Simulations of Capelin Migrations with Dynamic Energy Budget Theory and the Environment

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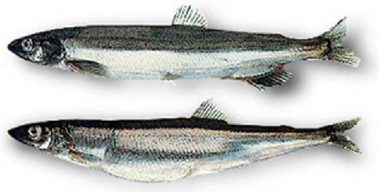
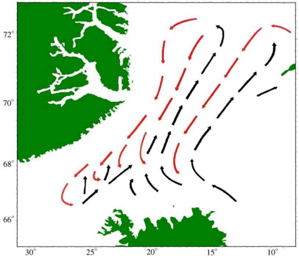
Outline

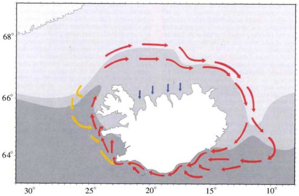
The Icelandic capelin (Mallotus villosus) is a species of pelagic fish which is very important to both the ecosystem and the economy.



Icelandic capelin spends the first 2-3 years of its life in the waters to the north of Iceland, along the edge of the continental shelf.

Every year a portion of the stock undertakes a feeding migration to the feeding grounds near Jan Mayen. They then return to the Icelandic waters north of Iceland in October and November and undertake a spawning migration to spawning grounds in the south of Iceland.





The capelin spawn in February-March and then die.

Mathematical Model

We let

$$\mathbf{q}_k(t) = (x_k(t), y_k(t))^\mathrm{T}$$

be the position of particle k and $v_k(t)$ it's speed at time t.

Next, we look at three zones around each particle, determining how neighboring particles affect the particle. (Based on Aoki, 1982, and Huth and Wissel, 1992)

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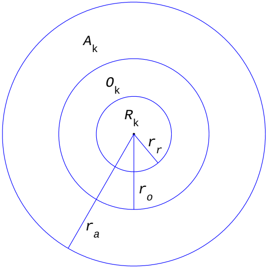
The zones are:

R_k, *Repulsion*,

O_k, *Orientation* and

A_k, *Attraction*.

- Let $|\cdot|$ be the
- number of particles
- in the above zones.



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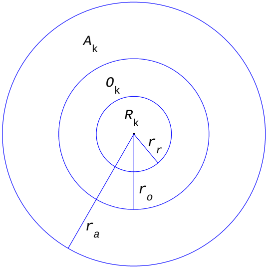


Particle k responds to another particle within...

- the zone of repulsion by heading away from that particle
- the zone of orientation by adjusting it's directional heading to the other particle's directional heading
- the zone of attraction by heading towards the particle

When many particles are withing these zones, these factors have to be weighed together.

Particle k updates it's position by

$$\begin{pmatrix} x_k(t+\Delta t) \\ y_k(t+\Delta t) \end{pmatrix} = \begin{pmatrix} x_k(t) \\ y_k(t) \end{pmatrix} + \Delta t \cdot v_k(t+\Delta t) \frac{\mathbf{D}_k(t+\Delta t)}{\| \mathbf{D}_k(t+\Delta t) \|} + \mathbf{C}(\mathbf{q}_k(t))$$

- Here $\mathbf{D}_k$ is the directional heading of particle k
- The current $\mathbf{C}$, only depends on the position of particle k and and is independent of its directional heading (see picture below)
- The speed is the average speed of particles within the zone of orientation. Later we will let it depend on the roe maturity of each fish.
- Time step Δt

The directional heading is updated as

$$\mathbf{D}_k(t+\Delta t) := \left((1-\beta) \underbrace{\begin{pmatrix} \cos(\phi_k(t+\Delta t)) \\ \sin(\phi_k(t+\Delta t)) \end{pmatrix}}_{\text{Reaction to neighbors}} + \beta \underbrace{\frac{\nabla r\left(T\left(\mathbf{q}_k(t)\right)\right)}{\| \nabla r\left(T\left(\mathbf{q}_k(t)\right)\right) \|}}_{\text{Reaction to temperature}} \right).$$

The reaction to the neighbors is as follows:

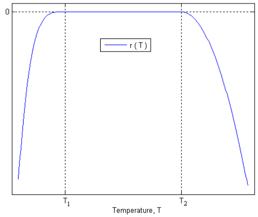
$$\begin{pmatrix} \cos(\phi_k(t+\Delta t)) \\ \sin(\phi_k(t+\Delta t)) \end{pmatrix} = \frac{\mathbf{d}_k(t+\Delta t)}{\| \mathbf{d}_k(t+\Delta t) \|}$$

where

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

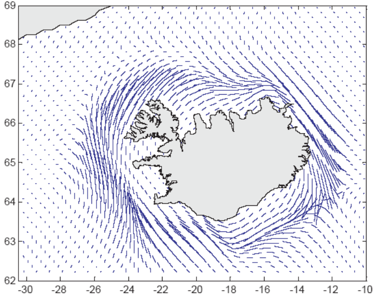
The function r describes the reaction to the temperature, T. The interval $[T_1, T_2]$ is the *preferred temperature range* which a particle tends to head into. Later, this range will depend on the roe content of each particle.

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

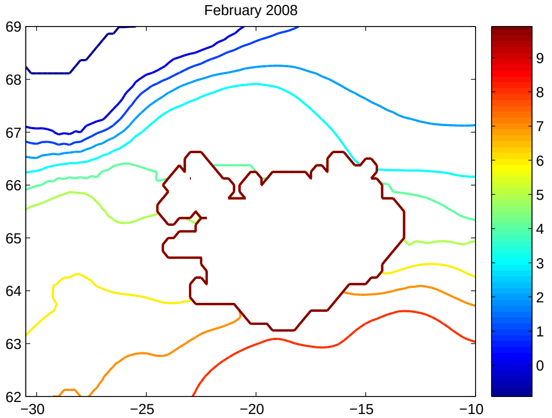


The environment

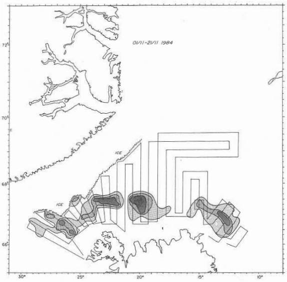
The simulated currents go clockwise around Iceland. The particles do not sense the current, i.e. it only translates them. The maximum speed of the current is 15 km/day, similar to the particles' swimming speed.



The temperature from February 2008:



1984–1985

(a) 

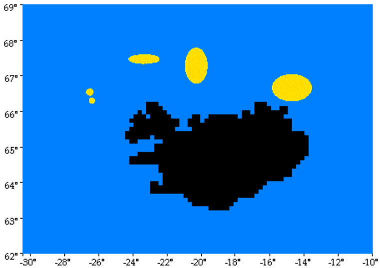
(b) 

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

1984–1985

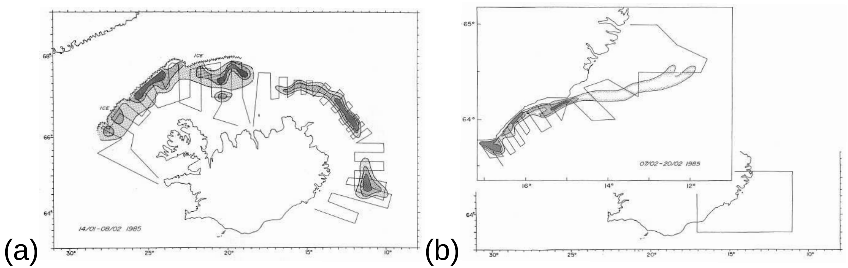
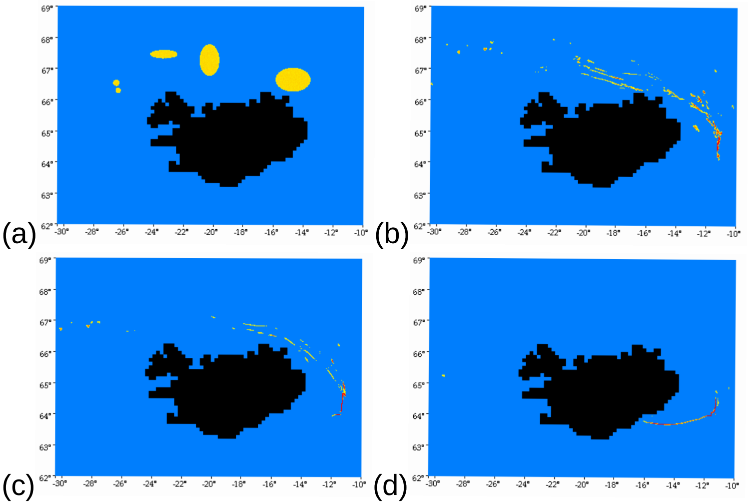


