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Publication Date

2008-01-24

Discrete and continuous models of the dynamics of pelagic fish: application to the capelin

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Abstract

In this paper, we study simulations of the schooling and swarming behavior of a mathematical model for the motion of pelagic fish. We use a derivative of a discrete model of interacting particles originated by Vicsek, Czirók et al. [6] [5] [23] [24]. Recently, a system of ODEs was derived from this model [2], and using these ODEs, we find transitory and long-term behavior of the discrete system. In particular, we numerically find stationary, migratory, and circling behavior in both the discrete and the ODE model and two types of swarming behavior in the discrete model. The migratory solutions are numerically stable and the circling solutions are metastable. We find a stable circulating ring solution of the discrete system where the fish travel in opposite directions within an annulus. We also find the origin of noise-driven swarming when repulsion and attraction are absent and the fish interact solely via orientation.

Key words: fish schooling, interacting particle model, capelin, swarming, migration

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1 Introduction

The capelin (*Mallotus villosus*) is a pelagic species of fish in the northern seas where there are several separate stocks of capelin [25] [26] [27]. We are interested primarily in modeling the capelin stock which lives in the ocean around and to the north of Iceland. This stock matures off the northern shelf of Iceland and each year the mature portion of the stock, generally two to three years old, migrates into the Arctic Ocean north of Jan Mayen, an island about 600 kilometers northeast of Iceland, to feed on the zooplankton that thrives on the vernal phytoplankton bloom in the Arctic waters. This portion of the stock returns to the northern shelf of Iceland and roughly four months later undertakes a spawning migration around Iceland, generally clockwise, to the southwestern coast of Iceland. There they spawn and almost all of the spawners die; the young drift with the tidal currents back to the northern shelf, where they remain until they are mature enough to undertake the migration [25] [26] [27].

The Icelandic fishing industry is interested in the capelin because is it a feeder fish for many larger, economically important species of fish such as the cod and the herring. Some fishing industry also catches the capelin for domestic use and export. Because of the ecological and economic importance of the capelin, it is vital that the capelin population be monitored to ensure that fishermen can find the stock and ensure that they do not overfish the species. Overfishing of the capelin could cause a population collapse not only of the capelin, but also of the cod and other species that depend on the capelin for sustenance.

We want to create a model of this migration cycle which can be used to estimate the location of the capelin stock at various times of year. Many environmental factors affect the migration, such as temperature, availability of food, size of the capelin population, and oceanic currents. While some studies are being performed incorporating some of these data, for example see [16] and [15] which build ocean temperature and currents into the model, these studies use forcing which models a homing instinct to reproduce the migration. We hope to model the migration using the physical factors mentioned above with no such forces affecting the migration route. In this paper, we focus on understanding all possible behaviors of our model and their properties. By analyzing the different solutions we can expect from the model, we gain insight into which behaviors will be useful to us in our eventual simulation of the migration.

The model we are using has an extensive history. It originated in 1995 when Vicsek, Czirók, Ben-Jacob, Cohen, and Shochet published a model intended to simulate interacting particles [23]. Their model has been modified and studied extensively, see for instance [4] [1]. In this paper, we use the following version of the model,

[1] For more information about models addressing similar issues, see [21] and [22] which treat a continuum model, and [7], which considers both an individual-based model and a

which simulates the tendency of fish to match neighbors in speed and direction:

$$\begin{pmatrix} x_k(t+\Delta t) \\ y_k(t+\Delta t) \end{pmatrix} = \begin{pmatrix} x_k(t) \\ y_k(t) \end{pmatrix} + v_k(t) \begin{pmatrix} \cos(\phi_k(t)) \\ \sin(\phi_k(t)) \end{pmatrix} \Delta t \tag{1}$$

This model was published by Hubbard, Babak, Sigurdsson, and Magnússon in 2004 [10]. It is a two-dimensional discrete model which is particularly well-suited to the capelin, since the species tends to stay close to the surface of the ocean and can therefore be reasonably modeled in two dimensions. Here, x and y are the x- and y-coordinates of the fish, v is the speed of the fish, and ϕ is the direction angle, i.e. the direction that the fish is heading. The subscripts track to which fish the variables correspond (for instance, x_k is the x-coordinate of the k^{th} fish). When N fish interact, ϕ and v are updated as follows:

$$\begin{cases} \cos(\phi_k(t+\Delta t)) = \frac{1}{N}\sum_{j=1}^{N}\cos(\phi_j(t)) \\ \sin(\phi_k(t+\Delta t)) = \frac{1}{N}\sum_{j=1}^{N}\sin(\phi_j(t)) \\ v_k(t+\Delta t) = \frac{1}{N}\sum_{j=1}^{N} v_j(t) \end{cases} \tag{2}$$

In the most basic form of the model, described by (1) paired with (2), directional alignment is achieved by averaging the cosines and sines of ϕ for all of the fish and normalizing to get the unit direction vector at the next time step. The fish choose their next speed by averaging the speeds of all of the fish. In more complex versions of this model, fish consider their distance from other fish when determining their next direction and speed and react to neighboring fish differently depending on their distance.

Biologically, studies have found that fish prefer to stay within a certain distance of their neighbors using vision and their lateral lines [18] [19]. The lateral line is a sense organ running the length of some fish's bodies that can detect pressure changes and velocity. Fish detect neighbors which are too close using their lateral lines and avoid them; they use their vision to find and move toward fish which are too far away [19]. This helps the fish form schools and protect themselves from predation, see [18]. In addition, there are hydrodynamic and navigational advantages to schooling [19]. Papers [28] and [29] provide further evidence of how repulsion and attraction affect the behavior of groups of fish in an experimental setting.

Many models of fish schooling have implemented different regions, often called zones, to try to mimic this tendency, see for example [4] [9] [12] [13]. Typically, three zones are specified around each fish: the *zone of repulsion*, defined by a radius of repulsion where the fish tries to head away from any others within this radius,

continuum model.

