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Modeling and Simulations of the Migration of Pelagic Fish

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Abstract

We model the spawning migration of the Icelandic capelin stock using an interacting particle model with added environmental fields. Without an artificial forcing terms or a homing instinct, we qualitatively reproduce several observed spawning migrations using available temperature data and approximated currents. The simulations include orders of magnitude more particles than many similar models, affecting the global behaviour of the system. Without environmental fields, we discuss how various parameters scale with respect to one another. In particular, we present scaling behaviour between the size of the time step, radii of the sensory zones and the number of particles in the system. We then discuss how environmental data are incorporated into the model.

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1 Introduction

Many species of marine animals travel great distances between feeding and spawning grounds, including pelagic species of fish like the capelin (*Mallotus villosus*) and herring (*Clupea harengus*) (Vilhjálmsón, 1994, 2002; Vilhjálmsón and Carscadden, 2002; Misund et al., 1998). Fish migrations are yet not completely understood and probably never will be in full detail. However, the general route the fish

take can be observed, as can the approximate timing, the surrounding environment and other characteristic factors. There are year-to-year variations which could be influenced by a number of variables including temperature and other environmental factors such as food density, salinity, bottom topography and oceanic currents. Internal variables, such as the physiological state, stage of maturity and egg content could also play a role.

The capelin is an example of a species of pelagic

fish which covers several hundred kilometers in the course of its migration. The stock upon which will be focused in this paper is the stock inhabiting the Iceland Sea, (*Mallotus villosus*), hereafter referred to as the Icelandic capelin. A brief account will be given of pertinent details of this species here, but the interested reader is referred to (Vilhjálmsson, 1994), which provides extensive details of the stock and the capelin's life cycle.

The Icelandic capelin spends the first 1-2 years of its life in the waters to the north of Iceland, along the edge of the continental shelf. When it approaches maturity, usually either during the spring of its second or third year, it undertakes an extensive migration, herein referred to as the *feeding migration*, to the plankton-rich waters of the Iceland Sea as far north as to the island of Jan Mayen. There, zooplankton are plentiful as they feed on the vernal phytoplankton bloom in the region. The maturing capelin eat these zooplankton and grow extensively. In October and November, fully-grown capelin return to the waters northwest and north of Iceland. In January, this portion of the stock undertakes a *spawning migration* around Iceland to the southern and western coasts. The spawning migration generally approaches along the continental shelf edge to the northeast and east of Iceland. However, in some years a portion of the capelin stock has been observed to migrate against the coastal current and take a westerly direction to the spawning grounds. The capelin spawn in February-March and then die, leaving the eggs to hatch and the larvae to drift with the coastal currents to the continental shelf waters north of Iceland and begin the cycle again.

A separate capelin stock resides in the Barents Sea (*Mallotus villosus* Müller), north of the coast of Norway and Russia. This stock has been widely studied and exhibits similar migration patterns between feeding and spawning grounds (Gjørseter, 1998; Gjørseter et al., 1998). Much effort has been put into modeling that stock, see (Sigurðsson et al., 2002; Magnússon et al., 2004a; Fiksen et al., 1995; Huse et al., 1999; Huse, 2001; Huse et al., 2004). However, the Barents Sea migration route differs from the Icelandic one, since they migrate within an ocean containing no islands or other obstacles.

In this paper, we use an interacting particle model based on the work of Hubbard, Babak, Sigurðsson, Magnússon, and Einarsson to simulate the spawning migration of the Icelandic capelin and predict their migration route given data about temperature and current (Hubbard et al., 2004; Magnússon et al., 2004b). The most notable difference is the absence of any artificial forcing terms attracting the particles to a specific spawning location.

The outline of the paper is as follows: in Section 2 the mathematical model is presented with no environmental factors added. Section 3 analyzes that model and presents various scaling behaviour between parameters. The environmental factors are incorporated into the model in Section 4. The full model is then applied to the Icelandic capelin stock and simulations from three different years are presented and then discussed in Section 5. Details of the implementation are also given in that section.

2 Mathematical Model

The model presented here is an interacting particle model. In the classical interacting particle models available in the literature such as (Vicsek et al., 1995), the models are discrete in time and spatially represent individuals rather than keeping track of the density of a population. Particles look to their neighbors to determine their directional heading at each time step, averaging the neighbors' directional headings to determine their own. This allows the particles to move together as a group. The model introduced in (Vicsek et al., 1995; Czirók et al., 1997, 1999; Czirók and Vicsek, 2000) is hereafter called the *CV model*. This type of model originated in physics and was adapted by the biological community to model group dynamics of social animals. It has been applied to herds of mammals, swarms of locusts, and schools of fish (Vicsek et al., 1995; Czirók et al., 1997; Buhl et al., 2006; Couzin et al., 2002). A European project called STARFLAG¹ uses similar models on swarms of starling and explores various interdisciplinary connections.

¹<http://angel.elte.hu/starling>

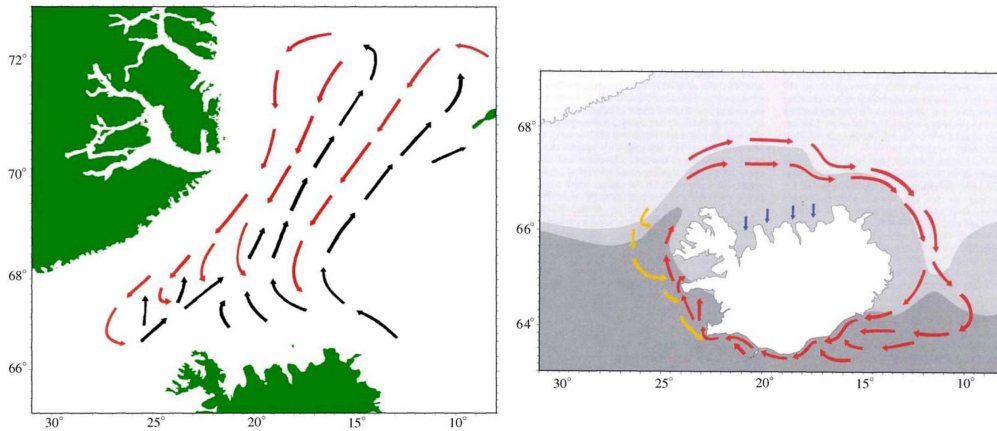


Figure 1: Feeding (top) and spawning (bottom) migration routes of the Central North Atlantic stock of capelin. From (Vilhjálmsson, 1994).

Partridge (Partridge, 1982) pointed out that fish tend to adjust their speeds according to their neighbors. This feature was first introduced into the CV model in (Hubbard et al., 2004) and is represented in equation (1). With this model, Birnir (Birnir, 2007), analyzed the continuous time limit of the model and found several solutions and symmetries.

Biologists have found that fish interact differently with each neighbor, dependent on the distance to the neighbor. Fish use both their vision and their lateral lines, sense organs running down the sides of many species of fish, to align themselves with neighbors and organize themselves into schools (Partridge and Pitcher, 1980; Partridge, 1982). Fish tend to aggregate and avoid collisions when traveling and distance to nearest neighbors seems to play a role in the organization of a school (Grünbaum et al., 2005).

