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Mathematical models for fish schools

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Preface

In this bachelor thesis we are going to investigate what kind of models exist to simulate fish schools. It is based on a search through literature in order to find these models. We are especially interested in the continuum models, which consider the whole school as a unit instead of simulating each fish individually. We are going to elaborate these models mathematically.

The choice for this subject arose from our interest in biology, so combining it with mathematics was a logical choice. Because it is a search through literature, we did not know in advance what kind of models we were going to find. The model(s) that we did find in the end, turned out to be too hard to analyse with elementary methods. Therefore this thesis gives a few starting points for future research, e.g. in a master project.

Contents

1 Biological and experimental background

The schooling behaviour of fish has always been very interesting to scientists. How they do it and why, and can we model this behaviour mathematically in order to get a better understanding about this schooling behaviour. There has been a lot of research on this subject. Different kind of studies of schooling fish have showed that it is more advantageous for fish to swim in a group than to live isolated. Fish were born with the ability to school. It protects them against predators, it gives them greater access to food resources and it saves energy. It is very dangerous to live isolated. A good example of saving energy by moving together, exhibited by a different type of organism, is that performed by a group of lobsters (*Panulirus argus*); one single lobster moves 25 cm/s, while when moving in groups, they go at a speed of 35 cm/s. It has been showed that fish live up to six time longer if they swim in schools compared to being on there own [1]. Over the years through natural selection, the fish who succeeded the most, survived. That is how the current schooling behaviour arose.

1.1 Major biological questions

The experiments performed by biologists are based on a couple of questions about the schooling behaviour of fish. They have a good idea why fish congregate, but have relatively little knowledge about how they congregate. In order to understand this better, they looked at the rules that seem to determine the individual behaviour in a school. They wondered what determined the movement of the fish and how the different kind of shapes of the school arose. They discovered that fish seem to use three kinds of zones around them. When other fish enter one of these zones, the fish will respond differently for each zone. The zone closest to the fish seems to be a zone where the fish will turn away if others enter this zone, some kind of territory. If there are no fish inside this zone, the fish takes notice of fish outside this zone. It seems to divide this in two different zones; one where it aligns with its neighbours, and one where it seems attracted by other fish. The area outside these zones is not in the field of perception of the fish.
Another import biological question is what the foci of attraction and repulsion from point of view of an individual group member are. There are different kind of foci imaginable, like predators and food. Is the strength of these forces strong enough to maintain the congregation, and can these forces explain the observed structure? To how many of their neighbours do fish pay attention? These are all questions biologists try to answer by experiments.

1.2 Collecting data

In order to make simulations about fish schools, we need to know how fish behave in a school. Experiments have been performed by biologist to collect

data. There are different ways to collect these data. Most studies use captured fish, so they can mark them. They put them in a tank, free of any distracting objects. First the fish have some time to get used to their new environment. After that they start filming the movement of marked fish, during a certain period, often from different angles in order to obtain information about the three dimensional position and velocity of each fish in the school. One of the difficulties is to determine how long you should monitor the fish and with how many frames per second. If there are too many frames per second, it turned out that there is too much autocorrelation. If there are not enough frames per second, there is a big loss of information. Parrish and Turchin analysed the individual trajectories of schooling fish and found out that the best option for their experiment was to look at every third frame, when there were 15 frames per second [5].

1.3 First conclusions from experiment

Biologists have done experiments with fish to investigate their schooling behaviour in fish tanks. First they looked at the individual behaviour of a fish in the school. It turned out that fish mostly use vision to determine their position with respect to their neighbours. They also use sensors on the side of their bodies to notice the water movement, the so called lateral line [3] (see Figure 1). This way the fish can determine how fast their neighbours are moving and in which direction. Without these two properties fish could not be schooling. If vision is decreasing, the fish will swim further apart from each other. Fish with more sensors in the lateral line swim closer to each other. The vision is used mostly to determine the distance and angle to their neighbours, while the sensors in the lateral line are used to watch their speed. To maintain the shape of the school, fish constantly have to watch their neighbours. They pay attention to their nearest neighbours, as well as to the school as a whole unit. The distance they keep to each other differs by the type of fish. This can explain why there are differences in the defense against predators and their movement through the water. It is difficult for the fish in the school to determine how to move without colliding with their neighbours and stay away from the predators.

In fish schools there is no leader, the fish change position in the school all the time. Once the school changes direction, the fish on the side suddenly become the leaders. Theoretical analysis of the experimental data which were mainly gained through simulations, has revealed that it is most likely that fish form a self-organization mechanism. In this mechanism they apply a few rules about how to use the information they get from there neighbours, in order to adjust their movement behaviour. This simple mechanism results in the high-level school structure of the group.
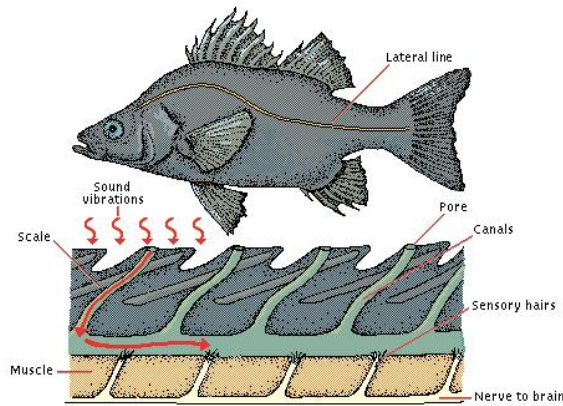
Figure 1: The lateral line of a fish

1.4 Objectives for mathematical modeling and simulation

After the (biological) experiments have been done, the theoreticians can start with their models and simulations. Biologists need these kind of models and simulations in order to get more information about the fish school. Before mathematics can be done, we need to know the question that need to be answered by the mathematical model. There are different questions possible which might need a different model. Sometimes we want to have more knowledge about how individuals behave in a group, whereas other times there can be more interest in the behaviour of all fish together, when considering migration of various schools over hundreds of sea miles. In that case there can be looked at the whole school as a unit on a large space scale.

The goal of Parrish and Turchin in [5] is to give a quantitative description of the rules of individual movement, based on the balance of attractive and repulsive forces. With the use of mathematics they wanted to investigate if the position of fish in a school were structured or completely random. They want to explore the data set for potential attraction and repulsion foci.

Individual-based (Lagrangian) multi-"particle" models are then much more appropriate than continuum (Eulerian) models, which seem to be more suited to answering the former. We will discuss this more in the next chapter.