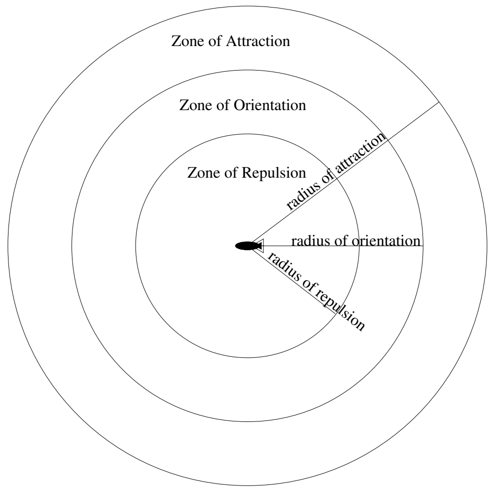

Fig. 1. At the center of this picture is a fish, and around it are drawn the three zones instituted in our discrete simulations: the zone of repulsion, the zone of orientation, and the zone of attraction. The radius of each zone is also shown. In our model, the fish wants to move directly away from fish in its zone of repulsion, align its heading and speed to that of the fish in its zone of orientation, and head directly toward fish in its zone of attraction. These desires are balanced by assigning a weight to each zone, so that the different, often conflicting, information can be weighed.

the *zone of orientation*, where the fish tries to align its direction angle and velocity with all fish inside this zone, and the *zone of attraction*, where the fish tries to go directly toward other fish within its radius of attraction and outside its zone of orientation. These zones are pictured in Figure 1. The information from the three zones is balanced by assigning a weight to each zone taking a weighted average of the input from these three zones.

In Section 2, we discuss the system of ordinary differential equations (ODEs) which Birnir derived from the simple discrete model (1) described above without the zones implemented [2]. This system of ODEs is easier to analyze than the discrete model and gives us insight into the types of behavior we may expect from the discrete system. We numerically solve the ODEs using MATLAB's ode23s solver. We find that the ODE system displays two main types of behavior: in Section 2.1, we describe *migratory* behavior where the simulated fish align with each other and head in one direction as a group; in Section 2.2, we describe *stationary* behavior, where the fish remain in place. The stationary solutions also give rise to *circling solutions* via small deterministic perturbations, see Section 2.3, and we will see in Section 4 that they play a key role in the formation of swarms.

We then analyze the discrete system. In our numerical exploration of the discrete system, implemented in MATLAB, adjusting angular noise and parameters such as the radii of the zones of attraction, orientation, and repulsion and the various weights that these zones carry, produces certain complex global behaviors. These behaviors include *migratory* behavior similar to that described above, see Section 3.1; *metastable circling* behavior, where the fish are positioned symmetrically around a circle and each fish traces out its own small circle, eventually dissolving into a migratory solution, see Section 3.3; *stable circling* behavior, where the fish form a circular loop and move around it with some fish traveling one way and others traveling the other, see Section 3.4; and *swarming*, where the fish come together and form a rough disk and the fish that leave the group are pulled back inside, see Section 3.5. These findings are important because biologists have observed behavior resembling the migration and swarming solutions in actual groups of fish. In addition to these solutions, we find an origin of swarming different from swarming motivated by repulsion and attraction. This new type of swarming depends only on the orientation interaction of the fish and on noise, see Section 4.

The various solutions discussed above interest us because they will be useful for simulating the capelin as it migrates around Iceland. In particular, we hope to use the migratory solutions while the fish move between Iceland and the Arctic Sea north of Jan Mayen and again when the fish undertake the spawning migration. The swarm solution will be useful while the fish are feeding north of Jan Mayen and when they are spawning.

We plan to introduce a dynamic energy budget (DEB) model to keep track of the size and reproductive maturity of the fish. Dynamic energy budget (DEB) models were created by biologists to study the lifecycle of populations of animals by considering the individuals within that population, see [8] [11] [17] [20]. These models use ODEs to solve for the carbon content and reproductive reserves for each individual in a population. The ODEs depend upon such parameters as food density, energy assimilation rate, and cost of maintenance; all of these parameters are species- and time-dependent. The individuals mature when the cost of maintenance is lower than the amount of energy that an individual has at a given time. We will use the information from the DEB model as internal triggers for the migration. For example, the fish achieving a specified carbon content might trigger the feeding migration and the fish reaching a certain reproductive reserve might trigger the spawning migration by changing the fish's temperature preferences. These triggers, along with external physical information, will enable us to transition between different solutions to the discrete model (1) during the course of the migration. For further information about DEB models, see [8] [11] [17].

2 The ODEs

In [2], Birnir derived a system of four ODEs from the discrete model (1) without the zones of interaction implemented; i. e., in the language used above, the zones of repulsion and attraction do not exist and the zone of orientation is infinite. Birnir's system is as follows:

$$\begin{cases} \dot{r}_k = v_k \cos(\phi_k - \theta_k) \\ r_k\dot{\theta}_k = v_k \sin(\phi_k - \theta_k) \\ \dot{v}_k = \frac{\alpha}{N^2}\sum_{j=1}^{N} v_j \sum_{j=1}^{N}\cos(\phi_j - \phi_k) - \alpha v_k \\ v_k\dot{\phi}_k = \frac{\alpha}{N^2}\sum_{j=1}^{N} v_j \sum_{j=1}^{N}\sin(\phi_j - \phi_k) \end{cases} \tag{3}$$

The position of each fish is now expressed in polar coordinates r and θ and a turning rate α has been introduced; in our analysis, we take $\alpha = 1$. Using this system, one can implement zones of attraction and repulsion using potentials and also introduce noise, but these alterations are not necessary to find simple behaviors exhibited by the model. Using system (3), Birnir found two types of solutions. He found the migratory solution, where all the fish move as a school in one direction. Using bifurcation theory, he also derived an infinite family of asymptotically stationary solutions. In these solutions, the fish slow down quickly and stop, remaining stationary thereafter. For information on the derivation of the ODE model (3) and its symmetries, refer to [2].

In our exploration of the system (3), we used MATLAB's ode23s function to solve the system. The solutions of this system give us insight into the kinds of behavior the discrete system might exhibit in the absence of noise. In our analysis of this system of ODEs, both analytical and numerical, we found three types of solutions detailed below: the *migratory solutions* and *stationary solutions* that Birnir's paper discusses, see Sections 2.1 and 2.2, respectively. When we added a deterministic perturbation to the stationary solutions, we also found *circling solutions* where each fish traces out its own circle.

2.1 Migratory Solutions

If the fish are given generic initial conditions, they will exhibit migratory behavior. Figure 2 shows an example of a migratory solution. Once the fish have found the migratory solution, they continue to display migratory behavior. The migratory solutions are stable, since they persist when the initial conditions are perturbed and arbitrary initial conditions lead to migratory solutions. The migratory solution results from the fact that the ODE system (3) has an infinite radius of orientation. This will, in most noiseless cases except the stationary ones, force the fish to align themselves and move as a group.

