotted in order to point out the favorable swimming positions.

This type of model is extremely flexible since further components of the state variable can easily be introduced. In further versions of our model the state of a cell can be described with a set of vectors. 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:

$$s_{i,j} = \{o, C_{\text{ox}}, v\}, \quad (2.4)$$

with

$$o = \{o_1, o_2, o_3, \dots\}, \quad C_{\text{ox}} \in \mathbb{R} \text{ and } v = \{v_x, v_y, v_z\}, \quad v \in \mathbb{R}^3. \quad (2.5)$$

Especially, we present simulations where oxygen consumption in a cell is modeled as

$$c_{\text{ox},t+1} = c_{\text{ox},t} + \rho(1 - c_{\text{ox},t}) - c_{\text{ox},t}\zeta n. \quad (2.6)$$

Here,  $c_{\text{ox}}$  is the oxygen concentration in a cell,  $\rho$  a replenishment rate,  $\zeta$  the oxygen consumption by a single fish,  $n$  the number of fish in a cell, and  $t$  and  $t+1$  refer to two consecutive time steps. Oxygen is supposed to be replenished due to the mixing of water, and the maximum oxygen concentration (depending on the water temperature) is normalized to one. Fish then only enter a cell if the oxygen concentration is above a critical value:  $c_{\text{ox}} > c_{\text{ox,crit}}$ , otherwise they turn away from the critical cell.

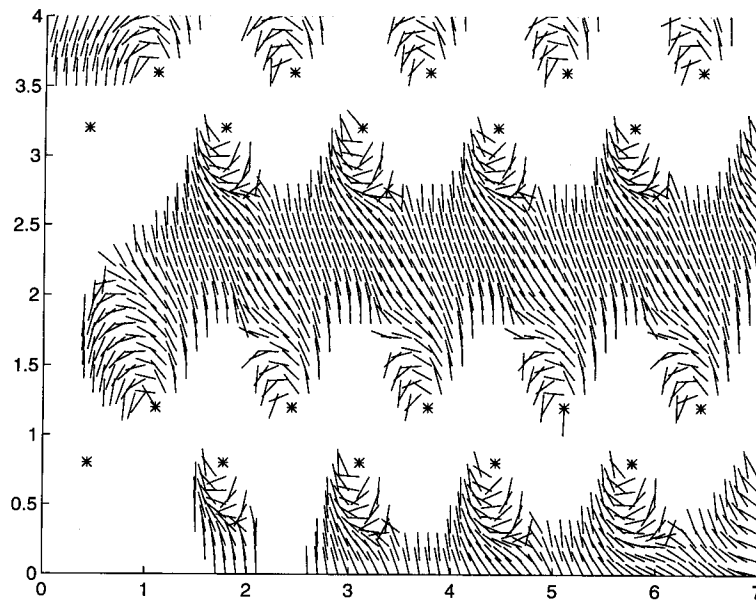


Fig. 3. Velocity field induced by two fish swimming to the left with tail strokes in phase. Only the favorable swimming positions with a component into the swimming direction of the school (here: to the left) are plotted. If the preceding fish move their tails in phase, the velocity vectors show a component perpendicular to the swimming direction of the school. The compensation of this component requires additional energy from the following fish. Again the vortex positions are marked with an asterisk. Here, two vortices with identical horizontal ( $x$ -), but different vertical ( $y$ -) positions have the same orientation, as the fish strike their tails in phase. In the previous two figures such two vortices have opposite orientation.

### 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 Fig. 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

$$\begin{aligned} &\{i, j + 2\}, \quad \{i + 1, j + 1\}, \\ &\{i + 1, j - 1\} \{i, j - 2\} \{i - 1, j - 1\} \{i - 1, j + 1\}, \\ &i, j \in \mathbb{N} \end{aligned}$$

keeping in mind that in our fixing the centers of the hexagons expressed in Cartesian coordinates allow  $x, y$ -coordinate pairs with even sums only.

The next concentric rings of cells consist of 12, 18, ... cells. The coordinates of these cells can easily be determined from Fig. 4. In our terminology we speak about a neighborhood of radius  $r$ , where  $r \in \{1, 2, 3, \dots\}$ . Even though the concentric rings of neighbor cells from 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.

#### 2.4. The state evolution

The rules for the state evolution are summarized in Fig. 5. These rules are according to the general rules of schooling models as mentioned in the introduction to this chapter.

