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A dynamic energy budget (DEB) model for the energy usage and reproduction of the Icelandic capelin (*Mallotus villosus*)

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ABSTRACT

We apply a dynamic energy budget (DEB) model to the Icelandic capelin (*Mallotus villosus*) and introduce a new state variable to capture the roe production of individual fish. Species-specific coefficients are found for the capelin such as the shape coefficient and the Arrhenius temperature. We show how to link the DEB model to measurable quantities such as weight, length, fat, and roe content. We use data on measured 3-year old female capelin from 1999 to 2000 season from the Marine Research Institute of Iceland (MRI) and Matis, an Icelandic Food and Biotech R&D. We then find plausible parameter values for the DEB model by fitting the output of the model to these data. We obtain good fits between theory and observations, and the DEB model successfully reproduces weight, length, fat percentage and roe percentage of capelin. We discuss the effect of maturity on the spawning route of capelin, and describe how we intend to incorporate these results with an interacting particle model for the spawning migration of capelin.

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1. Introduction

We focus our attention on the stock of capelin (*Mallotus villosus*) which resides in the oceanic area between Iceland, Greenland and the island of Jan Mayen. We refer to this stock as the Icelandic capelin and briefly describe their biology and spawning migration patterns. For a detailed description on the biology and behavior of the stock as well as a description on the oceanographic features of the Icelandic waters, we refer to Vilhjálmsson (1994). A concise description can be found in Vilhjálmsson (2002).

The mature spawning stock consists mostly of 2- and 3-year old capelin (which spawn at age 3 and 4), with the main proportion being 2-year old. After having spent the summer up north in the Iceland Sea and as far as the island of Jan Mayen, the fully grown capelin return to the waters north and northwest of Iceland in October and November. This portion of the stock then undertakes a spawning migration to the spawning grounds near the southern and western coasts of Iceland. The capelin generally takes a clock-wise route along the edge of the continental shelf to the spawning grounds via the eastern coast, but in some years a portion of the stock has been reported to take a western route. The capelin then spawn in February and March and the great

majority of the spawning stock dies after having fulfilled their destiny.

The importance of the Icelandic capelin to the ecosystem of the Icelandic waters and to the Icelandic economy is substantial. The capelin is a dominant element in the food web in the area around Iceland and brings yearly vast amounts of biomass from more northerly regions. It is the main diet of cod (*Gadus morhua*) and several other species (Magnússon and Pálsson, 1991; Magnússon and Aspelund, 1997). It is also important to the Icelandic economy as it is caught and made into fish meal and oil. Much research effort has been put into stock estimates (Vilhjálmsson and Carscadden, 2002) and modeling (Sigurðsson et al., 2002; Guðmundsdóttir and Vilhjálmsson, 2002; Magnússon et al., 2004a,b, 2005; Barbaro et al., 2009a).

As in Barbaro et al. (2009a) we are concerned with the spawning migration of the Icelandic capelin. There we used an interacting particle model as well as information about temperature and (an artificial map of) currents, to successfully reproduce the route of the spawning migration around Iceland from three different years. The continuous time limit of the model in Barbaro et al. (2009a) was analyzed by Birnir (2007), and numerical verifications are found in Youseff et al. (2008) and Barbaro et al. (2009c).

The model in Barbaro et al. (2009a) used no maturity model and only indirectly included that effect in the simulations. It is, however, well known that the stage of maturity has a significant effect on the behavior of migrating capelin (Vilhjálmsson, 1994, 2002). When mature capelin return from the feeding grounds to the continental

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shelf north off Iceland, they prefer relatively cold waters. As they start their spawning migration they have been reported to slow down and even come to a halt upon reaching warmer waters near the southeast of Iceland (Vilhjálmsón, 1994, 2002).

The capelin normally stay on the colder side of the sharp temperature boundaries between the warm Atlantic water and the colder water until the weight of the female ovaries is about 8–10% of their total body weight. They commonly increase their speeds at this point and have been recorded to swim at about 15 and 25 km d⁻¹ including the effect of translation by currents (Vilhjálmsón, 1994). As they enter the warm waters their roe production increases rapidly, as does their metabolism. They have a limited time to spawn after entering the warm waters and it is crucial for them to succeed in finding suitable spawning grounds rapidly. This happens relatively fast or in several days, compared to a migration that lasts months, and it is important for any model to capture this aspect.

It is clear that inner dynamics of individual capelin play an important role in the route and timing of the spawning migration. Following on the work of Barbaro (2008), who proposed a bioenergetics model to be integrated into a capelin migration model, and Barbaro et al. (2009b), we have implemented and developed a so-called dynamic energy budget (DEB) model to capture the growth, energy usage, and roe production of individual capelin. Below we describe the model and relate it to data from the Marine Research Institute of Iceland (MRI) and Matis, an Icelandic Food and Biotech R&D. We fit parameters to these data, and in Section 4 we discuss how we intend to combine the DEB model with the interacting particle model in Barbaro et al. (2009a). By doing so we hope to capture most of the characteristics of the spawning migration of the Icelandic capelin.