The ODEs are derived from the discrete model (1) and should therefore exhibit similar long-term behaviors. That the migratory solution is the most likely to appear when solving this system of ODEs indicates that the migratory solution should also

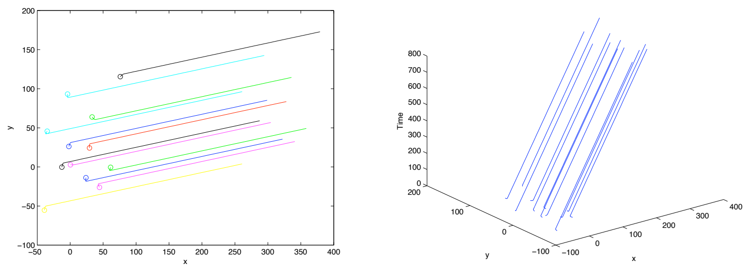

Fig. 2. These plots were generated from the ODEs (3) and illustrates a migratory solution. The figure on the left shows the positions of twelve randomly placed fish over time. Their initial positions are indicated by the circles and they are headed in different random directions. After a brief transitory period, they align themselves and once they are aligned, they move up and to the right as a group. The figure on the left shows the positions of the fish plotted against time and demonstrates that after the transitory period, they move at a constant speed.

be the most prominent solution in the discrete system. This is confirmed in Section 3.1.

2.2 Stationary Solutions

When we initialize the positions of the fish to be roots of unity around a circle or roots of unity around several concentric circles with direction angles tangent to the circle, they move forward, slowing down as they go, and quickly stop. When they stop, they are still arranged around concentric circles, and they stay in this position forever. Consequently, such solutions are called *stationary solutions*. Figure 3(a) shows a stationary solution for one circle of fish, and Figure 3(b) shows a stationary solution for three concentric circles, where the x- and y-positions of the fish are plotted against time. These solutions occur whenever the direction angles of the fish are roots of unity and also for all of the symmetries mentioned in [2]. For more discussion of stationary solutions, see Section 3.2.

2.3 Circling Solutions to the ODEs

To determine the solutions which lie close to the stationary solutions in phase space, we consider a perturbation of system (3):

$$\begin{cases} \dot{r}_k = v_k \cos(\phi_k - \theta_k) \\ r_k \dot{\theta}_k = v_k \sin(\phi_k - \theta_k) \\ \dot{v}_k = \frac{1}{N^2} \sum_{j=1}^{N} v_j \sum_{j=1}^{N} \cos(\phi_j - \phi_k) - v_k + \nu \\ v_k \dot{\phi}_k = \frac{1}{N^2} \sum_{j=1}^{N} v_j \sum_{j=1}^{N} \sin(\phi_j - \phi_k) + \omega \end{cases} \quad (4)$$

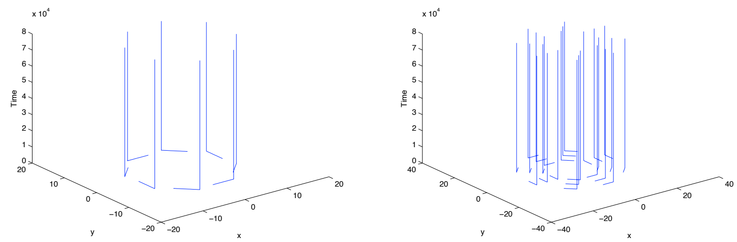

Fig. 3. This figure shows two simulations the ODEs (3) that resulted in stationary solutions. The figure shows the x- and y-coordinates of the fish plotted against time. In the left figure, eight fish begin set up as roots of unity on a circle heading tangent to the circle in a counterclockwise orientation. They then move forward and slow down as they go, stopping on another circle with larger radius. Their directions are tangent to this circle and they are placed as roots of unity. They remain in the position forever, as evidenced by their x- and y-coordinates remaining constant as time increases. The figure on the right is similar, showing instead of one circle of fish, three circles of eight fish, each one of which is arranged as in the figure on the left. Similarly to Figure (a), they move forward, slow down, and stop on three circles and remain stationary on this circle forever.

where ν and ω are small deterministic perturbations to the equations for $\dot{v}$ and $\dot{\phi}$. To create circling solutions, we initialize the fish so that with $\nu = \omega = 0$ they would move toward an asymptotically stationary solution. With nonzero ν and ω, the fish move toward the stationary solution where they would stop without the perturbation, pause there, and then each start tracing out a circle. These circles are not concentric but instead each fish traces out its own circle, see Figure 4. The size of the circle depends on the size of the perturbation, with smaller circles corresponding to smaller ν and larger circles corresponding to larger ν. Figure 4 juxtaposes the path of the fish for a certain stationary solution and the path for that stationary solution perturbed by $\nu = 5 \times 10^{-5}$ and $\omega = 1 \times 10^{-5}$ and then $\nu = 1 \times 10^{-4}$ and $\omega = 1 \times 10^{-5}$ for the velocity and direction angle perturbations, respectively. For more information about these circles, see [2].

3 The Discrete Model

Because our exploration of the associated ODEs revealed the migratory and stationary solutions, we sought these behaviors in the discrete model. We also implemented the zones of interaction discussed in Section 1: the *zone of attraction*, the *zone of orientation*, and the *zone of repulsion*, see Figure 1. These zones are biologically motivated and have been observed by biologists in schooling fish, see [18] [19]. Including these zones in the model differs from the work by Hubbard, Babak, Sigurdsson, and Magnússon, who worked solely with the zone of orientation [10].