To simulate the internal dynamics of a group of interacting animals, many interacting particle models therefore incorporate different sensory regions into their simulations. The distance between two particles determines how they react to each other and also, in some models, the strength of this interaction. These models include both individual and continuum (density) models, and the shape and size of the zones tends to differ depending on the model,

see for example (Chuang et al., 2007; Couzin et al., 2002; D’Orsogna et al., 2006; Hemelrijk and Kunz, 2005; Kunz and Hemelrijk, 2003; Kunz et al., 2006; Topaz et al., 2006).

We follow (Aoki, 1982; Huth and Wissel, 1992) and employ three sensory zones around each particle determining its reaction to the particles around it. Unlike similar models, including (Aoki, 1982; Huth and Wissel, 1992; Couzin et al., 2002; Kunz and Hemelrijk, 2003; Hemelrijk and Kunz, 2005; Kunz et al., 2006; Hemelrijk and Hildenbrandt, 2008; Viscido et al., 2004, 2005), we do not employ a blind region behind a particle. It is ambiguous whether or not this blind region is biologically relevant in the case of fish since the lateral line should allow a fish to sense the region behind it as it swims. In addition, the presense of such a region doesn’t seem to affect the outcome of the simulations (Huth and Wissel, 1994).

In (Barbaro et al., 2007), solutions to the model presented in (Birnir, 2007) were verified numerically. With sensory zones added, the model exhibits rich behaviour and swarming solutions induced by noise were found. The paper explored the interdependence of noise and the size and weights of the sensory zones in eliciting certain behaviours from the model.

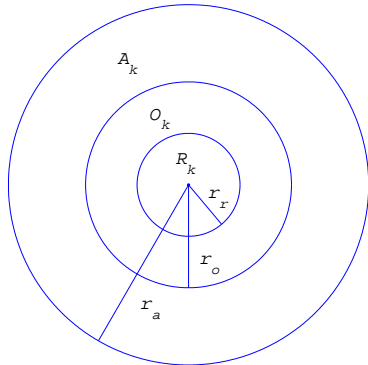


Figure 2: Zones of interaction (sensory zones) of particle k . A_k is its zone of attraction, O_k is its zone of orientation and R_k is its zone of repulsion. These zones have radii r_a , r_o and r_r , respectively.

We now describe the model in detail. The sensory zones are three annular regions around each particle, defined as follows, see Figure (2): The innermost region is the *zone of repulsion*, and a particle heads directly away from other particles in this region, thus avoiding collisions. The outer-most region is the *zone of attraction*, and a particle heads directly toward other particles in this region, adding to the cohesiveness of a group of particles. The annular region between the zones of repulsion and attraction is referred to as the *zone of orientation*, and a particle attempts to align itself in speed and in direction with particles within this zone. These directional headings often conflict, so each particle takes a weighted average of these directions, see (4) and (3).

We denote the set of particles within particle k 's zone of *repulsion* by R_k , its zone of *orientation* by O_k and its zone of *attraction* by A_k . We let $|\cdot|$ denote the number of particles within each zone. Let $\mathbf{q}_k(t) = (x_k(t), y_k(t))^T$ and $v_k(t)$ denote the position and speed of particle k at time t , respectively.

The particles update their speeds as follows:

$$v_k(t + \Delta t) = \frac{1}{|O_k|} \sum_{j \in O_k} v_j(t), \quad (1)$$

and their positions:

$$\mathbf{q}_k(t + \Delta t) = \mathbf{q}_k(t) \dots + \Delta t \cdot v_k(t + \Delta t) \begin{pmatrix} \cos(\phi_k(t + \Delta t)) \\ \sin(\phi_k(t + \Delta t)) \end{pmatrix}. \quad (2)$$

Here, $\phi_k(t)$ is the directional angle of particle k . At each time step, a particle chooses its next directional heading based on the previous positions and locations of its neighboring particles. Since this information can often lead to conflicts of interest, a weighted average is taken and $\phi_k(t + \Delta t)$ is calculated as

$$\begin{pmatrix} \cos(\phi_k(t + \Delta t)) \\ \sin(\phi_k(t + \Delta t)) \end{pmatrix} = \frac{\mathbf{d}_k(t + \Delta t)}{\|\mathbf{d}_k(t + \Delta t)\|} \quad (3)$$

where

$$\mathbf{d}_k(t + \Delta t) := \frac{1}{|R_k| + |O_k| + |A_k|} \times \left(\sum_{r \in R_k} \frac{\mathbf{q}_k(t) - \mathbf{q}_r(t)}{\|\mathbf{q}_k(t) - \mathbf{q}_r(t)\|} + \sum_{o \in O_k} \begin{pmatrix} \cos(\phi_o(t)) \\ \sin(\phi_o(t)) \end{pmatrix} + \sum_{a \in A_k} \frac{\mathbf{q}_a(t) - \mathbf{q}_k(t)}{\|\mathbf{q}_a(t) - \mathbf{q}_k(t)\|} \right). \quad (4)$$

3 Scaling

When working with discrete interacting particle models, it is important to know how parameters scale in relation to one another. When a particle represents many individuals, we think of the particle as a school of fish all behaving in an identical manner as a single individual. These particles we call *superindividuals*. We are assuming that the dynamics of a school of superindividuals is identical to the dynamics of a large school of individuals, which we justify with the scaling arguments presented below. Note that finding the correct interactions of superindividuals is a different problem which is not addressed in this paper.

Let F be the number of individual fish in the actual migration which, for the sake of simplicity, we take to be constant despite predation and other natural factors. Also, let N be the number of particles in a given simulation. Define $N^s := F/N$ to be the number of fish each particle, or superindividual, represents in that simulation.

We require the behaviour and spatial patterns to remain unchanged when a region is blown up in scale. To this end we let Δq denote the distance a particle travels in one time step. Letting v denote the particle's speed, we note that the simple relationship $\Delta q = v \cdot \Delta t$ indicates that there is a linear scaling between the spatial and temporal variables:

$$\Delta q \propto \Delta t. \quad (5)$$

Here, the time step Δt is a parameter in the simulations and we use Δq as a measure of the spatial resolution in the simulations.

The radii of the zones of repulsion, orientation and attraction are denoted by r_r , r_o and r_a , respectively. These are parameters which are known in the literature to affect the behaviour of the system (Aoki, 1982; Huth and Wissel, 1992, 1994; Couzin et al., 2002; D'Orsogna et al., 2006; Kunz and Hemelrijk, 2003; Hemelrijk and Hildenbrandt, 2008). We assume that $r_r \propto r_o \propto r_a$.

Each particle travels a distance of Δq at every time step and senses other particles within its sensory zones. In order for the movements and interactions amongst particles to be consistent across simulations, the radii of these sensory zones should therefore scale with Δq , i.e.

$$\Delta q \propto r_\gamma, \quad \gamma \in \{r, o, a\} \quad (6)$$

and from (5) we see that the same holds for Δq replaced with Δt .