In the following we explain the most simple set of rules for the state evolution, which 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 occupation of each cell is checked in the beginning of the updating algorithm. If a cell is occupied with more than one fish, any additional fish will

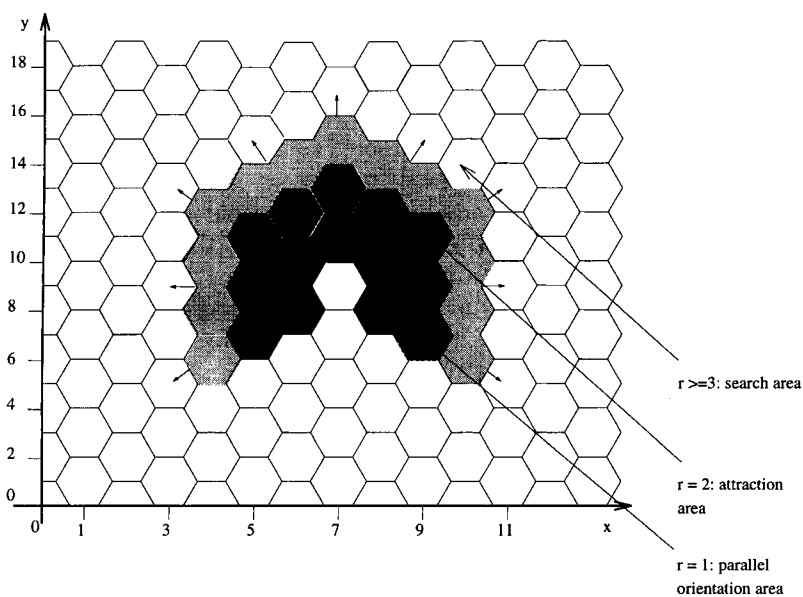


Fig. 4. The neighborhood of a cell in a hexagon grid.

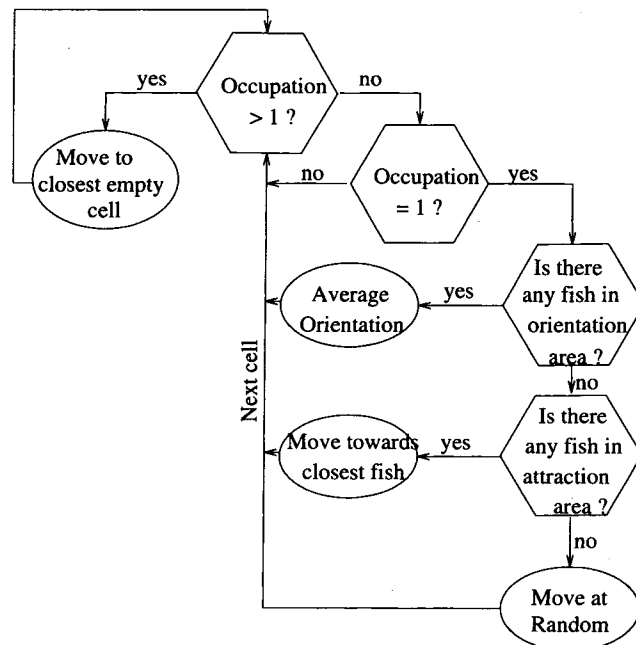


Fig. 5. A scheme for the cellular automaton model. These rules for the state evolution are applied to each occupied cell (i.e. to each fish) at each time step.

move towards the closest empty cell. That way the repulsion area of former schooling models is considered [22,17]. We assume that fish swimming too close to each other will disturb each other through their tail strokes. A fish never moves farther than to one of the six nearest neighbor cells at a time. If all neighbor cells are occupied, the additional fish moves nevertheless, and, thus, the double occupation is just shifted. At a further (third) time step the additional fish keeps moving 'away from the crowd'.

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 directions 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 closet 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 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 with center in the cell of the fish under consideration. The term radius as it is used on our hexagon 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 Fig. 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 distance between cell centers 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 with the fish occupying that 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.

Modeling the state evolution that way, we move away from the classical cellular automaton, where the scalar state variables of cells evolve according to deterministic rules and depending on the neighborhood. Our rules are not entirely deterministic: if two fish move towards the same cell, a random choice has to be made between the two of them. Indeed, classical cellular automata cannot be used to model migration as the contents of cells cannot be exchanged. A number of suggestions has been made how to repair this 'lack' of classical cellular automata. Usually, migration is implemented by means of a stochastic process: two cells are picked up at random and their contents are exchanged [37]. Another approach was suggested by introducing 'dimers': two cells are updated at a time, depending on both the neighborhoods [38].

### 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 Fig. 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 (Fig. 7). In any case, the boundary conditions should not have a major influence on the simulation results.