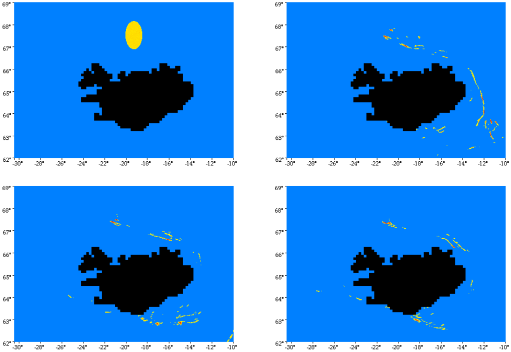
Figure: The distribution of capelin in mid-January to early February of 1985. a) Acoustic data from January 14 to February 8. b) Close up of the distribution of capelin from February 7 to February 20 of 1985.

The Simulated Spawning Migration 1984–1985



Simulations

Using the above model, we simulated several years with good results. Shown are snapshots from the 2008 spawning migration:



A sensitivity analysis in our recent paper (Einarsson *et al.*, 2009) showed that two parameters are key to recreating the migration route from a given year: β, the relative weight a particle places on the temperature term to determine its next directional heading, and $[T_1, T_2]$, the particles' preferred temperature range. With thousands of particles, a school effectively produces a global map of the environment.

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Dynamic Energy Budget Theory (DEB)

Dynamic Energy Budget, Kooijman og Nisbet *et al.*, 2000, describes some of the physiology of the capelin.

- the length or the weight V of the capelin, this is the lifemass of the capelin
- the inner energy, i.e. fat content, is energy E for procreation
- roe energy E_R is the roe portion of the weight of the capelin

We link this model with the particle model for the migration of the capelin and the environment, since the roe content of the capelin clearly influences the timing of the migration.

The DEB Equations

There are three variables: lifemass, V, energy reserves E and energy to make roe E_R.

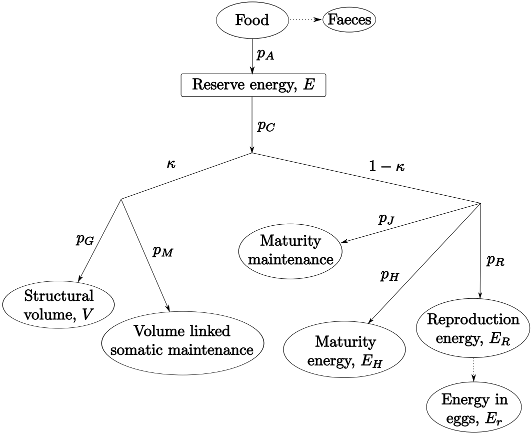
$$\frac{\mathrm{d}}{\mathrm{d}t}E = p_A - p_c \tag{1}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}V = \frac{\kappa p_C - p_M}{[E_G]} \tag{2}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}E_R = (1-\kappa)p_C - p_J \tag{3}$$

The last equation is valid after the capelin has reached (sexual) maturity.