We added angular noise to the system at each timestep, assigning an amplitude to be used throughout the simulation and adding random perturbations of this amplitude to the cosines and sines of the direction angle of each fish. We also experimented

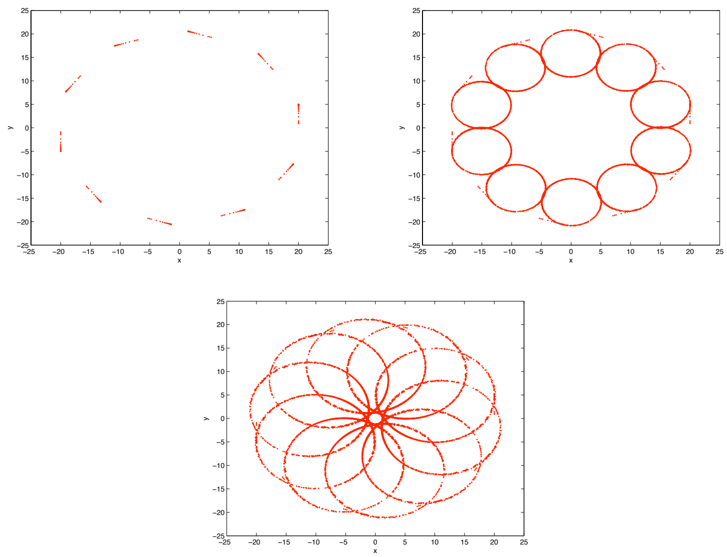

Fig. 4. All three of these pictures show the positions of ten fish set up as roots of unity on a circle of radius 20. The fish are headed tangent to the circle in a counterclockwise orientation. All three pictures have the same initial conditions. The first picture shows the paths of the fish with no perturbation of the ODE system (3). They move to the stationary solution, as in Figure 3. The second picture shows what happens when a perturbation of $\nu = 5 \times 10^{-5}$ is added to $\dot{v}$ and a perturbation of $\omega = 1 \times 10^{-5}$ is added to $\dot{\phi}$. The third picture shows the positions of the fish over time when a perturbation of $\nu = 1 \times 10^{-4}$ is added to $\dot{v}$ and a perturbation of $\omega = 1 \times 10^{-5}$ is added to $\dot{\phi}$. These pictures show that the circles that each fish makes grow as the velocity perturbation increases.

with varying the radii of the zones and the zonal weights; recall from Section 1 that each zone is assigned a weight so that the different, often conflicting, information from each zone can be balanced. When varying the weights for the different zones, we generally held the weight inside the zone of orientation at 1 and we called the weight for the zone of repulsion "repulsionWeight" and the weight for the zone of attraction "attractionWeight." We also assigned "selfWeight" to each fish, which allowed us to vary the weight that a fish gives its own directional heading.

We found several interesting behaviors as we varied the weights and the amplitude of the noise. The most prevalent solutions were the *migratory solutions*, see Figure 6. When the noise was increased, the path of the groups of fish became more erratic, but the fish still traveled together as a group, see Figure 5. The migratory solutions occurs without the different zones implemented and also with them, see Section 3.1. When there are no zones implemented, given certain initial conditions, the *stationary solution* appears, see Section 3.2. When the zones are implemented, under certain particular conditions, we can force fish to move in *(metastable) circles*, see Figure 9 and Section 3.3. If we vary the radii of the zones, change the orientation weight, and include noise, we find *stable circling solutions* in which the fish come together and form a circulating ring, with some fish going clockwise and some going counter-clockwise, see Figure 10 and Section 3.4. This solution seems to be stable: it continues as time goes on and it is not disturbed by the presence of reasonable noise. By varying the amount of noise and the zonal weights, we can

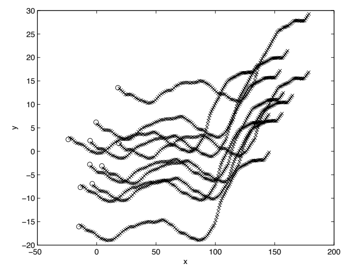

Fig. 5. This figure is a migratory solution of the discrete model (1) with no zone of repulsion and an infinite zone of orientation. In this simulation, the amplitude of the angular noise was very high. The plot shows the positions of the fish over time. The initial positions of the ten fish in this simulation are plotted as circles. All ten were placed in random positions with random directional headings. They immediately align themselves with each other and begin moving together as a group, and although the noise serves to make the group change directions and move on a more random path, they continue to move together as a group, essentially making a random migration.

also produce what we call *swarming solutions*. In these solutions, the fish come together as a group and although each fish weaves around inside this group, the group as a whole does not move, see Figure 11 and Section 3.5.

3.1 Migratory Solutions

As in the ODE system, the migratory solution is the most likely solution to appear and once it appears, it persists. In the simplest form of the model with an infinite zone of orientation, given generic initial conditions and random noise, the fish always find the migratory solution unless the noise is so large that the fish's directions are essentially random. If the noise is large but not unreasonable, then the fish tend to change direction as a group, all moving as a school albeit no longer linearly, see Figure 5. The migratory solution also appears when we implement the three zones. In this case, there is more diversity in the possible solutions and the initial conditions and the amount of noise paired with the weights and sizes of the zones seems to determine what type of long-term behaviors we see.

Given arbitrary initial conditions, the most likely outcome of any choice of weights and radii is migratory behavior. This indicates that these solutions are stable, whereas the other solutions are more sensitive to perturbations. Figure 6 shows one migratory solution. The radius of repulsion is 3, orientation is 20, attraction is 100; repulsionWeight and attractionWeight are 0.0032 and 0.0025, respectively, and the amplitude of the noise added to the velocity and direction angle at each step is 0.05. Depending on the proximity of initial conditions and the radii of the different zones, the fish occasionally split into several migrating schools. For example in Figure 7, the zones and weights are the same as they are in Figure 6, but the random initial conditions were sufficiently different to split the fish into three groups.

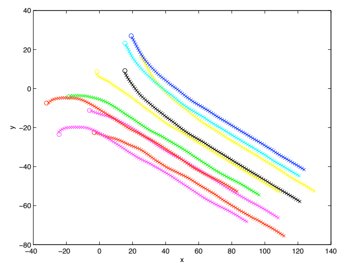

Fig. 6. This figure shows a migratory solution of the discrete model (1) with the radius of repulsion 3, the radius of orientation 20, and the radius of attraction 100. The initial conditions of the fish were random. The initial positions of the ten fish are plotted with circles. The fish immediately align themselves with each other and travel as a group from the upper left corner of the plot to the lower right corner. The repulsion and attraction weights were 3.2×10^{-3} and 2.5×10^{-3}, respectively. The amplitude of the noise added to the velocity and direction angle at each step is 0.05.

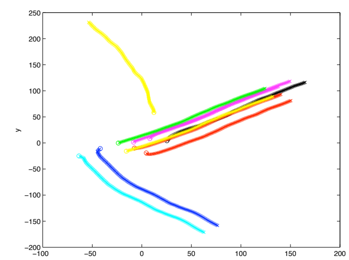

Fig. 7. This figure is another simulation using the discrete model (1). It was simulated under the same conditions as Figure 6, but the randomness of the initial conditions was enough to make the fish split into two groups, with one fish heading off on its own. The two groups from cohesive migrating groups, however, so it is still a migratory solution.