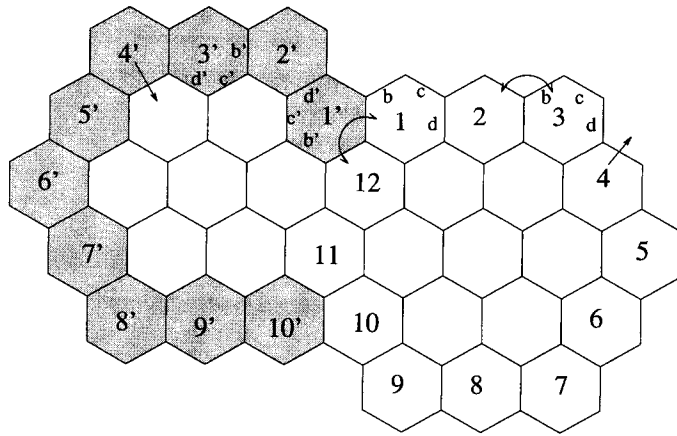


Fig. 6. Closing a lattice of hexagons to a transformed sphere. The hexagons printed in grey form the equator line. They are plotted twice and can be identified through their numbers. Some hexagons along the equator line only have five neighbors, because they touch one of their neighbors with two edges.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

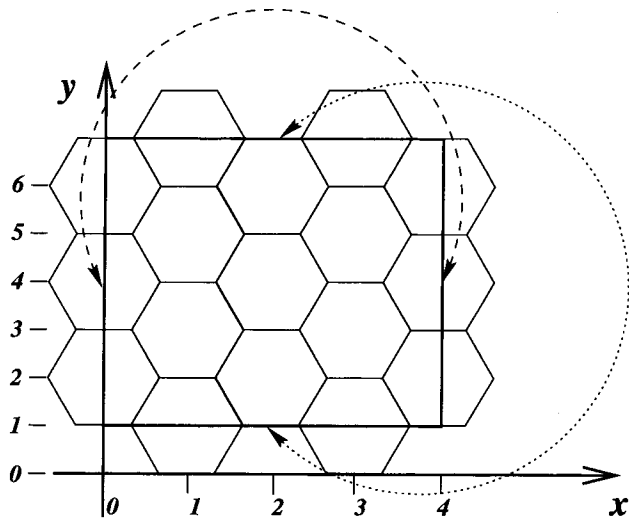


Fig. 7. Boundary conditions leading to a torus. The centers of the hexagon cells can be expressed in Cartesian coordinates. In our fixing, the centers of the hexagons have even sums of  $x$ - and  $y$ -coordinates.

### 3. Results

#### 3.1. Simulations

We present two simulations – with a higher and with a smaller number of fish – and one simulation where we additionally consider oxygen depletion as described in formula (2.6). 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 at random distributed. Also the initial swimming directions are determined at random out of the six possible swimming directions (on a hexagon 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 [39]. For this publication we show the final steps of three sample evolutions (see Figs. 9 and 10).

For the statistical analysis (Fig. 8), the number and size of schools is recorded as well as the polarization of each school after a certain amount of time steps (2000 in the example of Fig. 9, 10 000 for Fig. 10). The mean swimming direction of the school is given with reference to the (vertical)  $y$ -axis; this is against common use, but due to the hexagonal grid swimming directions along the  $x$ -axis it cannot occur. Therefore, we gave preference to our notation for the sake of clarity. In the tabular the angles  $\alpha$  between the swimming direction of the school and the  $y$ -axis are listed in degree ( $-180^\circ < \alpha < 180^\circ$ ).

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 1, 2 and 3. With an evaluation radius of 1, fish are considered to belong to the same school only if they occupy nearest neighbor cells. With an evaluation radius of 2 one empty cell may be between fish of the same school, and with an evaluation radius of 3 there may be a gap of two empty cells.

The table in Fig. 8 shows the statistical analysis for the final formations in Figs. 9 and 10. We calculate the average size of a school in 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 we evaluate

$$\sigma_n = \sqrt{(n - n_i)^2/n}, \quad i = 1, \dots, s, \quad (3.7)$$

```

12 fish, measure.radius = 1
school# size mean swimming direction standard deviation
  1     4           0                    0
  2     4          -60                   0
  3     2           0                    0
  4     2          -180                   0
average school size: 3
standard deviation: 1.1547

64 fish, measure.radius = 1
school# size mean swimming direction standard deviation
  1    12          -60                    0
  2     6         -120                    0
  3    11           0                    0
  4    22         -120                    0
  5    13          -60                    0
average school size: 12.8
standard deviation: 3.24519

64 fish, model with oxygen consumption, measure.radius = 1
school# size mean swimming direction standard deviation
  1     3           180                    0
  2    10           120                    0
  3    11          -60                    0
  4     7           -60                    0
  5     3            60                    0
  6     6          -120                    0
  7     2          -120                    0
  8     4          -120                    0
  9    10           -60                    0
 10     2            60                    0
 11     6            60                    0
average school size: 5.81818
standard deviation: 4.38035

```

Fig. 8. Statistical output data for the 3 simulations displayed in Figs. 9 and 10. The *mean swimming direction* is the angle between the vertical axis and the swimming direction of the school in degree.