One of our objectives is to understand the large scale, long-term behaviour of these schools, as may be encountered in the annual so called 'sardine run' near South Africa in spring time. There, trillions of sardines migrate away from their usual living ground without - apparently - any goal, except to be eaten by various predators in large numbers.

2 Models for animal grouping

It is often very difficult to collect data of movements of fish in schools in multi dimensions. This makes it more difficult than for example one-dimensional subjects like birth and death. The fact that it is difficult does not make it less interesting and it is a subject of which we would like to know more.

There are three different kind of models to simulate fish schools. The first one is the empirical studies with phenomenological models. The second one consists of theoretical analysis which are usually based on diffusion models, and the last one is the mechanistic approach, which is based on individuals and focus on a specific organism, using computer simulations.

Each of these three models have their advantages and limits. The first one is useful in quantifying dispersal in the field but it does not give us good insight in mechanisms of population redistribution [2]. The diffusion models are often too general as a result of the assumptions made about movement of organisms. The mechanistic models originate from very careful field observations, but they often focus too much on one specific kind of animal, which makes it difficult to draw general conclusions out of it. We will describe some outstanding models of this kind in Chapter 3 that have been able to shed light in universal principles regarding fish schooling, bird flocking and others.

The reason why not one of the models has replaced the others, is that most models are hard to compare. Each type is suited to answer different kind of questions, described in Chapter 1.4, so they are complementary. Most of them are too specific to compare the results of the simulations. The different assumptions made at the start of the simulation and the use of different parameters gives a different outcome. Besides that, the creators of the models often don't tell exactly how their models work, which makes it difficult to understand what it is actually doing.

Biologists have tried to find a solution for this problem. In [10] March and Jones came up with two possible solutions. They proposed that everyone who wanted to do such research, had to do this with an agreed structure. A consequence of an agreement like this, is that it should be flexible enough for different kind of organisms. A second solution is to try to close the gap between the too general diffusion models and the too specific simulations. In this thesis we pursuit this point. We are looking for continuum descriptions for fish schooling that bridges the gap between diffusion models and the detailed mechanistic models. Such models exist for example for chemotaxic movement ("chemotaxis") of cellular organisms, like bacteria and amoebae: kinetic chemotaxis models [12], [13]. A disadvantage of the second solution is that it does not give a good explanation for the behaviour of organisms. Therefore it is not really possible to use only one of the three models for movement simulation. Nevertheless, the need for a unifying framework that places them in proper (mathematical and biological) relationship is still wanted. The main point is, that the different types of models apply best to different space and time scales and that we should understand each

model's limitations regarding predictions derived from it in relation to other models.

2.1 Lagrangian versus Eulerian type models

The last two techniques of modeling are the most important ones because we get the best results out of it; the empirical approach does not give us sharp answers about mechanisms of population distribution. The second one is called the Eulerian approach, in which the congregation can be formulated as nonlinear diffusion problems and is centered on a point in space. The position and velocity of each fish is replaced by a distribution for the expected direction of fish in a specified region with velocity in a specified range. In this model we don't look at the individuals, but all the fish together in the school. The diffusion equation is a continuum approximation of the discrete random walk process. This model gives a lot of general insights into spatial population dynamics, but usually makes oversimplifying assumptions about movements of real organisms [2]. The last approach is called the Lagrangian model, which is centered on the individual behaviour of a fish. The individual movement is characterized by the position, velocity and acceleration of a fish. These models can be tightly linked to field observations.
If we compare the two different models, we can see a couple of advantages and disadvantages. In the Eulerian approach, all the fish are identical, which makes it easier to add a certain chance variable. In the Lagrangian approach there is the option to make a difference between individuals, which is an advantage, but adding a chance variable is not easy. Besides that, this mathematical model is relatively easy, but has a lot of equations, where the Eulerian model has one equation, but a rather difficult one. Because in this model we look at all the fish as if they are the same, we lose track of the individual fish.
In general, movement decisions of an individual group member can be viewed as a balance of forces, liked described in [11]. These forces are necessary to simulate multiple individuals, like in the Lagrangian model. The forces that have been taken in this balance are the attraction to and repulsion from their neighbours and the center of the school, and the tendency to align with their neighbours.

2.2 Physical diffusion

When we talk about the diffusion models we don't mean the physical diffusion, which is the diffusion of dissolved molecules or particles like heat conduction. In that case the fish would move away from each other instead of sticking together in a school. That is why a physical diffusion model is not a good model to simulate fish schools. Therefore we have to look at another kind of diffusion model, which transforms the diffusion model into a good model for fish schooling, the so called ecological diffusion model. First we will describe how a physical

diffusion equation is obtained.

The physical diffusion model is build in two steps:
1) one states the conservation equation that relates the change in spatial concentration of particles to their flux
2) one needs the empirical law connecting particle fluxes to their concentration gradients [2].

We can look at a one-dimensional example of the movement of particles in a thin tube and we assume that particles don't interact. We can investigate the change of concentration of particles at a small section of one end of the tube over time, between x and $x + \lambda$.

This gives us the following equation [2]

rate of change
of particle   net (entry minus   net (entry minus
number in   =   departure) at the + departure) at the   (2.2)
$(x, x + \lambda)$ x end $x + \lambda$ end
per unit time

If we take $u(x, t)$ the concentration of particles at a place x at a time t and we multiply this with the length of the interval λ, we get the total number of particles in $(x, x + \lambda)$. The quantities on the right are the fluxes $J(x, t)$; the rate at which the particles cross x in the positive direction [3]. Now we can write equation (2.2) in terms of the fluxes

$$
\begin{aligned}
\frac{\partial}{\partial t}[u(x, t)\lambda] &= J(x, t) - J(x + \lambda, t) \\
\frac{\partial u}{\partial t}(x, t) &= -\frac{J(x + \lambda, t) - J(x, t)}{\lambda}
\end{aligned}
\tag{1}
$$

and by taking $\lambda \to 0$, we get

$$
\frac{\partial u}{\partial t}(x, t) = -\frac{\partial J(x, t)}{\partial x}
\tag{2}
$$

Our following step is to apply Fick's law; the concentration within the diffusion volume does not change with respect to time, and if we take D to be the diffusivity, this gives us

$$
J(x, t) = -D(x, t)\frac{\partial u}{\partial x}(x, t)
\tag{3}
$$

If we substitute (3) into (2), we obtain the following diffusion equation

$$\frac{\partial u}{\partial t}(x,t) \quad = \quad \frac{\partial}{\partial x}\left(D(x,t)\frac{\partial u}{\partial x}\right)(x,t) \tag{4}$$

If $D(x,t) = D$ is independent of time, (4) simplifies to

$$\frac{\partial u}{\partial t}(x,t) \quad = \quad D\frac{\partial^2 u}{\partial x^2}(x,t) \tag{5}$$

One thing we have to take into account is that when the concentration is high, the interaction between particles become important and a consequence is that Fick's law is no longer accurate.