2. Dynamic energy budget model

Dynamics energy budget (DEB) theory is the study of the mechanisms of acquisition and use of energy by individuals, that has consequences in physiological organization and the dynamics of populations and ecosystems. It is closely related to bioenergetics that focuses on molecular aspects and metabolic pathways in a thermodynamic setting. DEB theory treats individuals as nonlinear dynamics systems that follow predictable patterns during their life cycle. This approach has firm physiological roots and provides a sound basis for population dynamic theories (Nisbet et al., 2000; Kooijman, 2010). We refer to Kooijman (2010) for a full description of the DEB theory. A conceptual introduction is given in Kooijman (2001), and further guides and discussion can be found in van der Meer (2006) and Sousa et al. (2008).

DEB theory is ultimately the theory of life. Its aim is to describe all life forms within the same framework. The complexity of the DEB model will depend on the complexity of the species at hand. For the Icelandic capelin, we use a basic form of the DEB model with one food substrate and one type of reserve. These assumptions can be generalized (Kooijman, 2010).

DEB theory has been successfully applied to anchovy (*Engraulis engrasicolus*) in the Bay of Biscay (Pecquerie et al., 2009), where their whole life cycle was modeled. The capelin and anchovies are similar fish in size and energetics, and both store energy mostly as lipids in their muscle. We fit the DEB parameters to the data on capelin and compare the resulting parameter values to those of the anchovies, obtaining similar results.

In Section 2.2, we give a brief account of the state variables of the standard DEB model which can be found in Kooijman et al. (2008). Furthermore, we introduce a new variable to account for the roe production of individuals in Section 2.4.

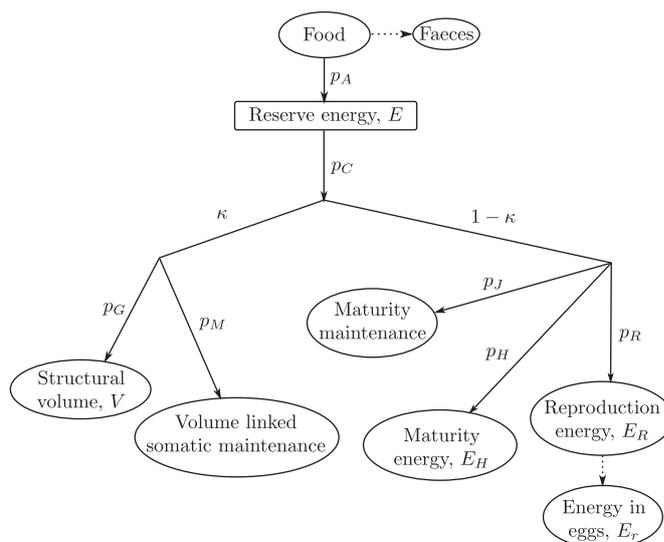


Fig. 1. Energy fluxes and the κ -rule. It is assumed that a fixed fraction κ of utilized energy flows to structural volume and somatic maintenance. See Section 2.1.

2.1. The κ -rule

According to DEB theory, each individual allocates a fixed fraction κ of utilized energy from reserves to growth and somatic maintenance. The rest, $(1-\kappa)$, is then allocated to maturity maintenance and reproduction. This energy flow can be seen in Fig. 1. The energy has been converted from food with constant efficiency. The DEB theory states that the value of κ stays fixed throughout the whole life cycle of an individual. It is species-specific and therefore is one of the characteristic parameters of each species. In Section 3.2, we obtain a relatively low value for κ compared to other fish, which we discuss in Section 4. We note that energy requirements due to swimming could be accounted for as part of the utilized energy for growth and maintenance. These requirements would depend on swimming speeds, but are not taken into account in this paper.

2.2. State variables of the standard DEB model

The state variables of the standard DEB model are structural volume, reserve energy, maturity energy and reproduction energy. The structural volume, V (cm³), is the amount of biomass. The dynamics are such that maintenance is assumed to take precedence over growth. The contribution of energy reserves and reproduction energy to structural volume is assumed to be small, hence we quantify structure with length (van der Veer et al., 2001). We let the variable $L = V^{1/3}$ denote the structural (volumetric) length of an individual, which relates to actual physical length as detailed in Section 2.6.1.

The reserve energy, E (J) is the energy available to the individual. Its source is food uptake and it is the energy an organism utilizes for growth and somatic maintenance on one hand, and maturity, reproduction and maturity maintenance on the other hand.

Following Kooijman et al. (2008) and Sousa et al. (2008), we let E_H denote a maturity energy. It is important to note that this variable is abstract and does not contribute directly to the weight of the fish. Initially, energy is allocated to this variable, and the maturity maintenance will be a fraction of this energy, $k_J E_H$. When E_H exceeds a certain threshold, E_H^P , the fish is mature and allocation of energy to E_H ceases.