3.2 Stationary Solutions

Looking for stationary solutions to the discrete model, we mimicked the conditions for the stationary solution to the ODE model. Using the simplest case of the discrete model where the only interaction between the fish is orientation and all fish interact with all other fish, we implemented the initial conditions in the discrete model that caused stationary solutions in the ODEs and found stationary solutions to the discrete model. The same initial conditions which lead to asymptotically stationary solutions in the ODEs also lead to stationary solutions in the discrete model. In the ODEs it takes a short time for the fish to find the stationary solutions. In the discrete model, because of the instantaneous averaging, the fish remain immobile from the first iteration.

In these stationary solutions, n fish are initialized with direction angles that are nth roots of unity. The same symmetries which apply in the case of the ODEs also apply here, i.e. we can add an arbitrary constant perturbation to all of the direction angles and still expect to see the stationary solution. This amounts to rotating the roots of unity arbitrarily clockwise or counterclockwise like turning a wheel. We also can set up any number of groups of fish each of which is arranged as above,

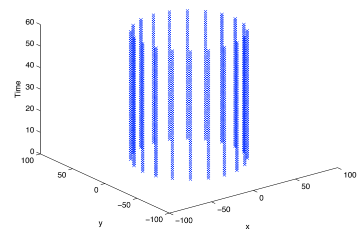

Fig. 8. This figure shows an example of a stationary solution to the discrete system (1), analogous to the stationary solutions in Figure 3. The fish begin and remain as roots of unity with direction tangent to the circle. This plot shows 20 fish set up in this way, with their x- and y-coordinates plotted against time.

for example two groups of fish where one set of five fish has angles as fifth roots of unity and the other group of 38 fish has angles as 38th roots of unity, and when we simulate them together, all the fish remain stationary. For derivation of this model and more discussion of these symmetries, refer to [2].

It is interesting to note that it is not necessary for the fish to have specific initial x- and y-coordinates. The only condition necessary for the fish to remain stationary is that their angles are arranged as described above. From the discrete model (1) and system (2), it is easy to see that if the average of all the cosines of the angles and the average of all the sines of the angles of the fish is zero, the fish will maintain their initial positions *independent of where they began*. This independence will be exploited in Section 4 to induce orientation-based swarming.

3.3 Metastable Circling Solutions

Given an adequate number of fish, when repulsion and attraction are implemented and there is only one circle of fish placed symmetrically on concentric circles heading tangent to the circle either all clockwise or all counterclockwise, there is a seemingly stable orbit during which each fish traces out its own circle. The fish head away from the others due to repulsion and being drawn back because of attraction.

When there are several concentric circles and adequately many fish, each fish initially traces out its own circle. The fish head away from their initial placements because there are other fish within their zone of repulsion, but as they head away, the zone of attraction starts to affect their direction and they turn back toward the other fish. Motivated by the interaction of these two zones, they each travel in a small circle. When viewed as a whole, the fish form a circular ring which slowly expands and contracts. However, this circular ring slowly pinches in, exhibiting a Kelvin-Helmholtz long-wave instability deforming the circle. The fish begin to cluster and clump and the pattern disintegrates into a migratory solution. Figure 9 shows one such situation as time goes on.

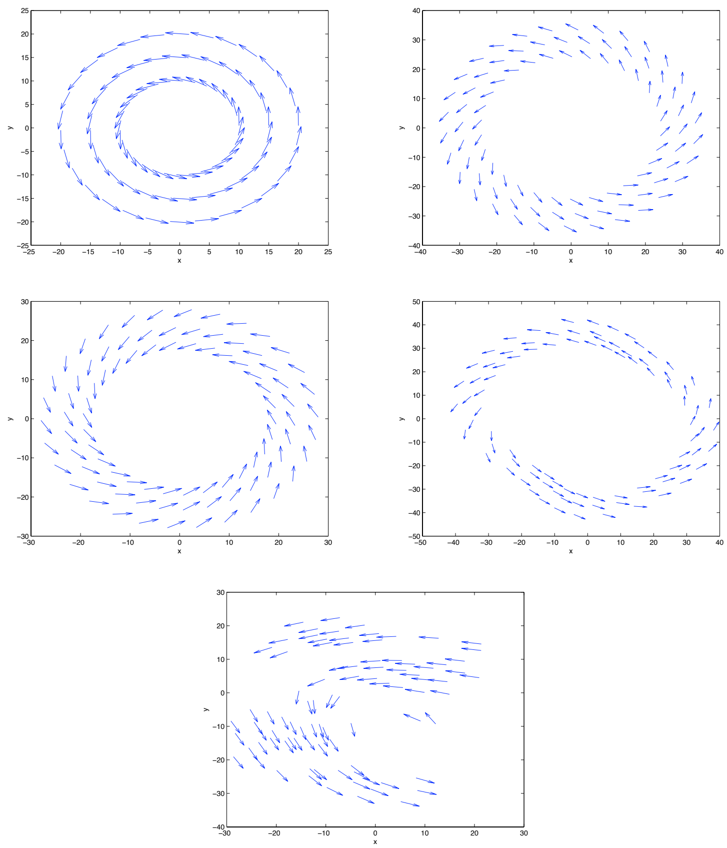

Fig. 9. This figure shows the instability of the circling solutions to the discrete model (1) with repulsion and attraction implemented. The first frame is at the first timestep, the second is at the 70^{th}, the third is at the 200^{th}, the fourth is at the 350^{th}, and the last frame is at the 500^{th} timestep. Each timestep is 0.25. The fish begin as roots of unity around three circles and move outward, each fish tracing out its own smaller circle. However, these circles are unstable, as one can see from the last two frames, during which the circles deform and the fish move toward a migratory solution.

Because the circling does not persist over time and is sensitive to perturbations in the initial conditions as well as to the magnitude of the noise, we conclude that multiple ring circling solutions are not stable; however, they persist for a long time and so can be considered metastable.