When adding more particles to the system, we require the dynamics of the simulations to be comparable. It can be shown that the spatial resolution, Δq , scales with the number of particles, N , as follows:

$$\Delta q \propto \frac{1}{\sqrt{N}}. \quad (7)$$

The scaling behaviour is summarized in Table 1.

Table 1: Scaling relationships between various parameters.

Δt	\propto	r_r	\propto	r_o	\propto	r_a
\dots	\propto	Δq	\propto	$\frac{1}{\sqrt{N}}$	$=$	$\sqrt{\frac{N^s}{F}}$

4 Environmental fields

Because the migration of the capelin is seasonal and varies by year, the environment clearly has a significant impact on the migration pattern (Vilhjálmsson, 1994, 2002; Carscadden et al., 1997). In order to accurately model the migration we must include environmental data in the simulations, allowing particles to respond to their environment, as done in previous models of the capelin (Reed and Balchen, 1982; Magnússon et al., 2004a; Hubbard et al., 2004; Magnússon et al., 2004b, 2005). We do this by introducing an *environmental grid* containing information about the current and the temperature at regular intervals. The grid also has information about landmasses, encoded as points on the grid with extreme heat. The data contained in the grid allow each fish to be translated by the current and adjust its direction depending on the temperature of the surrounding ocean. For details about the implementation of the grid, see (Youseff et al., 2008).

The speed of a migrating capelin has been recorded to reach over 25 km/day (Vilhjálmsson, 1994). The clockwise coastal current around Iceland is quite strong and its speed can be of the same order of magnitude as the speed of fish relative to the surrounding sea. As could be expected this seems to have a significant effect on the migration pattern.

Although the current has seasonal changes and even varies from day to day based on weather conditions, for simplicity we take it to be constant. Its maximum translation in the simulations is about 15 km/day, see Figure 3. We assume that the fish do not change directional heading depending on the current, hence it translates them independent of their own

movements. This assumption is reasonable since in some years a portion of the capelin stock has been known to migrate counter-clockwise around Iceland, against the current. We employ the same oceanic current field as (Magnússon et al., 2005). Henceforth, the current field will be denoted by $\mathbf{C}(x, y)$.

The capelin have been found to be sensitive to changes in temperature, and yearly variations are believed to affect the migration patterns (Vilhjálmsón, 1994, 2002; Carscadden et al., 1997). To model this we extrapolate measured temperature into a temperature field, denoted by $T(x, y)$. For more details regarding the temperature data and the extrapolations, see Section 5.3. Contour plots of the extrapolated temperature are shown in Figure 4. The particles sense the surrounding temperature according to the gradient of the following function r :

$$r(T) := \begin{cases} -(T - T_1)^4 & \text{if } T \leq T_1 \\ 0 & \text{if } T_1 \leq T \leq T_2 \\ -(T - T_2)^2 & \text{if } T_2 \leq T \end{cases} \quad (8)$$

Here T_1, T_2 are constants, and $[T_1, T_2]$ is referred to as the *preferred temperature range*. By looking at the gradient of r we see that fish should tend towards areas within the preferred temperature range, the tendency being stronger in colder waters.

As in Section 2, we let $\mathbf{q}_k(t)$ denote particle k 's position at time t . Factoring in the environmental fields, the model becomes

$$\begin{aligned} \mathbf{q}_k(t + \Delta t) = & \mathbf{q}_k(t) \dots \\ & + \Delta t \cdot v_k(t + \Delta t) \frac{\mathbf{D}_k(t + \Delta t)}{\|\mathbf{D}_k(t + \Delta t)\|} \\ & + \mathbf{C}(\mathbf{q}_k(t)), \end{aligned} \quad (9)$$

where

$$\begin{aligned} \mathbf{D}_k(t + \Delta t) := & \alpha \frac{\mathbf{d}_k(t + \Delta t)}{\|\mathbf{d}_k(t + \Delta t)\|} \\ & + \beta \frac{\nabla r(T(\mathbf{q}_k(t)))}{\|\nabla r(T(\mathbf{q}_k(t)))\|}. \end{aligned} \quad (10)$$

The speed is calculated as before in (1) and \mathbf{d}_k is the same unit vector as in (3). Furthermore, we let

$$\alpha + \beta = 1, \quad (11)$$

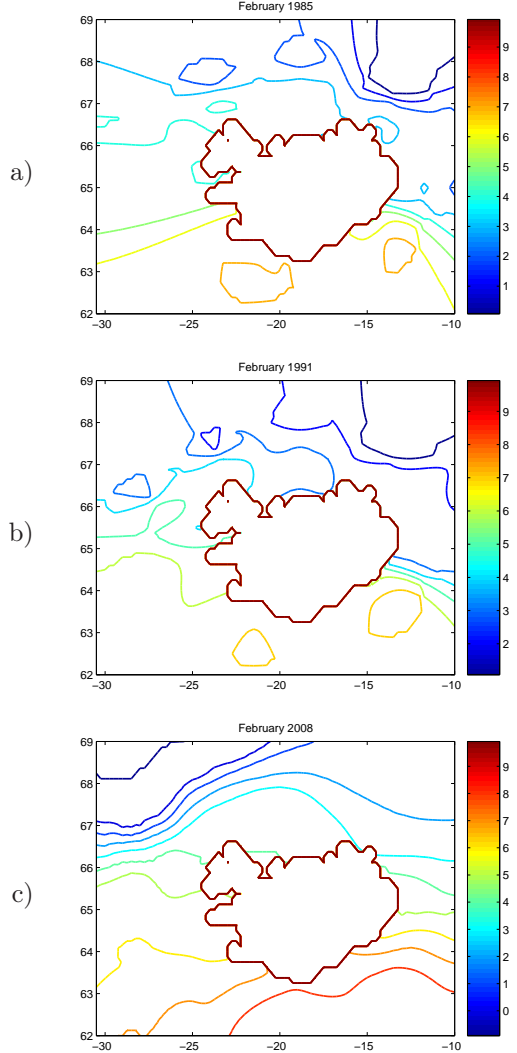


Figure 4: Contour lines of extrapolated temperature data used in the simulations, see Section 5.3. From February of a) 1985, 50 m depth, b) 1991, 50 m depth, c) 2008, surface temperature.