Thus E_H reaches a final value E_H^P which determines when an individual reaches puberty. It is important to note that puberty is,

therefore, neither determined by the volumetric length nor the physical length of a fish. This is the case with many species of fish.

After puberty has been reached, the energy starts to flow to E_R , which is the total energy available for reproduction. We note that the dynamics of the energy flow to maturity is the same as that to reproduction. This energy will, in turn, be converted into roe. We assume that there are no maintenance costs associated with E_R , but maturity still requires maintenance of $k_j E_H^p$, explaining the term in Eq. (8). In this paper we are focusing on the period of the spawning migration of capelin, where the individual has reached puberty. Therefore, the dynamics of E_H are zero but that of E_R will be non-zero.

In Section 2.4, we introduce E_r as the energy converted from the reproduction energy to eggs. We assume that there are no maintenance costs associated with roe. This quantity is not a state variable in the DEB theory and has to be specified for the species in question as well as its dynamics.

2.3. Equations of the standard DEB model

We non-dimensionalize the standard state variables of the DEB model, E , V , E_H , and E_R , and obtain the non-dimensional variables e , l , u_H , and u_R , respectively, where

$$E = [E_m] L_m^3 e l^3, \quad (1)$$

$$V = (L_m l)^3, \quad (2)$$

$$E_H = [E_m] L_m^3 u_H, \quad (3)$$

$$E_R = [E_m] L_m^3 u_R. \quad (4)$$

Here $[E_m]$ (J cm^{-3}) is the maximum energy density and L_m (cm) is the maximum volumetric length, the volumetric length being denoted with $L = L_m l$. The dynamics of the non-dimensionalized state variables are readily deduced from Kooijman et al. (2008) and are the following:

$$\frac{de}{dt} = \frac{v}{L_m l} (f - e), \quad (5)$$

$$\frac{dl}{dt} = \begin{cases} \frac{v}{3L_m} \frac{e-l}{e+g}, & l < e, \\ 0 & \text{else,} \end{cases} \quad (6)$$

$$\frac{du_H}{dt} = \begin{cases} \frac{v}{L_m} (1-\kappa) e l^2 \frac{l+g}{e+g} - k_j u_H, & u_H < u_H^p, \\ 0 & \text{else,} \end{cases} \quad (7)$$

$$\frac{du_R}{dt} = \begin{cases} 0, & u_H < u_H^p, \\ \frac{v}{L_m} (1-\kappa) e l^2 \frac{l+g}{e+g} - k_j u_H^p & \text{else,} \end{cases} \quad (8)$$

where v (cm d^{-1}) is called the energy conductance, f (dimensionless) denotes the functional food response (see Section 3.1.2 below), and g (dimensionless) is the energy investment ratio.

In DEB theory (Kooijman et al., 2008) maximum assimilation rate per surface area, $\{J_{EAm}\}$ ($\text{mmol d}^{-1} \text{cm}^{-2}$), and yield of structure from reserve in growth, y_{VE} (dimensionless), are taken to be primary parameters along with v , k_j , E_H^p and κ . The relationship of $[E_m]$ and g to these parameters is

$$[E_m] = \frac{\bar{\mu}_E \{J_{EAm}\}}{v} \quad (9)$$

and

$$g = \frac{v [M_V]}{\kappa \{J_{EAm}\} y_{VE}}, \quad (10)$$

where $[M_V]$ (mmol cm^{-3}) is the volume specific structural mass and $\bar{\mu}_E$ (J mmol^{-1}) the chemical potential.

We note that we fix the value of E_H^p to 3930 J which is the value used for anchovies (Pecquerie, 2009). We consider this appropriate here since we are not simulating the whole life cycle of the capelin. We are simulating capelin which we assume to have reached puberty, and thus discrepancies in E_H^p are corrected with the value of k_j . However, E_H^p will be a true parameter of the model once the full life cycle is simulated, and k_j might change accordingly.

We also note that $[E_m]$ is a biological constant characteristic to each species. Data on the energy density were reported in Anthony et al. (2000) to be 5866 ± 0.43 (J g^{-1}) for capelin (both sexes combined) in the northern Gulf of Alaska, collected from May to September in 1995 and 1996. We, therefore, take care choosing the parameters above such that the value of $[E_m]$ is close to that value, which we discuss further in Section 3.2.

The parameters v and k_j are temperature dependent as will be described in Section 2.5. In Table 1, we give values of the parameters and constants used in the simulations.