2.3   Ecological diffusion

Now we look at an easy example of a random walk in one dimension to obtain a simple ecological diffusion model. Imagine a small animal, e.g. a beetle, can move to the positions left and right and stay at his place with a certain probability, see Figure 2. It can move to the right with a probability $R(x,t)$, to the left with a probability $L(x,t)$ and stay at his place with a probability $N(x,t)$ being stated at position x. We make the assumption that the beetle can only make one step every time.
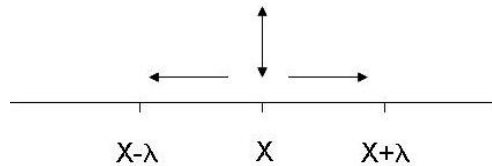

Figure 2: Movement of a small animal

We now want to formulate a recurrent equation for the probability that the beetle is at a certain place x on a time t, which we will indicate with $p(x,t)$. Because the beetle can only move one step, the probability that it is in x at time t, depends on the probability that it did not move, or was in the surrounding places $x - \lambda$ and $x + \lambda$ one moment earlier, $t - \tau$. In equation form, this gives us:

$$
\begin{aligned}
p(x,t) = \quad & N(x,t-\tau)p(x,t-\tau) \quad + R(x-\lambda,t-\tau)p(x-\lambda,t-\tau) \\
& \qquad\qquad\qquad\qquad\quad + L(x+\lambda,t-\tau)p(x+\lambda,t-\tau) \tag{6}
\end{aligned}
$$

Our next step is to make a differential equation expressed in terms of the deriva-

tives of $p(x,t)$ out of this recurrent one. Therefore we take the Taylor expansion:

$$p(x, t - \tau) \;=\; p(x,t) - \tau \frac{\partial p}{\partial t}(x,t) + O(\tau^2)$$

$$
\begin{aligned}
p(x - \lambda, t - \tau) \;=\;& p(x,t) - \lambda \frac{\partial p}{\partial x}(x,t) - \tau \frac{\partial p}{\partial t}(x,t) \\
&+ \frac{1}{2}\left(\lambda^2 \frac{\partial^2 p}{\partial x^2}(x,t) + 2\lambda\tau \frac{\partial^2 p}{\partial t \partial x}(x,t) + \tau^2 \frac{\partial^2 p}{\partial t^2}(x,t) \right) + O(\lambda^3)
\end{aligned}
$$

$$
\begin{aligned}
p(x + \lambda, t - \tau) \;=\;& p(x,t) + \lambda \frac{\partial p}{\partial x}(x,t) - \tau \frac{\partial p}{\partial t}(x,t) \\
&+ \frac{1}{2}\left(\lambda^2 \frac{\partial^2 p}{\partial x^2}(x,t) - 2\lambda\tau \frac{\partial^2 p}{\partial t \partial x}(x,t) + \tau^2 \frac{\partial^2 p}{\partial t^2}(x,t) \right) + O(\lambda^3)
\end{aligned}
$$

The Taylor expansion of R, L and N are similar.

Now we notice that $N + R + L = 1$. If we substitute these expansions into (6) and we neglect the terms of order τ^2 and λ^3, we get the following equation:

$$
\begin{aligned}
\tau \frac{\partial p}{\partial t}(x,t) \;=\;& -\lambda p \frac{\partial}{\partial x}(R-L)(x,t) + \frac{1}{2}\lambda^2 p \frac{\partial^2}{\partial x^2}(R+L)(x,t) \\
&+ \frac{1}{2}\lambda^2 \frac{\partial^2 p}{\partial x^2}(R+L)(x,t) - \lambda \frac{\partial p}{\partial x}(R-L)(x,t) \\
&+ \lambda^2 \frac{\partial p}{\partial x}\frac{\partial}{\partial x}(R+L)(x,t) \\
&+ \lambda\tau \frac{\partial p}{\partial x}\frac{\partial}{\partial t}(R-L)(x,t) + \lambda\tau p \frac{\partial^2}{\partial t \partial x}(R-L)(x,t) \\
&+ \lambda\tau \frac{\partial^2 p}{\partial t \partial x}(R-L)(x,t) + \lambda\tau \frac{\partial p}{\partial t}\frac{\partial}{\partial x}(R-L)(x,t) \\
\;=\;& -\frac{\partial}{\partial x}\left[(R-L)\lambda p\right] + \frac{\partial^2}{\partial x^2}\left[\frac{\lambda^2(R+L)p}{2}\right] \\
&+ \lambda\tau \frac{\partial p}{\partial x}\frac{\partial}{\partial t}(R-L)(x,t) + \lambda\tau p \frac{\partial^2}{\partial t \partial x}(R-L)(x,t) \\
&+ \lambda\tau \frac{\partial^2 p}{\partial t \partial x}(R-L)(x,t) + \lambda\tau \frac{\partial p}{\partial t}\frac{\partial}{\partial x}(R-L)(x,t)
\end{aligned}
$$

$$(7)$$

In the limit $\lambda, \tau \to 0, R - L \to 0$ where we assume $\displaystyle\lim_{\lambda,\tau \to 0}\frac{\lambda^2(R+L)}{2\tau} =: \mu$ and $\displaystyle\lim_{\lambda,\tau,R-L\to 0}\frac{\lambda(R-L)}{\tau} =: \beta$ to exist, we notice that the last four terms are of order τ^2 and will therefore disappear. This gives us formally the following approximation:

$$\frac{\partial p}{\partial t}(x,t) = -\frac{\partial}{\partial x}(\beta p)(x,t) + \frac{\partial^2}{\partial x^2}(\mu p)(x,t) \tag{8}$$

11

Our final step now is to look at the total number of moving beetles, N. If we multiply this with the probability of finding an individual at a certain place x, at a time t and we substitute $u(x,t) \equiv Np(x,t)$, we get a diffusion-approximation model for the movement of a population of organisms:

$$\frac{\partial u}{\partial t}(x,t) \quad = \quad -\frac{\partial}{\partial x}(\beta u)(x,t) + \frac{\partial^2}{\partial x^2}(\mu u)(x,t) \tag{9}$$

This equation is known as the Fokker-Planck equation and represents what is often called ecological diffusion.