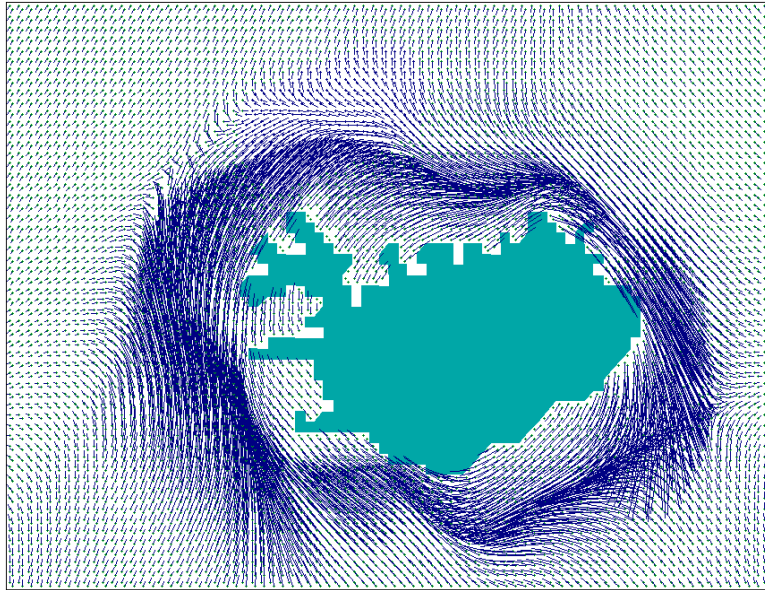


Figure 3: Simulated ocean current field around Iceland. The strength of the current is given by the length of the segments which originate at the green dots. The stronger current runs clockwise around Iceland.

where the weight factor α corresponds to each particle's interaction with its neighbors while β determines its reaction to the temperature field.

As we detail in Section 6, the tendency of fish to align with one another allows environmental information to propagate through a school of fish and produce a global environmental map to which the whole school responds.

5 Case studies

Using the model from Section 4, we are able to approximately recreate spawning migrations of the years 1984-1985, 1990-1991 and 2007-2008. In all three case studies, the simulation accurately captures distinguishing characteristics of the spawning migrations of each year along with the basic path of the main school. This is a significant achievement because it demonstrates that oceanic temperature and currents allow us to make predictions about the route that the stock will take in a given year.

We use temperature readings taken during February of each year, see Figure 4. Some artifacts appear in the 1990-1991 simulations which are addressed in Section 5.3.

We initially place particles in areas where data indicate high density of mature capelin (Vilhjálmsón, 1994). We hold the number of particles per “main school” to be between 40 000 and 50 000 particles in each simulation. This ensures that the dynamics of the migration are similar across years, although the total number of particles differs between simulations. According to the scaling laws in Section 3, by keeping the particle density constant in areas containing fish, we avoid the need to change parameter values between simulations.

5.1 Parameter and simulation specifications

In the simulations we use a general xy -coordinate system of dimensions 82 by 56. The temperature and oceanic currents are stored in a grid defined at points

$(i, j) \in \mathbb{Z}^2 \cap ([0, 82] \times [0, 56])$, corresponding to the area from $30.5\text{--}10.0^\circ\text{W}$ and $62.0\text{--}69.0^\circ\text{N}$. Hence, the spacing between points on the environmental grid is 0.25° in longitude and 0.125° in latitude. This means that the grid has a spatial resolution of roughly 12 kilometers in each direction, although the longitudinal length varies slightly depending on the latitude. This discrepancy is not significant and so is not taken into account in the simulations.

Icelandic capelin are generally found to spawn in water between 3° and 10°C (Vilhjálmsón, 1994). In the simulations, we set the temperature preferences to be between 3° and 6.5°C . Interaction among the particles paired with a high interaction weight enables particles to enter water which is outside their preferred range. Because of the form of the temperature preference function (8), the particles tend to leave water which is drastically different from their preferred range. This preference function combined with the fact that all the particles are reacting to the same temperature map keeps them in water of temperature close to the preferred range. The particles therefore stay within the actual temperature range of the capelin.

We measure the time t in days, the speeds v_k in grid units ($\simeq 12$ km) per day, and the radii of the sensory zones in grid units. We set $\Delta t = 0.05$ (i.e. $\simeq 1.2$ hours) and the speeds v_k are initialized uniformly in $[0, 0.375]$ (i.e. $[0, 4.5]$ km/day) and then updated according to equation (1). The initial direction angles are assigned randomly. Once the particles are east of 13.5°W , the algorithm sets $v_k = 1.25$, or about 15 km/day, which is significantly faster than the initial speeds and crudely models the increase in speed which has been observed by researchers as the spawning migration unfolds.

When we consider the spatial scale which our choice of Δt and v induces, we are considering on average Δq around 0.12 km. This means that it takes a particle about 10 time steps to move from one grid point to another. As described in Section 3, refining the temporal resolution will result in a refined spatial resolution. Taking time steps which are too large forces particles to skip over grid points and therefore miss the information located at these grid points. By choosing Δt and the v_k s as we have, we are simu-

lating with the resolution of the environmental data and using all of the information available to us, which therefore indicates that refining the time step will not change the behaviour and dynamics with respect to the environmental fields.

The other parameter values are $r_r = 0.01$ and $r_o = 0.1$, which correspond roughly to $r_r \simeq 120$ m and $r_o \simeq 1.2$ km. The zone of attraction is excluded from the simulations by setting $r_a = r_o$. The initial density of the particles within each school in the simulations is identical. In all simulations, the interaction weight factor is $\alpha = 0.99$ and the temperature weight factor is $\beta = 0.01$, see equation (10).

5.2 Three spawning migrations

Using parameters described in Section 5.1, we closely replicate three spawning migrations. The first is the spawning migration during the winter of 1984-1985. We run that simulation for 2200 time steps, or 110 days. Figures 5–7 show acoustic data from (Vilhjálmsón, 1994) juxtaposed with simulation pictures corresponding approximately to the same time period. In Figure 5, we show the acoustic data gathered between 1 and 21 November of 1984 alongside the simulation's initial distribution of particles. Initially, we place schools of particles according to where the density of capelin was measured to be highest. The 1984–1985 simulation begins in mid-November. Figure 6(a) shows acoustic measurements taken between 14 January and 8 February of 1985 and Figure 6(b) shows day 65 of the simulation, corresponding to mid-January of 1985. In this figure, we see that the main school in both pictures is traveling along the east coast of Iceland. Note that the simulation accurately captures the high density within the school farthest to the south, as can be seen by the red shading of this section of the school. To the northwest in the pictures, the difference between the acoustic data and the simulation could be explained by emergence of fish from beneath the ice sheet, whereas the simulation does not add particles over the course of the simulation. In Figure 7(a), we see the acoustic data from 7 to 20 February of 1985. Figure 7(b) shows day 109 of the simulation, corresponding roughly to late February. Both pictures show a school coming into

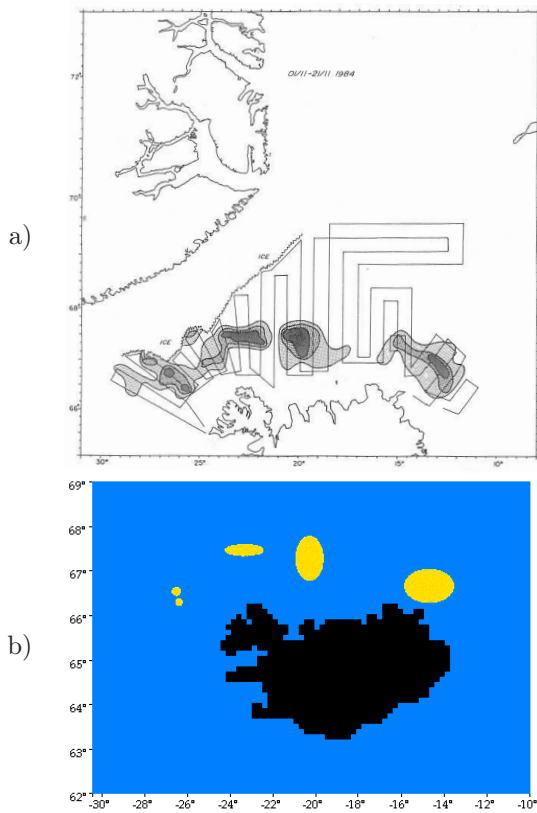


Figure 5: The distribution of capelin in November of 1984. a) Acoustic data from November 1 to November 21 (Vilhjálmsón, 1994). b) Initial distribution for the simulation.

shore on the east coast of Iceland. Note here that the simulation shows an elongated school of particles heading into shore at a similar latitude to that shown in the acoustic data, although the particles are not as close to the shore.