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

$$\sigma_{\bar{\alpha}_i} = \sqrt{(\bar{\alpha}_i - \alpha_{i,j})^2 / n_i}, \quad j = 1, \dots, n_i, \quad (3.8)$$

where  $\bar{\alpha}_i$  is the mean swimming direction of school  $i$  (counter-clock-wise with respect to the  $y$ -axis) and  $\alpha_{i,j}$  the swimming direction of a single fish in that school [22]. A perfect polarization is reached if  $\sigma_{\bar{\alpha}_i} = 0$ .

All results show a perfect polarization, i.e. no or only little deviation from the swimming direction. This is not surprising, since we discretized the possible swimming directions in only six. Therefore, the resolution of possible swimming directions is not higher than  $60^\circ$  ( $360^\circ/6$ ). 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.



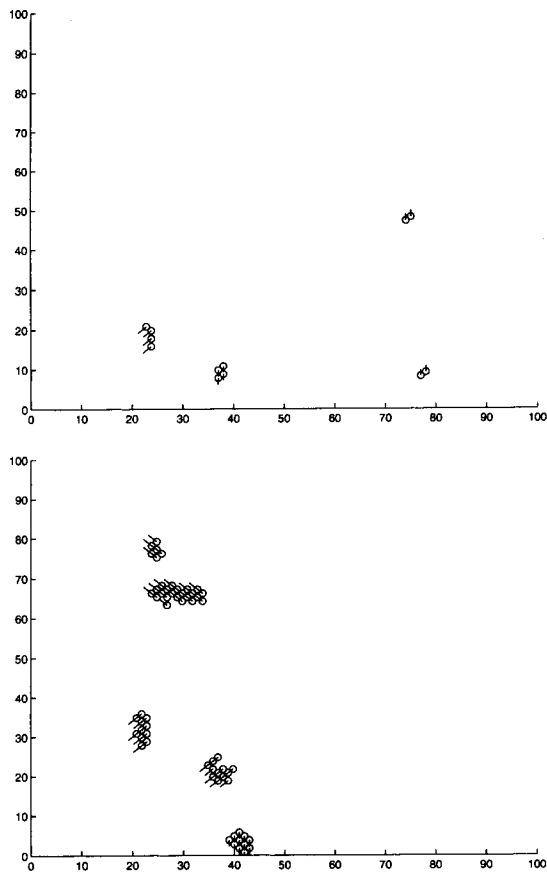


Fig. 9. Formation of schools after 2000 time steps for 12 (top) and for 64 (bottom) fish. The model parameters are: search-radius = 2, orientation-radius = 1.

The number and size of schools is stable after sufficiently long simulations. What is 'sufficiently long', i.e. the convergence speed, depends on the model parameters. Not only the radius of the attraction area, but also the radius of the orientation area affects the time needed for schooling: 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. In our simulations without oxygen consumption we present results after 2000 time steps. We could not observe any changes of the final pattern after 1000 time steps. In the case of models with oxygen depletion some solitary swimming fish without a specific (constant) orientation always remain, as the oxygen depletion does not allow them to join a school. However, the statistic of the number and average size of