3   Mechanistic models for fish schooling

As we described in Chapter 1, a fish uses his vision and his lateral line to determine the location and speed of his neighbours. The area around the fish can be divided in several spherical zones (see Figure 3). This corresponds with our presumption from Chapter 1.1, but now we give a more abstract description.
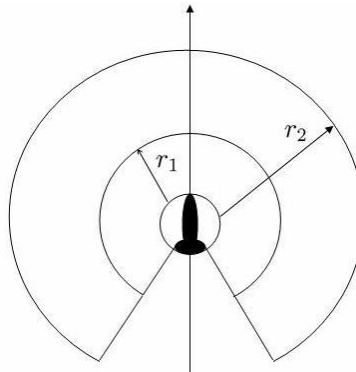

Figure 3: Areas around a fish

The zone closest to the fish is the zone of repulsion. When neighbours enter this zone, the fish will instantly move away from them. The sphere with radius r_1 around that is the zone of orientation or the alignment zone. In this area the fish will try to align with his neighbours. The area with the biggest distance to the fish is the zone of attraction which has radius r_2. When there are no fish in the first two zones, the fish will go looking for others. We notice that there is a zone behind the fish that is not in the field of perception; the fish cannot detect neighbours in this region. The size of this region can differ by type. Also the region outside the zone of attraction is not in the field of perception, it is just too far away from the fish to notice others.

From simulation of mechanistic models for fish schooling, one has concluded that the size of the alignment zone has a big influence on the shape of the school [6]. In simulations appear three shapes which are also known for natural fish schools, see Figure 4.
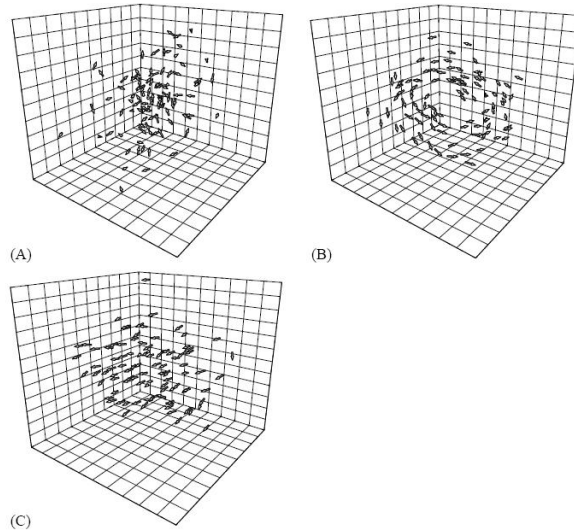

(A)

(B)

(C)

Figure 4: Different kind of shapes of a school [7]

The first one arises when there is almost no tendency to align (A). In this case the fish swim randomly. When this tendency gets stronger by enlarging the radius of the alignment zone, they suddenly start to follow each other, which results in a torus (or doughnut) shaped school (B). The final shape is when the alignment zone is large and the fish start to swim parallel to each other as in a migration (C). The transition between the different shapes is very sharp. Fish are able to adjust the size of their alignment zone. The tendency to align is important in allowing the group to transfer information [7].

It has been proven that individuals with a smaller repulsion zone tend to be closer to the center and front of the school than the fish with a larger repulsion zone. Fish that are hungry take a front position more often than those that are already satiated [7]. In multi-species schools, fish swim closer to their kind, and keep a bigger distance to other kinds. This might explain why the different species and fish of the same size tend to stay together, which is described as a sorting behaviour.

Now we look at the mechanistic models for fish schooling according to Couzin et. al. [8]. Here we simulate multiple individuals, lets say N. We want to investigate how the individuals change their direction when neighbours enter the different zones. Therefore we look at the desired direction the fish wants to go, the vector $d_i(t + \Delta t)$, where d stands for displacement. This direction is

mainly influenced by the fish in the zone of repulsion. For each individual i we define the sets:

$N_r(i) := \{j$— individual $j \neq i$ is in zone of repulsion $\}$

$N_o(i) := \{j$— individual $j \neq i$ is in zone of orientation$\}$

$N_a(i) := \{j$— individual $j \neq i$ is in zone of attraction$\}$.

This gives us, with c_j the position vector of the center of mass,

$$\mathbf{d}_i(t + \Delta t) \quad = \quad - \sum_{j \in N_r(i)} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|} \tag{10}$$

Avoiding neighbours is the highest priority.

If there are no neighbours in the zone of repulsing, the desired direction is constructed in a different way. To that end we use a unit direction vector derived from v_i. If there are only neighbours in the orientation zone, this gives us

$$\mathbf{d}_i(t + \Delta t) \quad = \quad \sum_{j \in N_o(i)} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|} \tag{11}$$

Similar, if there are only n_a neighbours in the zone of attraction, we get

$$\mathbf{d}_i(t + \Delta t) \quad = \quad \sum_{j \in N_a(i)} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|} \tag{12}$$

Whenever there are neighbours in the repulsion area, this desired direction vector is dominant. When this area is empty, the desired direction will be determined by the last two vectors

$$\mathbf{d}_i(t + \Delta t) \quad = \quad \frac{1}{a} \sum_{j \in N_o(i)} \frac{\mathbf{v}_j(t)}{|\mathbf{v}_j(t)|} + \left(1 - \frac{1}{a}\right) \sum_{j \in N_a(i)} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|} \tag{13}$$

where a depends on which zone is more dominant and differs by type of fish. This type of model is based on the work of Tamás Vicsek and collaborators e.g. see [14]. In [7] they use $a = 2$.

The position and the velocity of each fish are updated according to:

$$c_j(t + \Delta t) \quad = \quad c_j(t) + \frac{d_j(t + \Delta t)}{|d_j(t + \Delta t)|} \cdot v_0 \Delta t \tag{14}$$

$$v_j(t + \Delta t) \quad = \quad v_0 \frac{d_j(t + \Delta t)}{|d_j(t + \Delta t)|}$$

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where v_0 is a fixed speed.

As we have seen in Section 2.1, the simulation of individuals is based on the balance of forces. In [11] (p.254) they came up with a continuous time model which is comparable to the latter. Here we define $N_p(i) := \{j$— individual $j \neq i$ is in zone of perception$\} = N_r(i) \cup N_o(i) \cup N_a(i)$.