With set-up identical to the 1984–1985 simulation, we model the 1990–1991 spawning migration. We run the 1990–1991 simulation for 1900 time steps, or 95 days. In this case, the particles are placed where data indicates the capelin were between 8 and 27 November of 1990 (Vilhjálmsón, 1994). In Figure 8, we show this acoustic data next to the initial placement of particles for this simulation. Figure 9(a) shows the

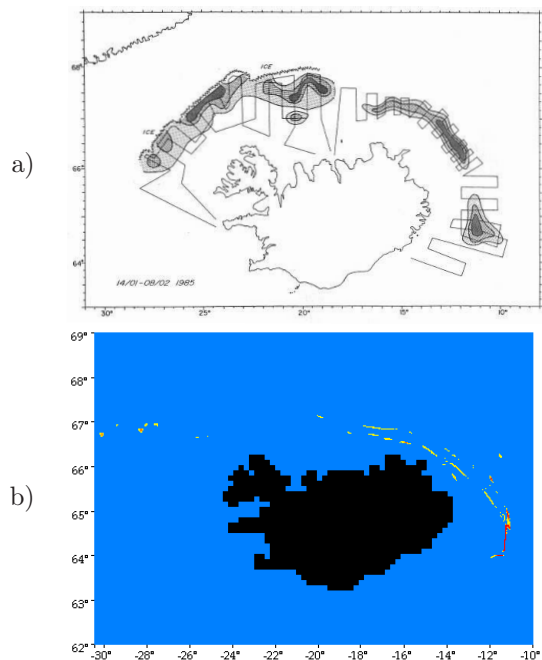


Figure 6: The distribution of capelin in mid-January to early February of 1985. a) Acoustic data from January 14 to February 8 (Vilhjálmsón, 1994). b) Simulated distribution in mid-January, day 65 of the simulation.

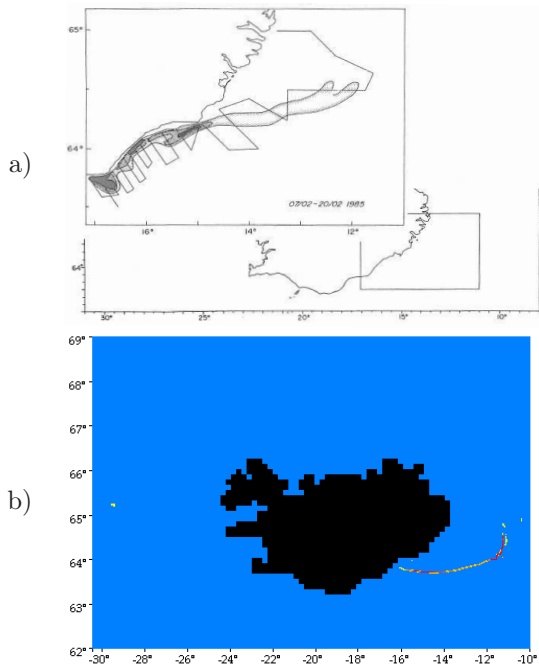


Figure 7: a) Close up of the distribution of capelin from February 7 to February 20 of 1985 (Vilhjálms-son, 1994). b) Simulated distribution in late February, day 109.

acoustic data gathered between 4 and 11 January of 1991, while Figure 9(b) shows the simulation of day 44, corresponding to early January. This figure shows in both pictures a cohesive school traveling clockwise to the east of Iceland. The location of the front of the school is very similar between the two pictures, although in the simulation the tail of the school is closer to Iceland than indicated by the acoustic measurements. The lines in Figure 9(a) show where research vessels searched for capelin, so we cannot assess the accuracy for the schools located outside this area in the simulation.

In Figure 10, acoustic measurements from 8 and 9 February of 1991 are shown alongside day 66 of the simulation, corresponding to early February. The simulation indicates that a school of particles heads into shore, as the acoustic data shows. However, the particles in the simulation are farther to the south and west than in the acoustic measurements. In Figure 10(b), there is also a large number of particles in the southeast corner of the simulation not corroborated by the measurements. This atypical route could be caused by the extrapolation used to make the temperature data for the simulations; see Section 5.3 for further details and discussion about temperature extrapolation. Figure 11 juxtaposes acoustic data gathered on 17 and 18 February of 1991 with the simulation in mid-February, on day 72. Note that the simulation shows two schools of particles near the southwestern shore of Iceland, precisely where the acoustic measurements indicate the highest density to be.

The most important result is the successful prediction of the route of the 2007-2008 spawning migration using initial fish density measurements taken by research and fishing vessels during January 2008. The capelin proved to be difficult to find this year and very little quota could be set. Subsequently, the fisheries were closed down in late February as a result of poor and low estimates of the stock size. Eventually, a large amount of capelin were found to have taken an unusual route, resulting in additional fishing quotas being set in the beginning of March.

We run the simulation for 1900 time steps, or 95 days, between January and early April. Figure 12 shows the simulated migration's initial placement and simulations of days 47, 59, and 65, roughly

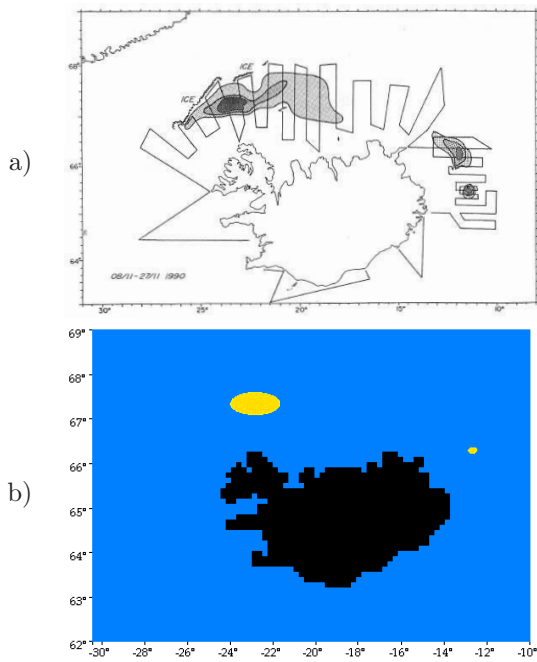


Figure 8: The distribution of capelin in November of 1990. a) Acoustic data from November 8 to November 27 (Vilhjálmsson, 1994). b) Initial distribution for the simulation.