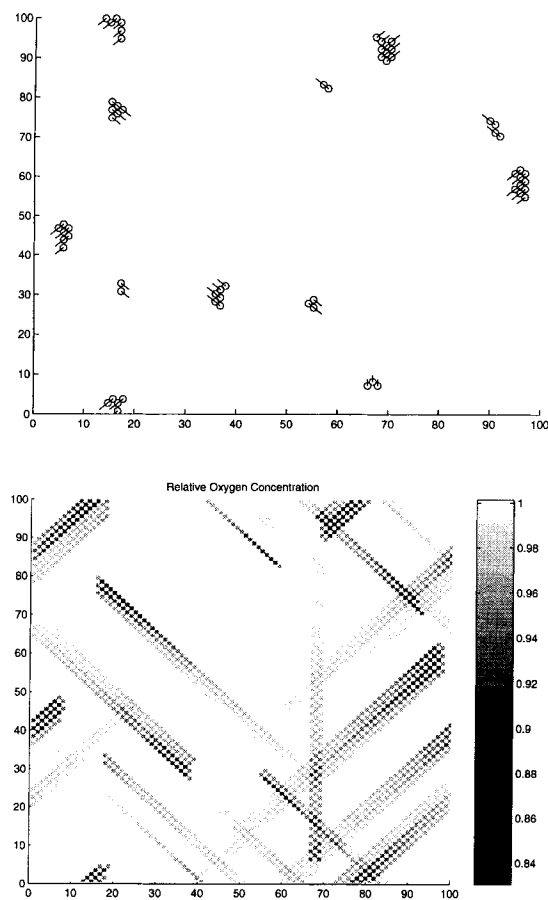


Fig. 10. Distorted formation of schools after 10 000 time steps for 64 fish. In the bottom figure the relative oxygen concentration in the cells is visualized. The swimming path of the school can be traced back. The parameter values are (referring to Eq. (2.6));  $\zeta = \rho = 0.05$ ,  $c_{ox} = 0.8$ , search and orientation radius as in the previous figures.

schools stabilizes also for models considering oxygen consumption. To be sure, we increased the number of time steps in that case. The bottom table in Fig. 8 shows that there are either schools with about 10 fish, or very small groups with about 3 fish. There are only a few patches with a medium size. This observation suggests that the small fish groups are detachments from originally larger schools due to a lack of oxygen. Additionally, we show the relative oxygen concentration in the lower part of Fig. 10. The very dark points represent cells with an oxygen concentration very close to the critical value, which is  $c_{ox} = 0.8$  for that simulation.

With an increasing number of fish the average size of schools increases, as more fish are available and the likelihood to find and join a school increases. For models with oxygen consumption basically the same can be observed, even though in a weaker fashion. The difference to the model without oxygen consumption is the increasing number of solitaire swimming, disorientated, detached fish.

### 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. Towards the rear of a school oxygen can be depleted due to the oxygen consumption of fish in front of the school. Oxygen reductions of about 30% are reported for schools of mullet. If fish in the end of the school actively roil the water surface, the school is close to break up [30].

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 are [40–42]: 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

$$O_{av} = u_{eff} \times A \times C_{ox}, \quad (3.9)$$

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

$$O_{need} = n \times GMR(u_{metabol})/E_{O_2}. \quad (3.10)$$

Oxygen is entirely depleted if

$$n_{max} = \frac{u_{eff} A C_{ox}}{GMR(u_{metabol})/E_{O_2}}. \quad (3.11)$$

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 results 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 no 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 in 4/3.

Another energy saving strategy is burst and coast swimming [43,44]. A fish can reach the same effective speed and reduce the required energy in 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 fish school formation and realistic school sizes. This is decisive for estimations of stock sizes.

As a technic 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 succeed in simulating the evolution of aligned fish schools. In a further model the oxygen concentration is introduced: oxygen is reduced when the cell is occupied and replenished when the cell is empty. By that means, we can simulate the detachment of single fish from larger schools. In two sample calculations we have shown how the school size can be related to oxygen depletion.

Previous studies have shown that so-called averaging models lead to better results than decision models [22]. 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 neighbor fish only.

We model behavior based on energetic advantages for the fish. We consider hydrodynamic advantages in introducing a hexagon 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 far fish swimming above each other influence each other, and if the mathematical assumptions made here are justified. Due to technical problems there are only a few studies and video recordings of large fish schools in the deep sea [45]. Lab conditions are different, and especially 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 hexagon grid, simplifies the consideration of energetic advantages, 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 [46,47]. Since tuna fish are not able to actively pump water over their gills, they need to swim for having an adequate oxygen supply. At the same time, swimming increases the metabolism and therefore the oxygen need [40–42].

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 [6].

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 [48]. 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 for 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 (chosen at random).

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?

The above discussed model belongs to a wider class of models, which describe the interactions of individuals (or objects) possibly resulting in patch information. These interactions depend on the relative positions and orientations of the individuals. A very comprehensive discussion of such models is given in Ref. [49]. The general description considers continuous positions and orientation angles, and gradual interaction intensities. This leads to a set of partial integro-differential equations. Bifurcations between different behaviors, such as spatially homogeneous alignment, formation of patches without alignment and the formation of patches with alignment can be described. We restricted ourselves to a discrete model, having a concrete application (to fish schools) in mind. A cellular automation is a convenient modeling tool for that purpose, allowing us to consider the anisotropy of the space due to wakes as well. It would be interesting to derive the discrete model from the above mentioned general class of models in view of the application of results.

In the model suggested here we merged a geometry stemming from hydrodynamical arguments with established assumptions on behavior. 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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