They give the following equation of motion for the ith individual in a group:

$$ma_i + mkv_i = b\frac{v_i}{|v_i|} + \frac{1}{N-1}\, \Sigma Q(R_{ij})\frac{c_j - c_i}{|c_j - c_i|} + \frac{1}{M} \sum_{c_j \in N_p(i)} h(v_j - v_i) + A_i(t)$$

(15)

where a_i is the acceleration, v_i the velocity and c_j the center of mass of the ith individual, thus $a_i = \frac{dv_i}{dt}$, $v_i = \frac{dc_i}{dt}$. R_{ij} stands for the distance between fish i and j and $A_i(t)$ models a random force. They describe that it was too difficult to solve equation (15) analytically, so they used computer simulations to examine the time variation of grouping pattern [11]. The result was the same as above, showed in Figure 4.

As we have already described, there is no leader in a school of fish. So how does the school determine where to go, how do they make a collective decision? That is a question I.D. Couzin et. al. [8] tried to answer by a simulation model. They used a simple model to show how information can be transferred within the school without signaling and when group members do not know which individuals, if any, have information. In their experiment, they gave a few individuals more information on where to go than others. They wondered if uninformed individuals recognize the informed ones and if that is even necessary. The way the school moves is described as above by the vector $d_i(t + \Delta t)$. The vectors of all the individuals together result in a new direction for the school. They showed that the larger the school, the smaller the proportion of fish with information could be in order to guide the whole school to the right place, that is for example away from a predator, or to a new food resource.

The model described in [7] reveals that two different collective states can occur for identical individual behaviour. This demonstrates the importance of the previous history of the group structure. It appears that when the tendency to align gets stronger, the shape of the fish school goes through the three different kind of shapes. First they swim randomly, then they start following each other and the school becomes doughnut-shaped and finally it becomes a well organised school. The transitions between the different shapes are very sharp. But if we look at the shape of the school when we are going the other way, we see a difference. We start with a very high tendency to align, so the school has the shape showed in Figure 4(C). If we start to lower the tendency to align, the school skips the doughnut-shape and goes directly to the shape showed in Figure 4(A) where the fish swim randomly in the school. So the shape of the

school depends on the previous shape. When the previous history is important to the group structure is called a hysteresis phenomenon.

4   Continuum models

We have discussed some mechanistic models. Now we move on to continuum, Eulerian models. Recall that our objective was to find continuum descriptions of fish schooling, that can be applied in settings where there is a very large ($\sim 10^9$ or more) number of individuals, moving on large scales in time and space. Moreover, we would also like to bridge the gap between mechanistic and diffusion models, as mentioned in Chapter 2. A partial result in this direction that we were able to find is Grünbaum's model, which we shall discuss in the next section.

4.1   Grünbaum's model

An equation given in [5], is expressed in terms of a probability density function $p(\theta, t)$, which, loosely speaking, is the frequency of fish with the tendency to align in the school with orientation in the range $[\theta, \theta + d\theta]$ at time t:

$$
\begin{aligned}
\frac{\partial}{\partial t}\rho(\theta,t) \;=\; & \frac{\partial^2}{\partial \theta^2}(D(\theta)\rho(\theta,t)) \\
& -\beta\frac{\partial}{\partial\theta}\left(\rho(\theta,t)\left[\int\limits_{\theta}^{\theta+\pi}\rho(\theta',t)d\theta' - \int\limits_{\theta-\pi}^{\theta}\rho(\theta',t)d\theta'\right]\right) \quad (16)
\end{aligned}
$$

We can rewrite this by taking

$$
\mathcal{G}(\rho)(\theta) \;=\; \int\limits_{\theta}^{\theta+\pi}\rho(\theta',t)d\theta' - \int\limits_{\theta-\pi}^{\theta}\rho(\theta',t)d\theta' \quad (17)
$$

so (16) becomes

$$
\frac{\partial}{\partial t}\rho(\theta,t) \;=\; \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta,t)) - \beta\frac{\partial}{\partial\theta}\left[\rho(\theta,t)\mathcal{G}(\rho)(\theta)\right] \quad (18)
$$

In this equation, the left-hand side describes probability of the movement of the fish. On the right-hand side, we recognize the diffusion part from the ecological diffusion models, equation (9), together with some kind of disturbance, like in

equation (9). Equation (16) can be read in the following way; the fish we are investigating has a vision range from $\theta - \pi$ to $\theta + \pi$. The first integral can be interpreted as the number of fish in the school with orientation to the left of θ, and the second integral as the number of fish with orientation to the right of θ. It represents the choice of direction of the fish; if there are more fish on the right-hand side, it will turn to them, and if there are more fish on his left-hand side, the fish will turn this way. β indicates the rate of turning towards his neighbours.

4.2 The extended Grünbaum model

In [9] we found a similar model, only this one is extended by that the authors call "an environment-induced preference" modeled by $F(\theta)$:

$$\frac{\partial}{\partial t}\rho(\theta,t) = \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta,t))$$
$$-\beta\frac{\partial}{\partial\theta}\left(\rho(\theta,t)\left[\int\limits_{\theta}^{\theta+\pi} F(\theta')\rho(\theta',t)d\theta' - \int\limits_{\theta-\pi}^{\theta} F(\theta')\rho(\theta',t)d\theta'\right]\right) \tag{19}$$

We suppose F is a continuous function and is periodic on $[0, 2\pi]$. Note that if $F(\theta) \neq 0$ for all θ, then F has fixed sign. We assume that $F > 0$ in that case and incorporate the sign into β.

As before we make the same simplication $\mathcal{G}$ as before, but now it depends on F as well, so

$$\mathcal{G}_F(\rho)(\theta) = \int\limits_{\theta}^{\theta+\pi} F(\theta')\rho(\theta',t)d\theta' - \int\limits_{\theta-\pi}^{\theta} F(\theta')\rho(\theta',t)d\theta' \tag{20}$$

and (19) becomes

$$\frac{\partial}{\partial t}\rho(\theta,t) = \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta,t)) - \beta\frac{\partial}{\partial\theta}[\rho(\theta,t)\mathcal{G}_F(\rho)(\theta)] \tag{21}$$

We can look at some properties of $\mathcal{G}_F$.

5 First steps towards analysis of the extended Grünbaum model

Whenever we are working on this kind of models, we should never lose track of the biological interpretation. We can take a look at equation (21) and integrate both sides from 0 to 2π. This gives

$$\int_0^{2\pi} \frac{\partial}{\partial t}\rho(\theta,t) = \int_0^{2\pi} \frac{\partial^2}{\partial\theta^2}(D(\theta)\rho(\theta,t)) - \beta\int_0^{2\pi} \frac{\partial}{\partial\theta}\left[\rho(\theta,t)\mathcal{G}_F(\rho)(\theta)\right]$$

$$= \left[\frac{\partial}{\partial\theta}(D(\theta)\rho(\theta,t))\right]_0^{2\pi} - \beta\left[\rho(\theta,t)\mathcal{G}_F(\rho)(\theta)\right]_0^{2\pi}$$

$$= 0$$

because D, ρ and $\mathcal{G}_F$ are all 2π-periodic.