3.4 Stable Circles

Given particular choices of the weights and radii for the different zones, increasing the parameter selfWeight to a very large value, decreasing the angular noise, increasing the attractionWeight and repulsionWeight, and making the fish place random weight (with mean 0 and variance 1) on their interactions in the zone of orientation, we find a circling solution that persists over time. That the fish are placing random weight on their interactions in the zone of orientation means that the fish are sometimes paying attention to which way the other fish are headed and

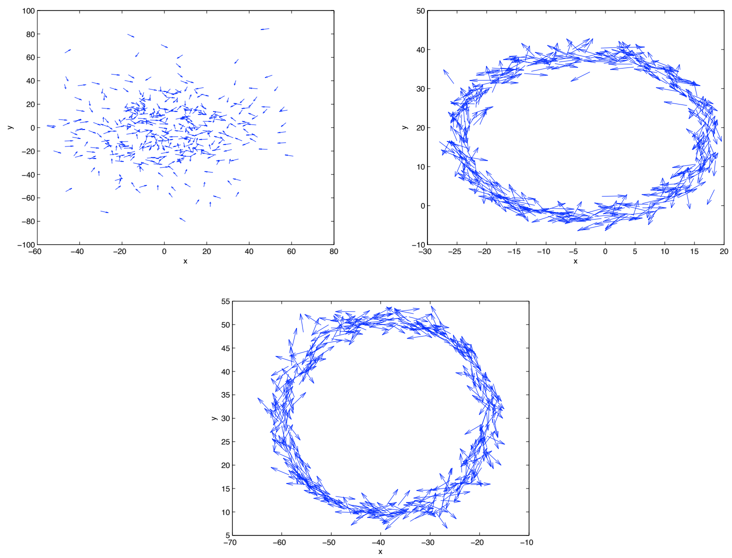

Fig. 10. This figure shows the stable circling solution to the discrete model (1). The first frame is at the first timestep, the second is at the 251^{st}, and the third is at the 800^{th}, with each timestep 0.25. In this solution, the zones of attraction and repulsion are implemented, the fish inside the zone of orientation are given random weight, the angular noise is low, and the parameter selfWeight is very large. The fish begin scattered, and then move toward each other, forming a ring with some fish going clockwise around the ring and some going counterclockwise around it. The solution is stable; once the fish find this solution, they stay on it. The ring shown here is stationary, although this is not always the case. The ring will sometimes move given different initial conditions and the same parameter values.

sometimes not paying attention to this. Under these conditions, when the fish begin scattered, they gather together to form a ring of fish, with about half of the fish moving clockwise and the other half moving counterclockwise around the ring. When this formation occurs, it persists, with fish that leave the ring they being pulled back in again. It differs from the circling solutions described above in Section 3.3 because the fish all travel along the same ring. Figure 10 shows such a solution over time. The ring sometimes stays stationary and sometimes moves slowly but maintains its shape as time goes on. It is possible to create rings which move and rings which remain in place using the same weights and radii, so this difference in behavior stems from the difference in initial conditions.

Behavior similar to this stable circling ring has been found by other groups working with models that include repulsion and attraction but are otherwise significantly different from this model. For example, Chuang, D'Orsogna, Marthaler, Bertozzi, and Chayes found similar behavior which they call "two interlocking mills" in a model using ODEs that included repulsion and attraction [3]. Similar behavior was also found by Levine, Rappel, and Cohen in a different discrete model employing zones of repulsion and attraction [14]. Accordingly, this behavior seems to be dependent on the zones of interaction and noise and not dependent on the particularities of the model studied here.

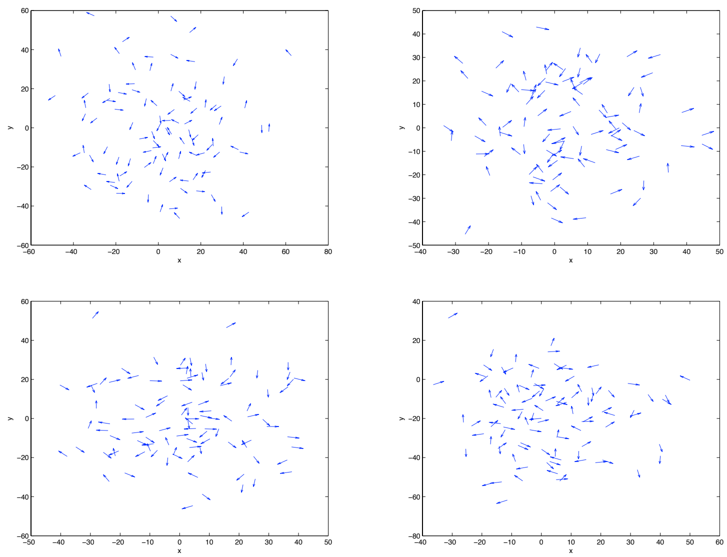

Fig. 11. In this figure, timesteps $1, 501, 751$, and 1000 of a swarming solution to the discrete model (1) are shown, where the size of each timestep is 0.25. In these solutions, the zones of attraction and repulsion are implemented and their associated weights are small, the parameter selfWeight is usually very high, and the angular noise is also high. The fish begin scattered and gather together, forming a group of unaligned fish with fish weaving through the group but not leaving it. Depending on the parameter values, the group sometimes moves and sometimes stays stationary, much like the situation with the stable circling solutions.

3.5 Swarming

We also see swarming behavior, where the fish come together into a group and the group stays more or less stationary as the individual fish weave throughout it. Figure 11 shows four iterations of a swarming solution over time. This behavior can be used to simulate the spawning and feeding behaviors of certain types of fish, and we hope to incorporate it into our simulation of the capelin's migration route in the Icelandic waters.

In our exploration of the swarming solution, we found that the solution was dependent on noise and the various zonal weights. To achieve a stable swarming school of fish we used the parameter selfWeight, see Section 3, which describes a fish's tendency to maintain its directional heading from one time step to the next. This parameter appears to correlate with the number of fish; the more fish are in the simulation, the higher selfWeight needs to be for the swarming solution to remain stable. In fact, we found selfWeight needed to be approximately 1.5 to 2 times the total number of fish to achieve a swarming solution. In exploring the effects of the selfWeight parameter, we found that a stable swarming solution can be made migratory by decreasing the selfWeight. Decreasing it a small amount will cause the swarm to drift around, but there is still no parallelism in the school. Adjusting it down more causes more drift, and some fish begin to align with each other. Further downward adjustment, approaching one quarter or less of the total number of fish, pushes the school over a tipping point where it assumes parallelism and travels in a well defined direction, transitioning to a migratory solution.

A stable swarming school also can be made migratory by adjusting only the amount of angular noise, although the numbers are less dramatic. One of our stable swarms used an angular noise coefficient of 0.72. When it was gradually adjusted downwards to around 0.12, the same continuum of behaviors was observed as when the selfWeight was decreased. By decreasing the angular noise, the school achieves parallel motion and migration, but each fish moves on a much smoother path than when we decrease selfWeight only.