Energy Fluxes and the κ-Rule



It is assumed that a fixed fraction of utilized energy flows to structural volume and somatic maintenance

Dynamics of DEB

Making some assumptions, about food consumption e.t.c, we get unitless equations:

$$\frac{\mathrm{d}e}{\mathrm{d}t} = \frac{\nu}{L_m l}(f - e)$$

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \begin{cases} \frac{\nu}{3L_m}\frac{e-l}{e+g}, & l < e \\ 0, & \text{else} \end{cases}$$

$$\frac{\mathrm{d}u_H}{\mathrm{d}t} = \begin{cases} \frac{\nu}{L_m}(1-\kappa)el^2\frac{l+g}{e+g} - k_J u_H, & u_H < u_H^p \\ 0, & \text{else} \end{cases}$$

$$\frac{\mathrm{d}u_R}{\mathrm{d}t} = \begin{cases} 0, & u_H < u_H^p \\ \frac{\nu}{L_m}(1-\kappa)el^2\frac{l+g}{e+g} - k_J u_H^p, & \text{else} \end{cases}$$

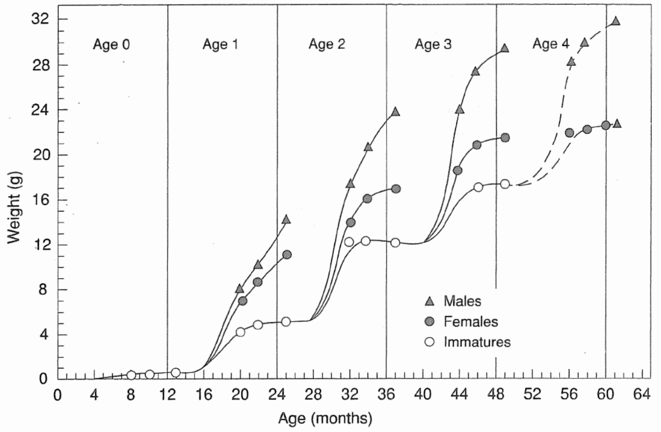
where l is the unitless length (weight) of lifemass

Data

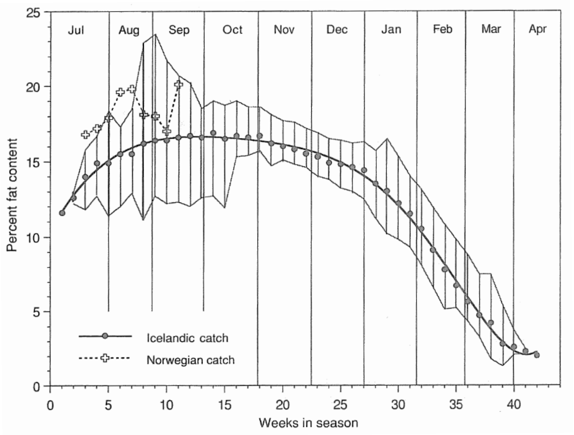
Use data from the Marine Research Institute and Matis.

- Compare to data from the 1999-2000 season.
- Species-specific parameters found
- Measurable quantities can be obtained from the DEB model.

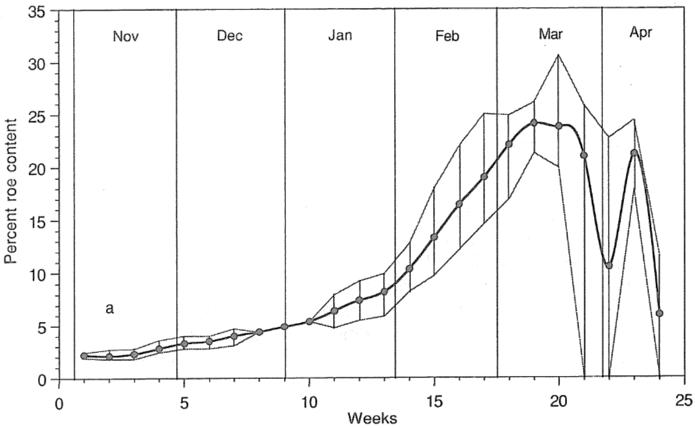
The capelin that participates in the spawning migration has reached full length (weight) in november, consequently we make the initial length $l(0) = 1$



We also let the energy be at its maximum $e(0) = 1$ at the initiation of the spawning migration