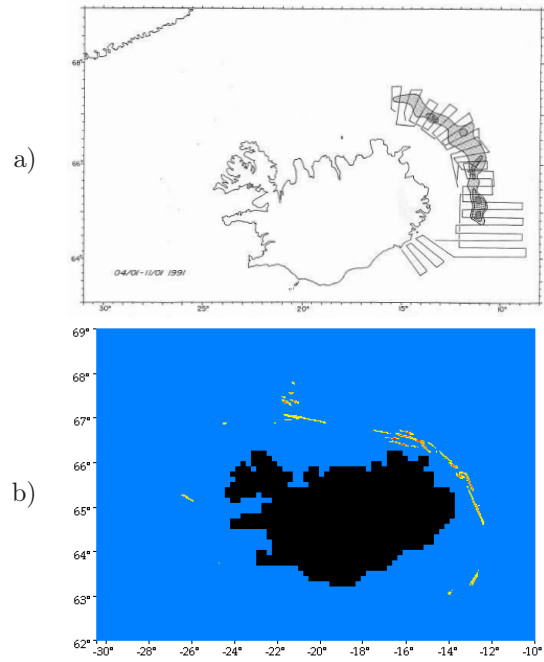


Figure 9: The distribution of capelin in January of 1991. a) Acoustic data from January 4 to January 11 (Vilhjálmsson, 1994). b) Simulated distribution in early January, day 44 of the simulation.

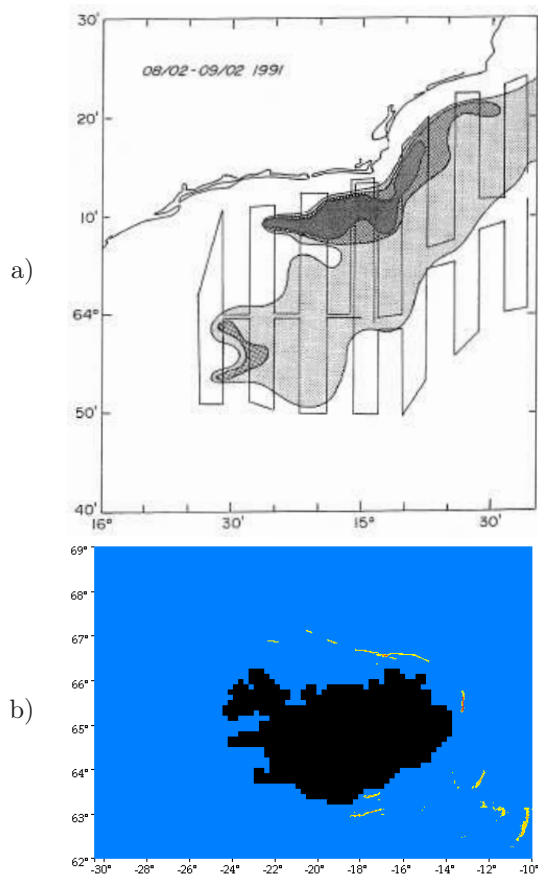


Figure 10: a) Close up of the distribution of capelin southeast of Iceland from February 8 to February 9 of 1991 (Vilhjálmsón, 1994). b) Simulated distribution in early February, day 66.

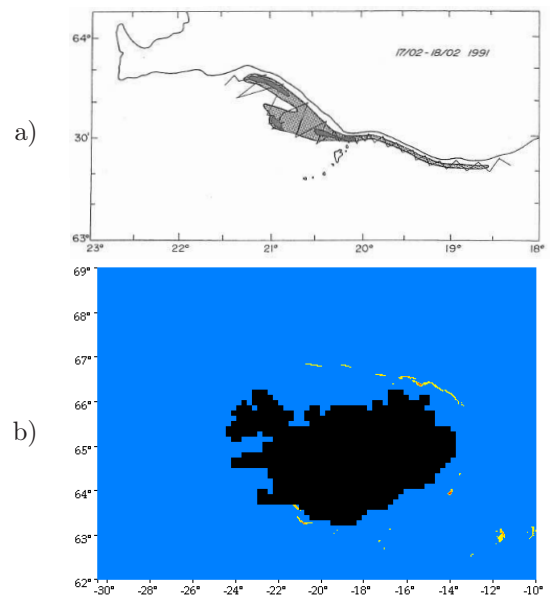


Figure 11: The distribution of capelin southwest of Iceland in February of 1991. a) Acoustic data from February 17 to February 18 (Vilhjálmsón, 1994). b) Simulated distribution in mid-February, day 72.

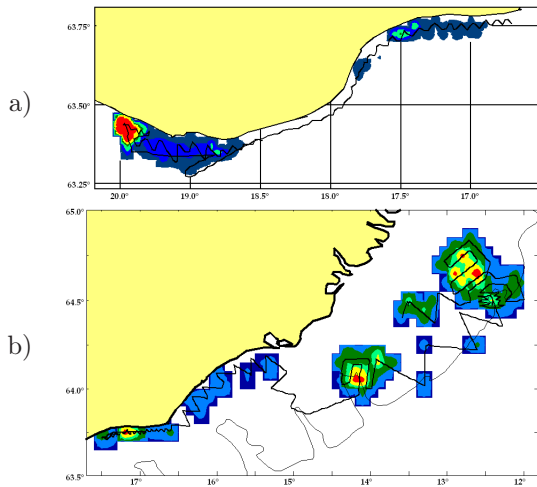


Figure 13: a) Measured distribution of capelin near the south coast of Iceland from February 26 to February 27 of 2008. b) Measured distribution of capelin near the southeast coast of Iceland from February 29 to March 3 of 2008.

mid-February, late February, and early March. Figure 13(a) shows acoustic measurements from 26 and 27 February, while Figure 13(b) shows observations gathered between 29 February and 3 March. Comparing Figure 12(c) with Figure 13(a) reveals that the bulk of the particles in the simulation head toward shore almost exactly where the acoustic data later found them to be. Furthermore, note that in Figure 12(d) there is a school of particles to the east of Iceland in almost precisely the same location as the school of fish farthest to the right in Figure 13(b). This indicates that the route and proportions of the particles in the simulated spawning migration was remarkably accurate, especially considering that the simulation was completed in early February of 2008.