4 The Origin of Orientation Induced Swarming

Swarming has been found in the discrete model with repulsion and attraction as described above. Similar swarming behavior has been studied in other models that include repulsion and attraction [21] [22] [4]. This type of swarming depends on the fish being pulled toward each other when they are far apart and repelled when they are close; the push-pull dynamics paired with noise produce the swarming solutions explored in Section 3.5. But can swarming solutions also be found in models with only one type of interaction, the zone of orientation? Or are the opposing effects of repulsion and attraction necessary to produce behavior resembling feeding or spawning fish?

When considering stationary solutions, it is interesting to note that the position of the fish does not affect their behavior, as the direction angles determine when the fish are stationary. In the discrete model (1) when the only zone of interaction is an infinite zone of orientation, any of the initial conditions which produce a stationary solution to the system of ODEs also produces a stationary solution to the discrete system. In fact, as long as we set up the fish so that the sum of the cosines of the directional heading of every fish and the sum of the sines of the directional heading of the fish are both zero, we will obtain a stationary solution to the discrete system without regard to the initial x- and y-coordinates of the fish. In Figure 13, for example, a stationary solution was produced when eight fish were started with directional headings as the eighth roots of unity but the initial x- and y-coordinates were random.

These stationary solutions offer a foundation for a new type of swarming independent of attraction and repulsion and motivated only by the zone of orientation and noise. When we perturb a stationary solution either by small uniformly distributed noise in the x- and y-coordinates at each time step, simulating currents or other ocean movement, or by small uniformly distributed noise in the directional angles of each fish, we produce a solution where the group of fish stays essentially stationary while each fish moves within the group. In other words, we produce a new type

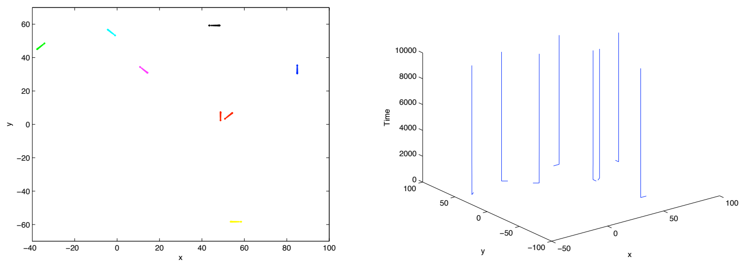

Fig. 12. This figure shows two simulations the ODEs (3) that resulted in stationary solutions given random initial positions. In the left figure, eight fish begin set up with initial direction angles as roots of unity and their x- and y-coordinates are plotted until t=10000. As in the stationary solutions described in Figure 8, the fish move forward, slowing down and eventually stopping. On the right, the same simulation can be seen with the fish's x- and y- coordinates plotted against time. It is clear from the plot on the right that the fish remain in the position forever, as evidenced by their x- and y-coordinates remaining constant as time increases.

of swarming solution.

In the case of the perturbations to x- and y-coordinates, each fish keeps its original directional heading and moves slightly without regard to its directional heading, generally staying close to its starting position. When the fish are placed randomly in x- and y-coordinates with directional headings in one of the symmetry groups of the stationary solution [2], these solutions form a convincing simulation of fish responding to chaotic ocean movement. Such a solution could simulate the behavior of shoals of fish being moved by the ocean, or fish which are feeding or spawning.

When small random perturbations with mean zero are added to the direction angle of each fish, we see swarming solutions closely matching the swarming solutions discussed in Section 3.5. Figure 3.5 shows an example of such a swarming solutions. That these solutions exist without zones of attraction and repulsion motivating the fish's behavior is important, since it means that the zone of orientation, together with noise, can force the fish to swarm. When we increase selfWeight under these conditions, essentially adding weight to the direction each fish is already moving, we see a convincing swarm in which each fish weaves through the group. These solutions persist for a broad range of selfWeight and a surprisingly large range of values for the amplitude of the random noise. The noise is necessary to the swarming solution, as it was in Section 3.5. Without adequate noise, the fish's desire to align themselves induces migration. Noise of amplitude greater than $.2\pi$ produces swarming solutions. However, with too much noise, the fish are jittery and exhibit little coherent movement.

5 Implementation in C++

We chose to reimplement our model in C++ for the following reasons:

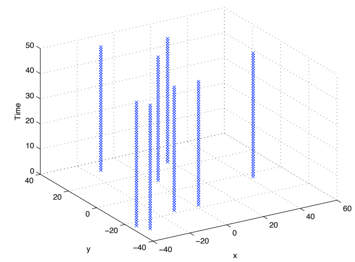

Fig. 13. In this figure, eight fish are initialized in the discrete Model 1 with directional headings as eighth roots of unity and random x- and y-coordinates. This figure is a plot of the x- and y-coordinates plotted against time; it is clear that the x- and y-coordinates do not change as time goes on.

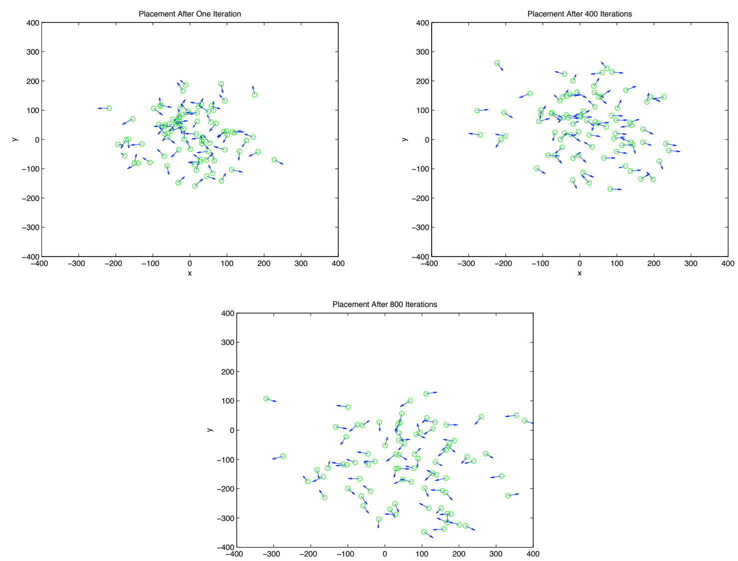

Fig. 14. This figure shows the initial placement and the placement after 400 and 800 timesteps of a swarming solution to the discrete model (1) with only the zone of orientation implemented. The circles are the positions of the fish and the arrows show the direction that the fish are heading. The parameter selfWeight is 10 and the amplitude of the angular noise is 0.1. There are 80 fish in this simulation and the initial angles of the fish are set to be 80^{th} roots of unity; without the angular noise, these initial conditions would effect a stationary solution.