By interchanging $\frac{\partial}{\partial t}$ and the integral we get $\frac{\partial}{\partial t}\left[\int_0^{2\pi}\rho(\theta,t)d\theta\right] = 0$, which gives $\int_0^{2\pi}\rho(\theta,t)d\theta = $ constant. This means that for $\rho \geq 0$, we find that the total amount of fish stays constant over time, which is preferable.

5.1 Existence, uniqueness an positivity of solutions

In this section we are going to look for the existence and the uniqueness of the solutions of the (extended) Grünbaum model. The case where $D(\theta) \neq 0$ is described in [9], where they use semigroup methods and functional analysis in order to prove existence, uniqueness and positivity of solutions (for finite time). They analyse the stability of the trivial equilibrium in case $D(\theta)$ is constant, but this is beyond the scope of this bachelor project. We tried to find out what can already be concluded with elementary methods, in scope with the requirements of this project. The case $D \equiv 0$ has not been treated in [9]; our results on equilibria in Section 5.3.1 suggest that uniqueness may fail in that case. We did not find results on existence of solutions for that case so far.
For interpretation of ρ it is necessary that $\rho \geq 0$. We did not consider proving this here. This has been done in [9], Theorem 2.3, p.421-424 for general θ-dependent D and F, both strictly positive.

5.2 Properties of $\mathcal{G}_F$

Let $C_{per}^k([0,2\pi])$ be the vector space C^k functions on $[0,2\pi]$ with $f^{(n)}(0) = f^{(n)}(2\pi)$ for all $0 \leq n \leq k$. A function $f \in C_{per}^k([0,2\pi])$ can be identified with

a 2π-periodic C^k-functions on $\mathbb{R}$.

Proposition 1. *The following statements hold:*

(i) For $F \in C_{per}([0, 2\pi])$, $\mathcal{G}_F : \rho \mapsto \mathcal{G}_F(\rho)$ is a linear map from $C_{per}([0, 2\pi])$ into $C^1_{per}([0, 2\pi])$.

(ii) For all $\rho \in C_{per}([0, 2\pi])$ and $\theta \in [0, 2\pi]$,

$$\frac{\partial}{\partial \theta}(\mathcal{G}_F(\rho)(\theta)) = 2\left[F(\theta + \pi)\rho(\theta + \pi) - F(\theta)\rho(\theta)\right]. \tag{22}$$

(iii) For all $\rho \in C_{per}([0, 2\pi])$ and $\theta \in [0, 2\pi]$,

$$\mathcal{G}_F(\rho)(\theta + \pi) = -\mathcal{G}_F(\rho)(\theta). \tag{23}$$

Proof

(i) Each of the two integral terms in the definition of $\mathcal{G}_F(\rho)$ is the integral over the product of two continuous functions if $F \in C_{per}([0, 2\pi])$. This gives a function which is $C^1_{per}([0, 2\pi])$. Thus $\mathcal{G}_F$ maps $C_{per}([0, 2\pi])$ into $C^1_{per}([0, 2\pi])$. It is clear that $\mathcal{G}_F$ is linear.

(ii) If we take the derivative of $\mathcal{G}_F(\rho)$, we first integrate and then differentiate with respect to θ. This means that the result is equal to the integral, evaluated at the endpoints of the domain of integration. This yields (22).

(iii) We can rewrite $\mathcal{G}_F(\rho)(\theta + \pi)$ in order to prove (23).

$$
\begin{aligned}
\mathcal{G}_F(\rho)(\theta + \pi) &= \int_{\theta+\pi}^{\theta+2\pi} F\rho \, d\theta' - \int_{\theta}^{\theta+\pi} F\rho \, d\theta' \\
&= \int_{\theta-\pi}^{\theta} F\rho \, d\theta' - \int_{\theta}^{\theta+\pi} F\rho \, d\theta' \\
&= -\left[\int_{\theta}^{\theta+\pi} F\rho \, d\theta' - \int_{\theta-\pi}^{\theta} F\rho \, d\theta'\right] \\
&= -\mathcal{G}_F(\rho)(\theta)
\end{aligned}
$$

$\square$

5.3 Equilibria for the extended Grünbaum model

It is easily verified that the homogeneous distributions $\rho \equiv c$, yield equilibria for the the Grünbaum model when D is constant. In order to find nontrivial equilibria of the extended Grünbaum model, we take $\frac{\partial}{\partial t}\rho(\theta, t) = 0$. Then (21) becomes

$$0 = \frac{\partial^2}{\partial \theta^2}(D\rho) - \beta \frac{\partial}{\partial \theta}[\rho \mathcal{G}_F(\rho)]$$

By integrating this, we get

$$c = \frac{\partial}{\partial \theta}(D\rho) - \beta \rho \mathcal{G}_F(\rho) \tag{24}$$

We can divide the determination of the equilibrium into three cases:

1. $D \equiv 0$

2. $D > 0$

3. $D \geq 0$, but $D \not\equiv 0$

We shall concentrate on what equilibria may exist in case 1 and 2.

5.3.1 Case $D \equiv 0$

Lemma 1. *Let $D \equiv 0$. ρ is an equilibrium in $C^2_{per}([0, 2\pi])$ iff $\rho \mathcal{G}_F(\rho) \equiv 0$.*

Proof
If we suppose that $\mathcal{G}_F(\rho) \not\equiv 0$, this implies that there exists θ^* such that $|\mathcal{G}_F(\rho)(\theta^*)| \neq 0$. By using Proposition 1(ii) from Chapter 5.2, this implies that there exists θ_0 with $\theta^* < \theta_0 < \theta^* + \pi$ such that $\mathcal{G}_F(\rho)(\theta_0) = 0$.
So if $\rho \mathcal{G}_F(\rho) \equiv c$, this implies that $\rho \mathcal{G}_F(\rho) \equiv 0$. $\qquad \square$

In order to find an equilibrium, we first use Fourier series. We can determine the kernel of $\mathcal{G}_F$ in the Grünbaum case, $F \equiv 1$. We write $\mathcal{G}$ instead of $\mathcal{G}_1$ as in Section 4.1.