2.4. Roe maturity

We note that the development of eggs is not a part of DEB theory and has to be dealt with separately. We, therefore, introduce E_r which denotes the energy translated from the reproduction energy, E_R , to roe. We assume that the rate of increase of this energy is proportional to the amount of energy already in roe as well as to energy available to reproduction. We non-dimensionalize and get the following equation for $e_r = E_r / ([E_m] L_m^3)$:

$$\frac{de_r}{dt} = \gamma (u_R - e_r) e_r. \quad (11)$$

We note that the parameter γ (d^{-1}) depends on temperature in the same way as v and k_j as detailed in Section 2.5 below. Also worth mentioning is that we have assumed that the energy invested in roe grows logistically to the asymptote u_R , which is a variable. We do not address here the implications this has on the timing of the actual spawning since we are working with data on capelin before spawning takes place.

2.5. Arrhenius temperature

Physiological rates depend on temperature and we use the Arrhenius temperature T_A to express this effect (Kooijman, 2010). We assume that all rates are affected in the same way for a species-specific range of temperatures according to

$$p(T) = p(T_r) \exp\left(\frac{T_A}{T_r} - \frac{T_A}{T}\right), \quad (12)$$

where T_r (K) is a chosen reference temperature, T_A (K) is the species-specific Arrhenius temperature, and p is the physiological rate (J d^{-1}).

In Frank and Leggett (1981), the relationship between egg development time D (d) and temperature T (K) for the Icelandic capelin was reported to be $\ln(D) = 4.29 - 0.63 \ln((T - 273) + 1)$, derived from experimental data, from Friðgeirsson (1976) amongst others. Also, Frank and Leggett (1981) found a near identical relationship by field experiments on beach spawning capelin in Newfoundland.

To estimate the Arrhenius temperature for the Icelandic capelin we used the data reported in Frank and Leggett (1981). Plotting $\ln(1/D)$ against $1/T$ results in a straight line scatter. We obtained $T_A = 9100$ K ($n=9$, $r^2=0.981$), as the slope of the linear regression.

We emphasize that Eq. (12) applies to a temperature range specific to the species in question. Data from a temperature range,

Table 1
Values of parameters and constants.

κ	0.4	–	Fraction of energy to somatic growth and maintenance ^a
ν	0.02	cm d ⁻¹	Energy conductance ^a
$\{J_{EAm}\}$	0.23	mmol d ⁻¹ cm ⁻²	Maximum assimilation rate per surface area ^a
y_{VE}	0.8	–	Yield of structure from reserve growth ^b
k_j	0.001	d ⁻¹	Fraction of maturity maintenance ^c
E_H^p	3.93	kJ	Maturity energy at puberty ^d
γ	0.20	d ⁻¹	Growth rate of roe ^a
T_A	9100	K	Arrhenius temperature ^e
T_r	6.5 + 273	K	Reference temperature ^c
$[M_V]$	4.4	mmol cm ⁻³	Volume specific structural mass ^a
$\bar{\mu}_E$	500	J mmol ⁻³	Chemical potential ^d
δ	0.161	–	Shape coefficient ^e
L_m	2.82	cm	Maximum structural (volumetric) length ^e
d_V	1	g cm ⁻³	Density of structural volume ^f
ρ_E	39.30	kJ g ⁻¹	Energy reserve density ^g
ρ_R	10.00–8.33	kJ g ⁻¹	Energy density of roe (see Fig. 4(b)) ^a

- ^a Calibrated to data.
^b From Pecquerie et al. (2010).
^c Chosen.
^d From Pecquerie (2009).
^e Estimated from data.
^f From van der Veer et al. (2001).
^g From Anthony et al. (2000).

which the species experience during their life cycle, should be used. The temperature used in Frank and Leggett (1981) ranged from 0 to 18 °C. We have chosen to exclude the last data point, since it is a temperature the capelin do rarely experience, if at all, in the waters around Iceland, and that data point is a clear outlier as well.

2.6. State variables and observations

The state variables of the DEB model are not directly observable. Rather, the observable variables are weight, length, fat content, and roe content. In turn, the state variables have to be obtained from these measurable quantities as we detail here below.

Physical weight, \mathfrak{W} , has contributions from structure, the energy reserves, the reproduction energy and roe. These are general compounds, which are rich in lipids, which are mostly stored in the muscle, but also contain, e.g. protein. We assume that the reserve energy and reproduction energy have the same composition and thus the same energy content.

The roe has a different energy content than the reserves, and thus the weight of roe needs to be treated separately from the fat content. It is characteristic to capelin to convert almost all of its available fat content into roe, and we thus subtract the energy already converted into roe from fat.

$$\mathfrak{W} = d_V V + \frac{E + E_R - E_r}{\rho_E} + \frac{E_r}{\rho_r}, \quad (13)$$

where the constant d_V (g cm⁻³) denotes the density of the structural volume, ρ_E (J g⁻¹) denotes the energy content of one gram of reserve, and ρ_r (J g⁻¹) denotes the energy content of one gram of roe. This representation of physical weight is found in a similar way as in Kooijman (2010).