(1) The simulation with many fish lends itself to an object-oriented model. Not only can the fish themselves be objects, but the data structures in C++ facilitate the division of the geographic region into cells.
(2) Because it is a lower-level language, algorithms which we implement ourselves run faster in C++.
(3) Our scheme does not require much in the way of higher-level functions for numerical computations that MATLAB provides. Because we use more basic algorithms, our scheme did not use the advantages offered us by MATLAB.
(4) In C++, we can use MPI for parallelization.

It is a common obstacle in interacting particle models such as ours that in order for each particle to interact with each other particle requires $O(n^2)$ computational work. With fish populations in the millions, we must contend with this. Our fish have a limited range of interaction, and we may take advantage of this to prune away unnecessary comparisons. First, we divide the grand body of water home to our simulation (which we call the world) into a grid of rectangular regions called oceans. The dimensions of these oceans are significantly larger than the radius of attraction and also large enough that fish cannot skip over an ocean in one time step. Each ocean has a list of fish inside it. At the beginning of each timestep, we iterate through each pair of adjacent oceans O_1 and O_2. Ocean O_1 makes a copy of all the fish in its list which are within the radius of attraction of fish in ocean O_2. These fish are added to O_2's list with a flag set. When a fish updates its velocity, it need only consider other fish in its ocean's list. After the fish interact and their velocities are updated for the timestep, fish with the flag set are removed from each ocean. Since fish only interact with other fish in their ocean's list, this helps limit the total number of comparisons required.

For an extra speed gain, we also sort fish in an ocean by x-coordinate. For each fish F, we find the range of fish in the sorted list whose x-coordinate is within the radius of attraction of F's x-coordinate, and then only compare F against these fish. In practice we found that these modifications save enough comparisons to make more complex data structures like BSP-trees unnecessary. Furthermore, this geographic division of work lends itself well to parallelization since the interaction of fish on any one ocean may be computed independently of all the other oceans. In practice we make the number of oceans bigger than the number of processors and dynamically assign oceans to processors to balance computational load. For further work on this model, including parallel implementation, see [1].

For testing purposes, it is convenient to modify the world so that it is connected like a torus, i.e. the top edge is identified with the bottom edge and the left with the right. As a fish moves beyond the boundary of the world, it simply reappears on the other side and enters the appropriate ocean. Each ocean on the boundary is considered adjacent to oceans on the other side as well. Running the simulation on a torus allows us to observe behavior on an arbitrary timeline, because fish never exit the simulation. It also allows us to ensure that every fish starts out surrounded by other fish, so we might expect behavior we observe in the torus to also occur in the interior of a much larger, uniformly dense school.

We ran our program on a torus with repulsion implemented. The behavior we observe indicates that as time progresses in a large school, the fish spread out and create belts transverse to their direction of travel, see Figure 15. This could explain why scientists find the area through which capelin schools have traveled to be completely devoid of the plankton which the capelin eat. Our simulations on the torus indicate that the fish essentially spread to sweep the food out of the entire area that they travel through.

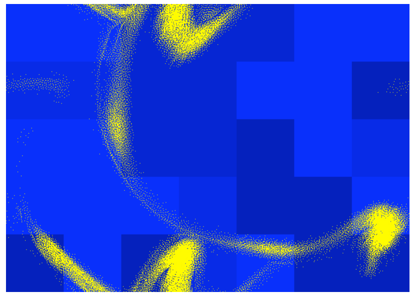

Fig. 15. This figure shows the behavior of a school of fish in a toroidal world. The right and left sides of the world are identified as are the top and bottom. The rectangular divisions behind the fish indicate which region belongs to which processor; for more information, see [1]. The fish eventually spread out and form belts transverse to the direction of travel. This formation may help the fish absorb the most nutrients from a given area.

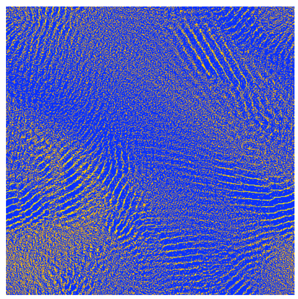

Fig. 16. This figure demonstrates the complex internal structure which can be observed within the schools. This simulation was performed on a torus. The light dots are areas of high fish density.

In these simulations, we also noticed interesting internal structures within the schools as time went on. Once the fish had dispersed over the entire surface of the torus, they formed a rippling pattern which can be seen in Figure 16. This rippling suggests complex internal dynamics within the traveling schools which merit further investigation.

6 Conclusion

Our exploration of the discrete model for motion of pelagic fish has turned up several interesting solutions. The most prominent of these are the migratory and swarming solutions. Guided by the ODEs, we found metastable and stable circling solutions, in addition to stationary solutions with the same symmetries as those of the ODEs. Most importantly, we found a new mechanism for the initiation of swarming that relies neither on repulsion nor attraction, but only on the existence of the stationary solution. These swarming solutions occur with only the zone of orientation implemented and in the presence of noise.

The ODE system was important to our analysis because it allowed us to look for possible solutions to both systems analytically. We found stationary and migratory solutions to both systems and by adding noise and zones of interaction into the discrete system, we also found a circulating ring solution and a swarming solution. The stationary solution that we found in both systems offers a different perspective on the swarming solution in the discrete system, since in the presence of noise, the stationary solution can become a swarming solution.

What remains to be done now is the simulation of the feeding and spawning migration of the capelin. The swarming solution and the migratory solution are the most important to us in our simulation of the migration. While the fish are moving from one area to another during the feeding and spawning migration, we will use the migratory solution to approximate their behavior. During the feeding and the spawning, we will use the swarming solution to model the fish's movement. That this discrete model is capable of producing both behaviors makes it possible to use it for the simulation of the migration. We will pair this model with the DEB model mentioned in Section 1, which will provide the internal triggers required to initiate the transition between the different behaviors.

Acknowledgements The authors were supported by grants number DMS-0352563, DMS-0112388 from the National Science Foundation whose support is gratefully acknowledged.

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