Proposition 2. $\mathrm{Ker}(\mathcal{G}) = \{\rho \in C_{per}([0, 2\pi]) | \rho \text{ is } \pi\text{-periodic }\}$

Proof For $\rho \in C_{per}([0, 2\pi])$ we have the Fourier Series $\rho(\theta) = \sum\limits_{k=-\infty}^{\infty} r_k e^{ik\theta}$. If we substitute this in $\mathcal{G}(\rho)$, we get

$$\mathcal{G}(\rho)(\theta) \quad = \quad \int\limits_{\theta}^{\theta+\pi} \sum_{k=-\infty}^{\infty} r_k e^{ik\theta'} d\theta' - \int\limits_{\theta-\pi}^{\theta} \sum_{k=-\infty}^{\infty} r_k e^{ik\theta'} d\theta' \tag{25}$$

By interchanging the sum and integral, we get

$$\mathcal{G}(\rho)(\theta) \quad = \quad \sum_{k=-\infty}^{\infty} r_k \int\limits_{\theta}^{\theta+\pi} e^{ik\theta'} d\theta' - \sum_{k=-\infty}^{\infty} r_k \int\limits_{\theta-\pi}^{\theta} e^{ik\theta'} d\theta' \tag{26}$$

$$= \quad \sum_{k \ odd} \frac{-4r_k}{ik} e^{ik\theta}$$

Thus $\rho \in \mathrm{Ker}(\mathcal{G})$ if and only if each $r_k = 0$ for k odd. Now we can conclude that ρ is π-periodic. $\qquad\square$

If we look at the extended Grünbaum model with $F \neq 1$, we can do a similar thing, so for $F(\theta) = \sum\limits_{k=-\infty}^{\infty} s_k e^{ik\theta}$ we get

$$\mathcal{G}_F(\rho)(\theta \quad = \quad \int\limits_{\theta}^{\theta+\pi} \sum_{k=-\infty}^{\infty} r_k e^{ik\theta'} \sum_{l=-\infty}^{\infty} s_l e^{il\theta'} d\theta' - \int\limits_{\theta-\pi}^{\theta} \sum_{k=-\infty}^{\infty} r_k e^{ik\theta'} \sum_{l=-\infty}^{\infty} s_l e^{il\theta'} d\theta'$$

$$= \quad \sum_{k=-\infty}^{\infty} t_k \int\limits_{\theta}^{\theta+\pi} e^{ik\theta'} d\theta' - \sum_{k=-\infty}^{\infty} t_k \int\limits_{\theta-\pi}^{\theta} e^{ik\theta'} d\theta'$$

$$= \quad \sum_{k \ odd} \frac{-4t_k}{ik} e^{ik\theta}$$

where $t_k = \sum\limits_{k} \left(\sum\limits_{i,j | i+j=k} r_i s_j \right) e^{ik\theta'}$. So once again we conclude that $\rho \in \mathrm{Ker}(\mathcal{G}_F)$ if and only if each $t_k = 0$ for k odd. This is all we can say about this case right now, so we leave the rest of this for future studies.

We can also investigate the equilibria from a different direction, by first looking for the solutions of the equation $\rho \mathcal{G}_F(\rho) = 0$, so for each $\theta \in [0, 2\pi]$, either $\rho(\theta) = 0$, or $\mathcal{G}_F(\rho)(\theta) = 0$.

Proposition 3. *The following statements hold:*

(i) $\rho \in \mathrm{Ker}(\mathcal{G}_F) \iff F(\theta + \pi)\rho(\theta + \pi) = F(\theta)\rho(\theta)$ *for all* $\theta \in [0, 2\pi]$.

(ii) The set $\left\{\theta \mapsto F(\theta + \pi)\hat{\rho}(\theta) \mid \hat{\rho}(\theta) \in C^1_{per}([0, 2\pi]), \pi\text{-}periodic\right\}$ is a subspace of $\mathrm{Ker}(\mathcal{G}_F)$.

Proof

(i) " $\Longleftarrow$ ": This follows directly from equation (20).
" $\Longrightarrow$ ": If $\rho \in \mathrm{Ker}(\mathcal{G}_F)$, this is equivalent to $\mathcal{G}_F(\rho) \equiv 0$, which implies that $\frac{\partial}{\partial \theta}\mathcal{G}_F \equiv 0$, and by using equation (22) we find that $F(\theta)\rho(\theta) = F(\theta + \pi)\rho(\theta + \pi)$ for all $\theta \in [0, 2\pi]$.

(ii) If we take $\rho(\theta) = F(\theta + \pi)\hat{\rho}(\theta)$ we get
$F(\theta)F(\theta+\pi)\hat{\rho}(\theta) = F(\theta+\pi)F(\theta)\hat{\rho}(\theta+\pi)$. Now if we take $\hat{\rho} \in C^1_{per}([0, 2\pi])$ and π-periodic and $\rho(\theta) = F(\theta + \pi)\hat{\rho}(\theta)$, we conclude from part (i) that $\mathcal{G}_F(\rho) \equiv 0$.

$\square$

Let us now consider the case that F is continuous and nowhere equal to 0. Then we can define the map $\xi : C([0, \pi]) \longrightarrow \mathrm{Fun}([0, 2\pi])$ by

$$\xi\hat{\rho}(\theta) := \begin{cases} \hat{\rho}(\theta) & \text{for } 0 \leq \theta \leq \pi \\ \frac{F(\theta-\pi)\hat{\rho}(\theta-\pi)}{F(\theta)} & \text{for } \pi \leq \theta \leq 2\pi \end{cases} \tag{27}$$

It holds that ξ is linear;
$\lim_{\theta \uparrow \pi} \xi\hat{\rho}(\theta) = \hat{\rho}(\pi)$ and $\lim_{\theta \downarrow \pi} \xi\hat{\rho}(\theta) = \frac{F(\pi)\hat{\rho}(\pi)}{F(0)}$
Thus $\xi\hat{\rho}$ is in $C([0, 2\pi])$ whenever

$$F(\pi)\hat{\rho}(\pi) = F(0)\hat{\rho}(0) \tag{28}$$

This implies that $\xi\hat{\rho}$ is 2π-periodic.

Proposition 4. $\mathrm{Ker}(\mathcal{G}_F) = \{\rho \in C_{per}([0, 2\pi]) | \rho = \xi\hat{\rho}, \hat{\rho} \in C_{per}([0, \pi])$ and satisfies equation (28}$).