5.3 Extrapolation of temperature data

To create the temperature field for the simulations, we use available data from February of the years which we simulate. In the 1984-1985 and 1990-1991

case studies, we use temperature data recorded by the Marine Research Institute of Iceland. The measurements are taken at a depth of 50 m, at several locations in the sea around Iceland. The collection of data points for 1991 is shown in Figure 14. We extrapolate the temperature field using *Ocean Data View*.²

In the 2007-2008 case study, we use temperature data which we extracted from a German weather website³ on 5 February, 2008, a source commonly used by fishermen. These data were then extrapolated using *Ocean Data View*. The nature of these data is different from the data from the Marine Research Institute of Iceland; the website averages data from various surface measurements from buoys, satellites and ships. If data are missing or beyond a certain distance from available measurements, the website uses the average temperature of the current month from 1961 to 1990. Strong winds and storms in the winter cause turbulent mixing of the water near the surface down to a few dozen meters, as temperature data corroborate. It is therefore reasonable to assume that these surface data approximate the temperature at a depth of 50 meters. This makes the temperature data comparable among these three case studies. Contour plots of the extrapolated temperature for the three years we simulate are shown in Figure 4.

We have found the extrapolation of the temperature measurements to greatly affect the simulations. We were able to best recreate the migrations of 1984-1985 and 2007-2008. We had more difficulty recreating the migration of 1990-1991 due to artifacts of the temperature extrapolation. In the 1984-1985 simulation, the particles stay generally within the area for which we have true temperature readings, so the data the particles react to are reasonably sound since these data are interpolated as opposed to extrapolated. For the 2007-2008 simulation, we use data from the German weather map, so we have a more complete temperature map of the entire region than we have for the other years. Because of this, the particles in the simulation are reacting to actual temperature data regardless of their placement within the grid.

²Schlitzer, R., Ocean Data View, <http://odv.awi.de>, 2007

³<http://www.wetterzentrale.de/topkarten/fsfaxsem.html> [→Bracknell →Wassertemperatur]

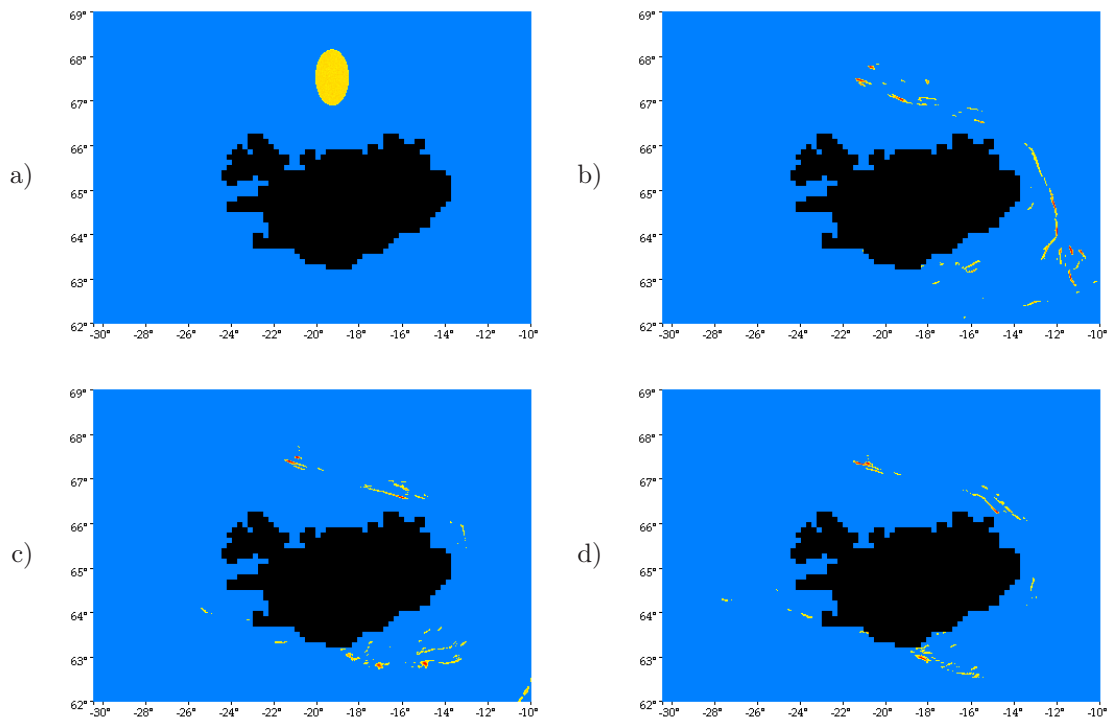


Figure 12: Simulation of the 2007-2008 spawning migration. a) Early January, day 0 b) Mid-February, day 47 c) Late February, day 59 d) Early March, day 65.

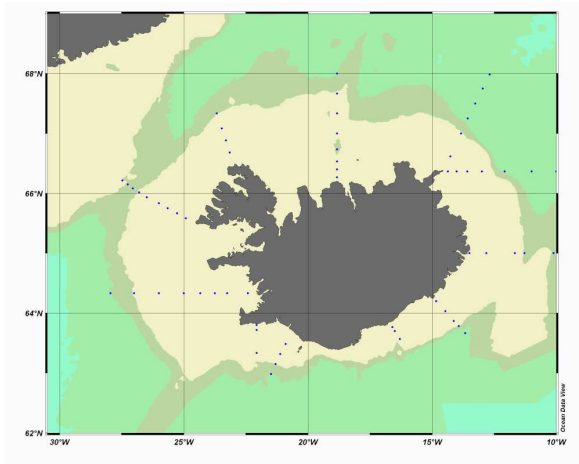


Figure 14: Locations of temperature data collection points (blue) around Iceland in February of 1991. The different colours show bottom topography around Iceland.

However, for the 1990-1991 temperature data, the particles leave the area for which we have accurate temperature readings and go into an area over which we have extrapolated the temperature data. The details of the extrapolation then come into play, and, as can be seen from Figure 15, the extrapolated data map which we use in the simulation creates an artificial “bump” of high temperature surrounded by cooler water. This means that the particles are likely to travel off the bottom of the grid due to the effects of the temperature once they enter this region. Using a different extrapolation drastically changes the temperature map for the area outside the region for which we have measurements, see Figures 4 and 15. Because of the issues that the incomplete temperature data create in the simulations, it would be worth investigating the possibility of creating a more accurate temperature extrapolation using a good estimate of the temperature along the boundary of the grid.

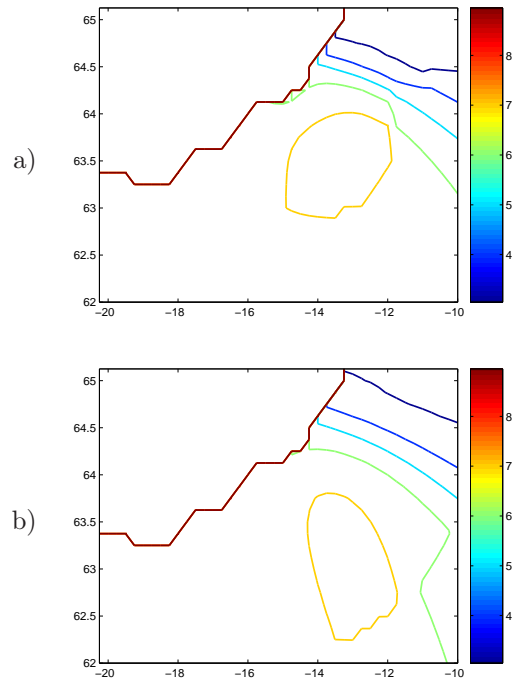


Figure 15: Contour lines of extrapolated temperature from the southeast coast of Iceland in February of 1991. Different extrapolation parameters cause variations between pictures. See Section 5.3 for discussions. a) Data used in the simulations, from Figure 4(b). b) An example of extrapolation parameters yielding a different temperature data.