Lipid content (in dry mass) is the primary determinant of energy density (Anthony et al., 2000), and since the capelin store most of their energy as lipids in their muscle, we let $\rho_E = 39.3$ (kJ g⁻¹), which is the energy content of lipids reported in Anthony et al. (2000). We do not have a measured value of ρ_r , and therefore find a plausible value for the simulations. We find a value for ρ_r which is lower than ρ_E , as expected, since the roe have

considerable more water. The water content of roe has to be taken into account, which we detail in Section 3.1.3.

We denote the fat content of individuals by

$$W_{fat} = \frac{E + E_R - E_r}{\rho_E}, \quad (14)$$

and the weight of roe by

$$W_{roe} = \frac{E_r}{\rho_r}. \quad (15)$$

We denote by R the percentage of the roe weight of the total body weight, i.e.

$$R = 100 * \frac{W_{roe}}{\mathfrak{W}}, \quad (16)$$

and also by F the percentage of the fat weight of the total body weight, i.e.

$$F = 100 * \frac{W_{fat}}{\mathfrak{W}}. \quad (17)$$

2.6.1. Shape coefficient and the physical length

In order to link the volumetric length, L , to the actual length of the capelin, ϱ , we treat the capelin as an isomorph (Kooijman, 2010) after it develops from the larvae stage, and estimate the shape coefficient, δ , such that

$$\varrho = \frac{1}{\delta} L. \quad (18)$$

We have assumed that the immature capelin have no reproduction reserves, and neglected the contribution of the reserves to the total weight. The latter assumption is justified by the fact that capelin do hardly feed much or at all during the winter (Vilhjálmsson, 1994). An approximate value $\delta = 0.161$ ($n=22$, $p < 0.001$) was obtained by fitting a weight–length relationship of the type $\mathfrak{W} = (\delta \varrho)^3$ to immature capelin measured in January–February (Vilhjálmsson, 1994). The value of the shape coefficient for capelin is similar to the shape coefficient 0.172 found for anchovy, reported in Pecquerie et al. (2009).

3. Results

3.1. The 1999–2000 season

DEB theory is the theory of energy uptake and utilization of individuals, but not of whole populations comprises individuals. In order to compare the theory to measurements we would need data on individuals from their whole life cycle. Then we would have growth curves which are true to the nature of DEB theory.

However, capelin is quite small and far from trivial to locate. Also, tagging individual capelin is quite costly and difficult. When individuals are caught for measuring, it usually costs them their lives. We use MRI data from 1999 to 2000 season because of numerous data available. The data include location as well as length, wet weight, and weight of reproductive organs. About 100 individual capelin were caught on each of 56 different days, resulting in a total of 5596 measured capelin. Plots of the daily averages can be seen as (blue) dots in Fig. 5.

Here, we choose to compare the DEB to the daily averages of these data. To be as consistent as possible, we look at mature 3-year old female capelin. The great majority of the spawning stock is 3- and 4-year old capelin, contributing on average 70% and 27%, respectively. The spawning stock of 3-year old is usually divided between females and males in a 3:2 ratio, since the males usually mature at an older age (Vilhjálmsson, 1994).

Fig. 5(c) shows the data from Matis of the fat percentage of capelin. Those data are different from the MRI data since they are from commercial capelin catches, where samples were collected and processed on land. We do, therefore, not have any location associated with these data. We, however, believe that these data represent the same schools of fish as the MRI measurements sampled during their research expeditions, and are therefore comparable.

3.1.1. Temperature

As equations governing metabolic rates are dependent on temperature (see Eq. (12)) we need to estimate the temperature the capelin experienced in the 1999–2000 season. In Fig. 2(a), we see the location of the capelin measurements in the 1999–2000 season. Fig. 2(a) was created in Ocean Data View (Schlitzer, R., Ocean Data View, <http://odv.awi.de>, 2010). Using temperature data from the CODE model (Logemann and Harms, 2006), we estimate the temperature at 45 m depth for each individual measured capelin. In Fig. 2, we show the daily averages of these estimates as (blue) dots. We fit a quintic polynomial through these estimates, shown as a (red) curve, which will be the

temperature we use in the simulations of Eqs. (5)–(11). We believe that by doing so we have a fairly accurate and the best available estimate of the temperature the schools of capelin experienced.

3.1.2. Food availability

Food availability in the cold seas around Iceland in fall and winter is low compared to the plankton-rich areas north of Iceland. During the spawning migration, mature capelin have been observed to feed only when they encounter food, but not to actively seek it out (Vilhjálmsson, 1994). Measurements are rare and hard to acquire and we, therefore, choose the simple form of the function for the functional food response, f , in Eq. (5), shown in Fig. 3.

3.1.3. Water content of roe

We note that the energy content of roe is low compared to the energy content of the energy reserves. Data from Matis show how the water content of capelin roe increases as the roe matures, and becomes the best measure on roe maturity once the roe percentage exceeds 20% (Gissurarson et al., 2009). In Fig. 4(a), we show data from Matis and in Fig. 4(b), we show how we take the water content into account by changing the value of ρ_r over time. The change in ρ_r corresponds to a 20% increase of water over a period of one month.