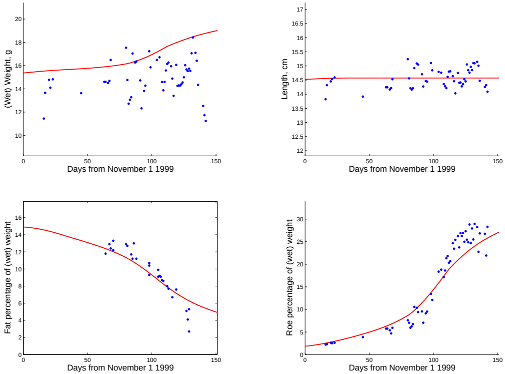


The initial roe weight is set equal to 0.46*grams*



Results of DEB model

The DEB model captures the weight, length, fat and roe percentage:



- The capelin is sensitive to the temperature of the surrounding ocean and stays in colder water until the roe percentage reaches 10%. We let the roe percentage determine the preferred temperature of each fish, when it reaches 10% we let the preferred temperature change.
- The swimming speed of the capelin increases in the warm water
- The behavior of the whole school is also determined by the synchronization of the fish in the school. Not all the fish have to have reached the 10% roe percentage for the school to head into a warmer region of the ocean
- In the warmer ocean the roes mature much faster

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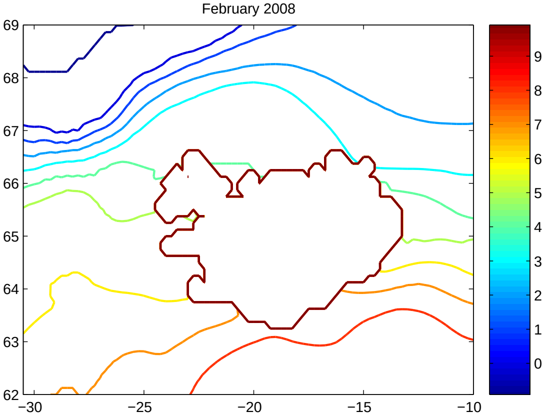
The temperature distribution in the ocean in February 2008:



- We incorporate the DEB into the model by letting the speed of a particle be determined by the roe percentage:

$$\nu_k(t) = \frac{1}{|O_k(t)|} \sum_{j \in O_k(t)} v_j(t) \tag{4}$$

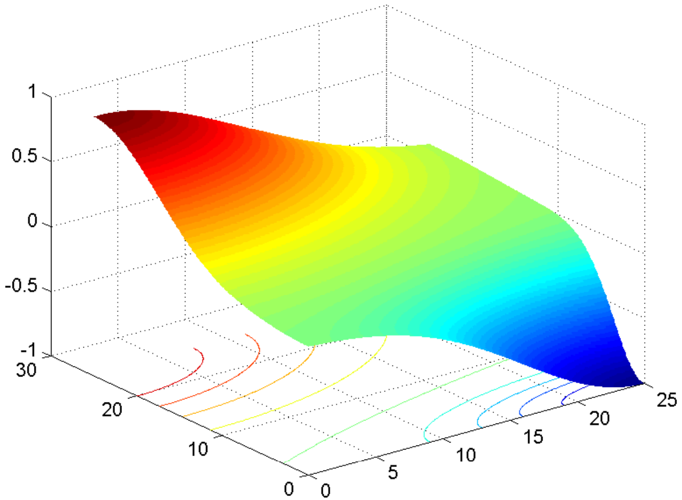
and

$$v_k(t + \Delta t) = \nu_k(t) + \Gamma\left(\nu_k(t), u_{Rk}(t)\right) \tag{5}$$

where Γ determines the acceleration of a particle

- We can also let the preferred temperature range $[T_1(u_R), T_2(u_R)]$ depend on the roe percentage

The Γ function:



Here is a movie from February of 2008 (without the DEB). It was used to make a prediction of the spawning migration.

Conclusions

- The value of $\kappa = 0.4$ for the capelin
- This is *much lower* than κ values for other types of fish
- Even anchovies have $\kappa = 0.65$, Pecquerie *et al.* 2009, and κ values are frequently in the range 0.85 (flounder) to 0.9 (sole)
- Thus the capelin put a minimum of energy into structural volume and somatic maintenance
- Most of the energy goes into reproduction, that has *only one chance* of succeeding
- The DEB model seems capable of determining the timing of the different parts of the spawning migration

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