Proof
From Proposition 3(i) we have for $\rho \in \mathrm{Ker}(\mathcal{G}_F)$ that $F(\theta+\pi)\rho(\theta+\pi) = F(\theta)\rho(\theta)$ for all $\theta \in [0, 2\pi]$. Thus $\rho = \xi\hat{\rho}$ where $\hat{\rho}$ is the restriction of ρ to $[0, \pi]$. Now, let $\hat{\rho} \in C([0, \pi])$ satisfy equation (28), then $\rho = \xi\hat{\rho}$ satisfies

$$\rho(2\pi) = \frac{F(\pi)\hat{\rho}(\pi)}{F(0)} = \hat{\rho}(0) = \rho(0) \tag{29}$$

Thus $\rho \in C_{per}([0, 2\pi])$. By construction, ρ satisfies the condition of Proposition 3 (i). $\square$

We can conclude from Proposition 2 and its generalisation Proposition 3, that the case $D \equiv 0$ will be degenerate in comparison to $D > 0$. Both ways of determining equilibria lead to infinitely many solutions.

5.3.2 Case $D > 0$

Like we have seen in the previous chapter, assuming that fish do not make random movements, leads to a infinitely many equilibria. So apparently, taking $D \equiv 0$ does not simplify the dynamics, nor simplifies the mathematics. We have found that there exists at least one equilibrium for the case $D > 0$.

Proposition 5. *Let $F > 0$, $D > 0$ be π-periodic continuous functions. Then $\rho(\theta) = \frac{c}{D(\theta)}$ is an equilibrium for the extended Grünbaum model.*

Proof
We can proof this by substituting $\rho(\theta) = \frac{c}{D(\theta)}$ in the extended Grünbaum model. Clearly $\frac{\partial^2}{\partial \theta^2}(D\rho) = 0$. Proposition 3(i) yields that also $\mathcal{G}_F \equiv 0$, thus

$$\frac{\partial}{\partial t}\rho = \frac{\partial^2}{\partial \theta^2}(D\rho) - \beta \frac{\partial}{\partial \theta}(\rho \mathcal{G}_F) = 0 \qquad (30)$$

$\square$

As we have said before, the case where $D > 0$ is studied in [9] although the question of stability of equilibria is only considered for constant D and F. We leave the search for more equilibria in this case for future studies.

6 Discussion and open problems

The (extended) Grünbaum models are not able to resolve the delicate spatial structure of the total fish school (Figure 4). If we look at the different shapes the school can adopt, we see that these models cannot determine the difference between the doughnut shaped school, Figure 4(B), and the school in which fish swim in totally random directions, Figure 4(A). When fish swim randomly, like we described in Chapter 3, there are the same amount of fish orientated one direction as the other. This means that $\int_{\theta}^{\theta+\pi} \rho(\theta',t)d\theta' - \int_{\theta-\pi}^{\theta} \rho(\theta',t)d\theta' = 0$. If we compare this to the case where the school has the shape of a doughnut, we see that there are also equally as many fish orientated one way as the other, so our model gives the same result. So this kind of models is not able to distinguish spatial differences between fish schools. This is one reasons why we referred to it as a partial result.

The question whether the (extended) Grünbaum model with $D \equiv 0$ is well-posed remains open: whether solutions to the initial value problem exist (local in time) are unique and depend continuously (in some sense) on the initial value. The results on equilibria suggest it is not.

Another point of discussion is mentioned in [9]. There they comment on the biological interpretation of the solutions of the extended Grünbaum model. The angular orientation of a fish is placed in a arbitrary horizontal plane, but this has nothing to do with the actual location of the fish in the water volume.

Preparatory studies have found a symmetry axis which have been used as the origin for the angular orientation. However, this axis is by no means connected to a specific horizontal direction in the sea. Besides that there is also no relationship between a given orientation and the actual location of the fish with this orientation. The determination of a suitable model is announced in [9] as a subject for future research.

What will happen in the case $D \not\equiv 0$ and F or D is not π-periodic? Or when $D \not\equiv 0$ but $D(\theta) = 0$ for some θ? And similar for $\mathcal{G}_F$ with $F(\theta) = 0$ for some θ. These are all questions which are still unanswered. It may be necessary to consider the underlying stochastic models to verify that these cases make sense altogether.

Another point of discussion has to do with equation (13). In this equation we introduced the parameter a that models the balance between the tendency to align and the attraction to neighbours. One can wonder how the simulations based on this equation as in [7] depend on the choice of a. This problem is not addressed in [7], but seems to be interesting to investigate to us in further detail.

We would like to make a final comment on the extended Grünbaum model. We can try to find equilibria in another way than described in Section 5. If we rewrite equation (24) we get

$$-\beta\rho\mathcal{G}_F(\rho) = c - \frac{\partial}{\partial\theta}(D\rho)$$

If we substitute this into the equilibrium equation multiplied by ρ

$$
\begin{aligned}
0 &= \rho\frac{\partial^2}{\partial\theta^2}(D\rho) - \beta\rho\frac{\partial}{\partial\theta}\left[\rho\mathcal{G}_F(\rho)\right] \\
&= \rho\frac{\partial^2}{\partial\theta^2}(D\rho) - \beta\rho\mathcal{G}_F(\rho)\frac{\partial\rho}{\partial\theta} \\
&\quad +2\beta\rho^2\left[F(\theta)\rho(\theta) - F(\theta+\pi)\rho(\theta+\pi)\right]
\end{aligned}
\tag{31}
$$

we get the following functional differential equation

$$
\begin{aligned}
0 &= \rho\frac{\partial^2}{\partial\theta^2}(D\rho) + \left(c - \frac{\partial}{\partial\theta}(D\rho)\right)\frac{\partial\rho}{\partial\theta} \\
&\quad +2\beta\rho^2\left[F(\theta)\rho(\theta) - F(\theta+\pi)\rho(\theta+\pi)\right]
\end{aligned}
\tag{32}
$$

It may be interesting to see whether this may be approached with techniques for delay equations.

As found in [9] for D and F constant, there turns out to be a critical value β_0 for β such that there is an additional (stable) equilibrium for $\beta > \beta_0$ apart

from the (then unstable) trivial equilibrium. This may be recovered from (32) as well.

We did not survey the literature for (large scale) fish migration models. This field of research may be looked at in the future in search for continuum models for fish schooling. It remains to be seen to what extent these models incorporate the underlying behaviour of individual fish or are mainly phenomenological.

So, summarizing, there is plenty of opportunity for mathematical research concerning Eulerian models for fish schooling. These may turn out to be very useful in fish migration studies.

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