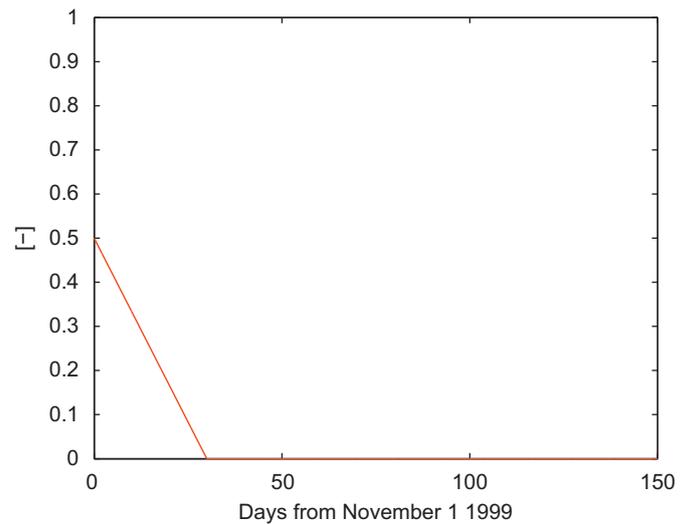


Fig. 3. Food availability and utilization used in Eq. (5).

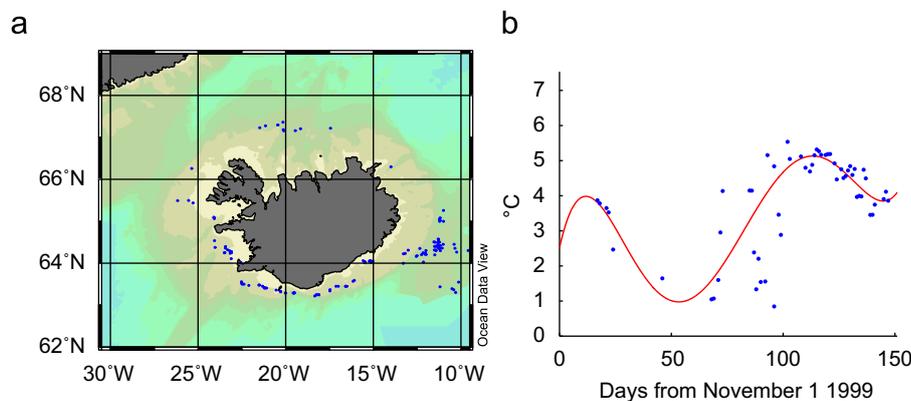


Fig. 2. (a) Location of measurements on 3-year old spawning capelin from the Marine Research Institute during the 1999–2000 season. (b) Estimated temperature (blue dots) from locations of measurements on capelin in 1999–2000 along with the temperature which was used for the DEB simulations (red curve). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

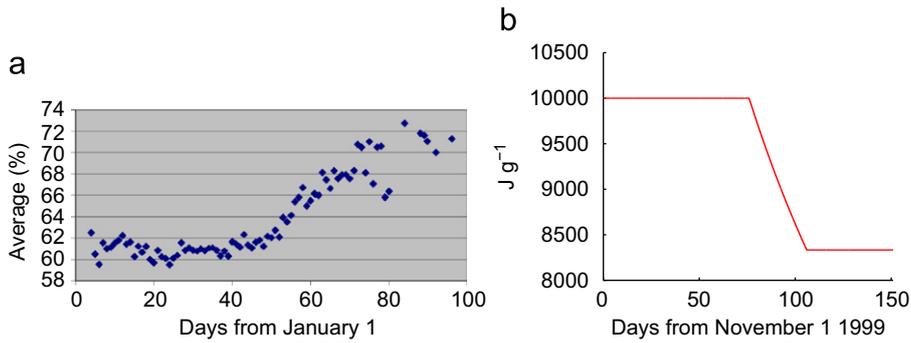


Fig. 4. (a) Water content of capelin roe. Averages from 1984 to 2009. Data from Matis (Gissurason et al., 2009). (b) The parameter ρ_r , see Eqs. (13) and (15). It assumes an increase of the water content of roe of 20% in about one month.