6 Discussion

One contribution of this paper is that we are able to qualitatively reproduce the spawning migrations of the capelin without an external forcing term. The papers (Sigurðsson et al., 2002; Magnússon et al., 2004a) as well as the papers (Hubbard et al., 2004; Magnússon et al., 2004b, 2005) all use some sort of guidance toward the feeding or spawning grounds. This is done explicitly with a spawning potential inducing a preferred direction as in (Magnússon et al., 2004b; Hubbard et al., 2004) whose model includes this feature as directional noise. Promising results of the Barents Sea stock were presented in (Huse et al., 2004) using only environmental factors, but with some discrepancies between predictions and observations. Our work indicates that it is possible to explain the migration route of the Icelandic capelin stock without a homing instinct and also, as suggested in many of the papers above, that oceanic temperature is of great importance.

One ambitious goal of our research is to be able to simulate each individual fish in the migration. Because parameters were found which reproduce observed migration patterns with about 42 000 particles, the scaling behaviour given in Table 1 gives an estimate of parameter values at the level of individual fish.

We are now in a position to analyze how the parameters should scale when we take $N^s = 1$, i.e. when each particle in the simulation corresponds to one fish, recall relation (7). In the simulation which accurately reproduces the spawning migration of 2008, the number of particles is on the order of $5 \cdot 10^5$. A conservative estimate of the stock size of the migrating capelin is $F \simeq 5 \cdot 10^{10}$ individual fish. Thus, the number of fish each superindividual represents is roughly 10^5 . The spatial resolution in the simulation is $\simeq 1.2$ km.

When we move to the level of simulating individuals, i.e. $N = F$, the spatial resolution can be calculated to be 4 m and the temporal resolution to be 27 s. The radius of repulsion should scale down to $r_r \simeq 38$ cm, which is roughly 2 body lengths. The radius of orientation should scale to $r_o \simeq 3.8$ m. It is worth noticing that all of these values are quite rea-

sonable from a biological point of view (Partridge and Pitcher, 1980; Partridge, 1982). Furthermore, recent computational capabilities should allow for simulations at this scale, enabling us to model at the level of an individual.

Another implication of our work is that greater number of particles allows the school to sense its environment through local interactions and thus create a map of the environmental fields. A similar observation was made in (Couzin et al., 2002) regarding predator and obstacle avoidance. A subtle issue in this type of model is how the time step indirectly affects the behaviour of a group of particles and how information from the environment propagates. The time step and the spatial resolution of the grid directly affect neither the strength of the interactions nor the number of particles within the zones of interaction. However, once the system is endowed with dimensions, the time step determines the number of times a particle interacts with other particles each day. A smaller time step therefore enables particles to align with other particles much faster, as pointed out in (Hemelrijk and Hildenbrandt, 2008).

One possible solution for this inconsistency could be to enforce a maximum turning angle per time step (Huth and Wissel, 1992). As discussed in (Hubbard et al., 2004), reaction times to both the environment and the interactions depending on the time step could be introduced. In this work, we chose not to address this issue since the time step was set $\Delta t = 0.05$ days which corresponds to 1.2 hours and a school of fish should align itself completely in that time. However, when we scale the model to the level of individual fish, we will need to account for the fact that a smaller time step increases the number of times each day the particles interact with each other and sense their environment. Information from the environment could propagate more quickly through a school and thus could become magnified. Those issues, however, should be partly taken care of if we adhere to the scaling in Section 3.

Another point of interest is the difference between the weight factors α, β and the radii of interaction, r_r, r_o, r_a . Since the radii depend on the number of particles as described in Section 3, one might conclude that the weight factors should do the same. How-

ever, the weight factors govern the balance between the environmental data and the interactions and thus determine a behaviour which is indeed independent of the number of particles.

We note that the schools of particles in the simulations seem “thin” compared to acoustic measurements. Adding noise to the directional angle of the particles could have the effect of spreading them out. Noise has not been added into the simulations on this stage, which facilitates the interpretation of the behaviour of the system. Future simulations will incorporate noise, which requires a statistical interpretation of the simulations.

The fact that some groups of particles in the simulations tend to take different routes than expected from existing data indicates that additional factors affect the migration route. Good temperature measurements are available but a more accurate and dynamic current field is needed. However, the most obvious information which needs to be included in simulating the spawning migration is the sexual maturity of the fish. The fish have been observed to wait on the boundary between warm and cold water until the mass of the roe content in the females reaches 8-10% of their body weight. Once they enter the warmer water, their maturation accelerates, which seems to drive them to seek out desirable conditions for spawning (Vilhjálmsson, 1994). The model currently uses no maturity cues and so cannot be expected to reproduce the precise location of where fish come to land. However, the success of the biologically simplistic simulations demonstrates the profound effect which temperature and local interaction among the fish have on the migration route.

Using a bioenergetic model based on Dynamic Energy Budget (DEB) theory from ecology, we plan to explore the effect of maturation on the path of the spawning migration (Kooijman, 2000; Gurney and Nisbet, 1998; Nisbet et al., 2000). The DEB model simulates the conversion of carbon uptake from food sources into carbon content, internal reserves, and egg content of individuals over time. For more information on DEB models, see (Gurney and Nisbet, 1998; Kooijman, 2000). Incorporating this bioenergetic model into the simulations will allow us, for example, to change a fish’s temperature preference and

speed over time in response to the individual’s energy reserves and sexual maturity. This flexibility and individuation will enable us to modify the preferences for each fish as it matures, which we hope will aid us in reproducing the observed behavioural differences between varying age groups and sizes.

We have found a range of parameters qualitatively producing the migration of several years. One of the next steps is to quantitatively explore the parameter space using acoustic data from recent years and introduce DEB into the model. We will compare simulations of several years and see if a common parameter range can be found. If that turns out to be the case, we have further support for the hypothesis that the route of the migration of the capelin is largely affected by environmental factors.

7 Summary

In Section 2 we started out with a mathematical model describing local interactions between particles. We then discussed scaling behaviour between the parameters of the model in Section 3. In order to maintain the same dynamics between different simulations, there is a linear relationship between the time step, radii of interactions and the spatial resolution. However, the time step scales as $N^{-1/2}$, where N is the number of particles in a simulation. These results are summarized in Table 1.

In Section 4 we described how environmental factors are included in the model. We applied the model to the Icelandic capelin stock, using approximated currents and available temperature data. We presented simulations from three different years in Section 5: from 1984-1985, 1990-1991 and 2007-2008. In all three cases we qualitatively produced the route of the spawning migration of the capelin. The main achievement of this paper is the prediction of the route of the spawning migration of the capelin in 2007-2008.

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