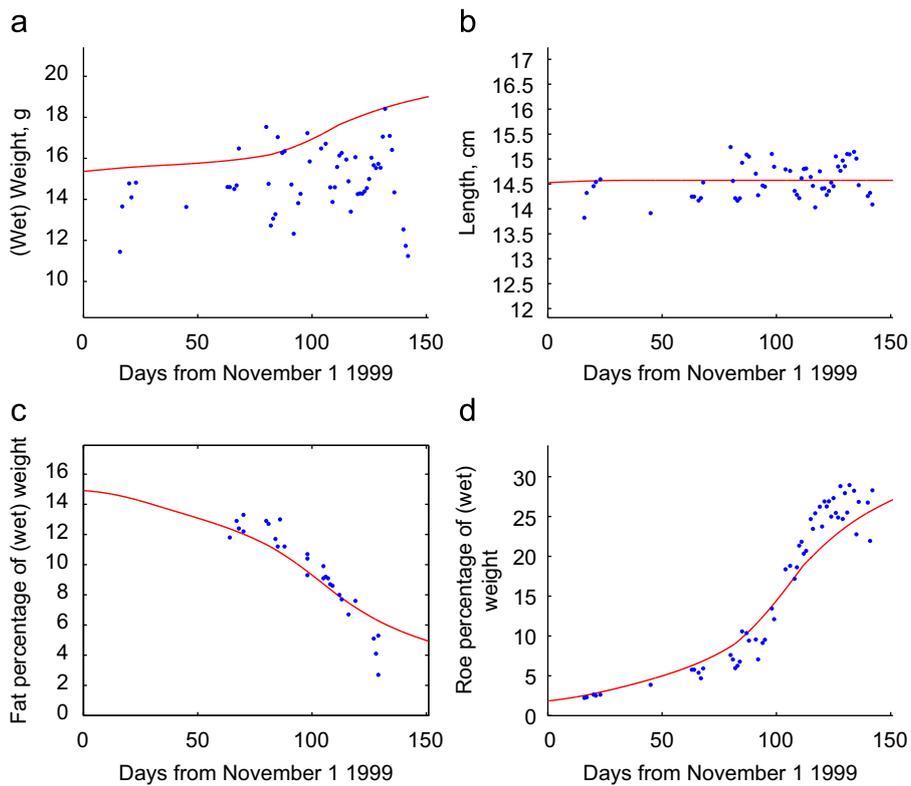


Fig. 5. Comparison between measurements of 3-year old mature female capelin during the 1999–2000 season (blue dots) and the DEB model (red curves), see Eqs. (13)–(18). (a) Weight, (b) length, (c) fat percentage and (d) roe percentage. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. DEB simulations

We now simulate Eqs. (5)–(11) using a fourth-order Runge–Kutta method with the parameter values as described in Table 1, the first five parameters being primary DEB parameters.

As described in Section 2.6, we plot as solid curves in Figs. 5(a), (c), and (d) the derived quantities: weight, \mathfrak{W} , fat percentage, F , and roe percentage, R , respectively. Fig. 5(b) shows the physical length from Eq. (18) as described in Section 2.6.1.

Firstly, we look at Fig. 5(a) of the weight. The data from the MRI are shown as (blue) dots and the derived physical weight \mathfrak{W} from Eq. (13) as a (red) solid curve in the figure. We obtain a weight which is higher than measurements, but the difference is relatively small. Note that the derived weight increases as the individual comes closer to spawning. We notice that the scatter of the data does not seem to render this increase in weight implausible. We are plotting wet weight in both cases, and thus

this increase can be explained by the water content of roe increasing, as discussed in Section 3.1.3.

We show in Fig. 5(b) the measured length of the capelin and the DEB simulations of the length in Eq. (18). We see that the simulated length is very similar to the measured one, but note that the simulations are sensitive to the shape coefficient δ in Eq. (18). Because the shape coefficient is only a parameter in the model it indirectly affects the simulations. A smaller value of δ would increase the length, but other parameters would have to be changed to get similar results.

Fig. 5(c) shows the fat percentage from data from Matis as (blue) dots. The DEB simulations of the derived quantity F from Eq. (17) is shown as a (red) solid curve. The fit is reasonably good, although the data suggest a sharper drop in the fat percentage, which could be explained by the roe production not fully reaching its maximum fast enough close to spawning, as described below.

Finally, and most importantly, Fig. 5(d) shows the roe percentage from data from MRI as (blue) dots. Here we clearly see the sharp increase in roe production of the capelin once they start maturing. The DEB simulations of the roe percentage R is shown as a (red) solid curve. The DEB theory gives a good fit, with the main discrepancies towards the end of the migration. The maximum roe percentage eventually reaches values similar to measurements, but the data suggest an even faster increase of roe production. On the other hand, most notably we see that the sharp increase of roe production starts at the same time as the measured one. This will allow us to use the DEB theory to model behavioral triggers in the interacting particle model in Barbaro et al. (2009a), which we discuss further in Section 4.3.

Finally, we calculate the values of several derived quantities which the parameter values in Table 1 give. First, the value of g , the energy investment ratio from Eq. (10), becomes

$$g = \frac{v[M_V]}{\kappa \{J_{EAm}\} y_{VE}} = 1.20, \quad (19)$$

which for anchovies was reported as 6 (Pecquerie et al., 2009). The value of $[E_m]$, the maximum energy density from Eq. (9) turns out to be

$$[E_m] = \frac{\bar{\mu}_E \{J_{EAm}\}}{v} = 5750, \quad (20)$$

where $\{J_{EAm}\}$ was chosen, so that $[E_m]$ would have a similar value to the one given in Anthony et al. (2000), where a value of 5860 J cm^{-3} is reported. Similarly, we get the value of $[E_G]$ (J cm^{-3}), which is the volume specific cost of growth, as the following:

$$[E_G] = \frac{\bar{\mu}_E [M_V]}{y_{VE}} = 2750, \quad (21)$$

where $[M_V]$ was chosen, so that the value of $[E_G]$ is similar to the value 2800 for anchovies (Pecquerie, 2009). The volume specific somatic maintenance rate, $[p_M]$ ($\text{J d}^{-1} \text{ cm}^{-3}$), can be calculated as follows:

$$[p_M] = \frac{\kappa \bar{\mu}_E \{J_{EAm}\}}{L_m} = 16.3, \quad (22)$$

where Pecquerie (2009) gives the value 19.0 for anchovies. The maximum structural volumetric length of the capelin was chosen, so that the maximum physical length of capelin, according to Eq. (18) with $L=L_m$, would be 17.5 cm, which was estimated from the data from the MRI.

4. Discussion

4.1. Low value of κ

We note that the value of κ or the fraction of utilized energy each individual spends on somatic growth and maintenance, which was calibrated to be 0.4, is quite low compared to other species of fish. For example, in van der Veer et al. (2001) the value of κ is given for four different species of flatfish; plaice *Pleuronectes platessa* (L.), flounder *Platichthys flesus* (L.), dab *Limanda limanda* (L.), and sole *Solea solea* (L.). The values given for these species is 0.85, 0.65, 0.85, and 0.9, respectively. If we compare to anchovy, Pecquerie et al. (2009) found the value $\kappa=0.65$. However, the anchovy can spawn up to 20 times per season (Motos, 1996), whereas capelin spawns only once.

The spawning behavior of capelin is quite dramatic in the sense that once it has decided to spawn it puts nearly all its efforts into roe production. After spawning the spawning stock dies. This strong requirement for success probably explains the low value of κ . It is possible that during the earlier life stages of

the capelin this value is higher, which is reminiscent of the “bang–bang” strategy for organisms (e.g. Bulmer, 1994). In future work, when the whole life cycle of the capelin is modeled, it will be interesting to see if this is the case and the DEB model needs to be modified, or if a single value for κ will suffice.

4.2. Scatter in data plots

In Figs. 5(a)–(d) of the data from the MRI and Matis we note that there is considerable scattering. The plots show average values of all caught fish each day from various locations. When investigating the data set we find that the locations (i.e. the data points) are mostly close to each other, both spatially and temporally, but discrepancies in the measurements could explain some of the scattering.

We also note that we do not have the history of the whole life cycles of each individual, but rather we have samples from schools of fish. It would be optimal, and true to the essence of DEB theory, to follow individuals and measure them several times on their migration, if this were possible. We have, however, samples of capelin which experienced similar conditions and therefore hopefully give a reasonable representation of a typical life cycle of the capelin.

4.3. Links to an interacting particle model

We have presented a DEB model for the growth, energy utilization, and reproduction for mature 3-year old female capelin. Good fits of parameter values were found for the season 1999–2000 based on a large data set of 5596 individuals. We intend to incorporate this model of the capelin's inner dynamics with the interacting particle model presented in Barbaro et al. (2009a).

The most important contribution of the DEB model to the interacting particle model is the timing of the onset of increased roe production. With the DEB model we are now in a position to let the sexual maturity of individuals act as triggers for changes in their behavior.

In Barbaro et al. (2009a), the individual particles have a preferred temperature range which they seek out. As mentioned in the introduction, the capelin have a tendency to time their entry into warmer waters according to their roe percentage. By letting, e.g. 9% trigger the change in the preferred temperature range we hope to obtain the desired effect, thus improving the simulations of the interacting particle model.

In Barbaro et al. (2009a), particles also have a preferred speed depending on how close they are to spawning, although the actual speed also depends on the average speed of certain neighboring particles. This preferred speed is somewhat crudely modeled by increasing it when the particles reach a geographical location, east of longitude 13.5°W . By integrating the DEB model into the particle model it is possible to let the preferred speed depend, e.g. on roe content.

The DEB model will further help to explain variations in migration patterns based on environmental factors. In particular, the DEB equations depend on oceanic temperature which allows us to determine the effect that the environment has on the migration routes of the capelin, and thus predict what effect changes in the oceanic temperature will have on the behavior of the capelin.

Although DEB theory deals with individuals, and not populations as a whole, we hope that by combining the DEB model with the interacting particle model in Barbaro et al. (2009a) it will be possible to explain phenomena of large schools of fish by the physiology of individual fish, resulting in a powerful model of the spawning migration of the Icelandic capelin and hopefully the migrations of other species of fish as well.

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