Critical threshold size for overwintering sandeels (Ammodytes marinus)

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Critical threshold size for overwintering sandeels (*Ammodytes marinus*)

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Abstract Several ecologically and commercially important fish species spend the winter in a state of minimum feeding activity and at lower risk of predation. To enable this overwintering behaviour, energetic reserves are generated prior to winter to support winter metabolism. Maintenance metabolism in fish scales with body size and increases with temperature, and the two factors together determine a critical threshold size for passive overwintering below which the organism is unlikely to survive without feeding. This is because the energetic cost of metabolism exceeds maximum energy reserves. In the present study, we estimated the energetic cost of overwintering from a bioenergetic model. The model was parameterised using respirometry-based measurements of standard metabolic rate in buried *A. tobianus* (a close relative to *A. marinus*) at temperatures from 5.3 to 18.3°C and validated with two independent long-term overwintering experiments. Maximum attainable energy reserves were estimated from published data on *A. marinus* in the North Sea. The critical threshold size in terms of length (L_{th}) for *A. marinus* in the North Sea was estimated to be 9.5 cm. We then investigated two general predictions: (1) Fish smaller than L_{th} display winter feeding activity, and (2) size at maturation of iteroparous species is larger than L_{th} to ensure sufficient energy reserves to accommodate both the metabolic cost of passive overwintering and reproductive investments. Both predictions were found to be consistent with data on size at maturation and total body energy in December and February.

Introduction

In temperate and boreal regions, planktivorous fish experience strong seasonal fluctuations in food availability often relying on a single transient increase in zooplankton production (Winder and Schindler 2004; Varpe and Fiksen 2010). Yet our understanding of how strong seasonality in food availability shapes life-history traits of planktivorous fish is limited (e.g. Hurst 2007).

To endure long winters and periods of low food availability, many high latitude fish species build up energy reserves which are mobilised during periods of food shortage (e.g. Hislop et al. 1991; Schultz and Conover 1997). Several ecologically and commercially important species generate enough energy reserves prior to winter to allow them to *overwinter* in a passive state of minimum feeding activity and therefore at lower risk of predation (Winslade 1974; Ultsch 1989; Huse and Ona 1996; Paul and Paul 1998; Schultz and Conover 1997; Varpe and Fiksen 2010). This type of overwintering strategy optimises the trade-off between energy uptake and predation risk on an annual time scale (Garvey et al. 2004; van Deurs

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et al. 2010), and this definition applies to all subsequent use of the terms overwinter or overwintering.

Size-dependence of metabolic maintenance requirements theoretically dictates a critical threshold size below which the organism is unlikely to survive winter without feeding (van de Wolfshaar et al. 2008). Experiments and field studies implying the existence of size-dependent bioenergetic constraints in relation to winter conditions include studies of Atlantic silversides (*Menidia menidia*), yellow perch (*Perca flavescens*), Eurasian perch (*P. fluviatilis*), smallmouth bass (*M. dolomieui*), and largemouth bass (*M. salmoides*) (Conover 1992; Schultz et al. 1998, 2002; Schindler 1999; Garvey and Marschall 2003; Biro et al. 2005; Shuter and Post 1990; Fullerton et al. 2000).

The notion that a critical threshold size must exist arises from the differences in allometric scaling of maximum energy reserves and metabolism (van de Wolfshaar et al. 2008). Maximum energy reserves for a given fish length ($R_{\max}$) are proportional to the maximum body weight ($w_{\max}$) attainable for a fish of that length (allometric scaling exponent of 1), whereas mass-specific standard metabolic rate (SMR) decreases as body weight increases (allometric scaling exponent of c. 0.8) (e.g. Clarke and Johnston 1999; Schultz and Conover 1999; Garvey et al. 2004). If the fish is successful in reaching $w_{\max}$ prior to the overwintering period and we know the relationship between fish length and $w_{\max}$, we can define the threshold size required for overwintering in terms of length (L_{th}) in the following way: $L = L_{\text{th}}$ when $R_{\max}(L) - \Delta E_{\text{ow}}(L) = 0$. A schematic plot of the analytical solution to $R_{\max}(L)$ and $\Delta E_{\text{ow}}(L)$ reveals that fish larger than L_{th} have surplus energy after paying the metabolic cost of overwintering, whereas fish smaller than L_{th} will experience an energy deficit (Fig. 1).

Lesser sandeel (*Ammodytes marinus*) represents an archetypical example of the overwintering strategy, and thus offers an ideal subject species for a test of the theoretical framework introduced above. *A. marinus* is the most abundant of all fish species in the central regions of the North Sea, where they overwinter buried in sandy bottom habitats. They are the main target for a wide range of predators, as well as a large-scale industrial fishery. Commercial catches of *A. marinus* show a steep decrease in catches between August and April indicating that the overwintering period for adult *A. marinus* on average lasts for 8 months (Winslade 1974; Wright et al. 2000; Høines and Bergstad 2001) interrupted only by spawning in December/January (Macer 1966; Bergstad et al. 2001; Boulcott and Wright 2008). In addition to the pronounced overwintering behaviour, *A. marinus* in the North Sea are non-migratory, and local patterns of ocean currents retain most *A. marinus* larvae near hatching locations (Christensen et al. 2008; Jensen et al. 2011). These characteristics promote adaptations to local environmental conditions and allow sampling from the same pool of fish multiple times over the course of a year.

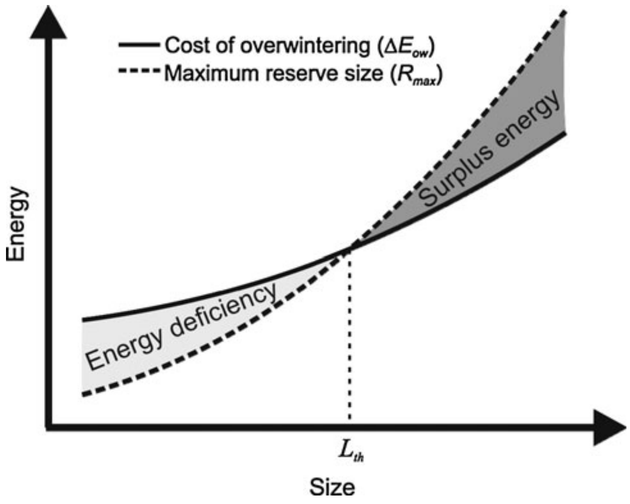

Fig. 1 Schematic illustration of the theoretical argument for the existence of a critical threshold size (L_{th}). Dashed curve represents the relationship between fish length and maximum energy reserves prior to winter. *Solid line* represents the total energetic cost of overwintering (ΔE_{ow}) (reproductive investment excluded) as a function of fish length. L_{th} is where ΔE_{ow} equals $R_{\max}$ (the intercept of the two curves). For sizes smaller than L_{th}, there is a deficit of energy (*light grey* area) which must be paid by compensatory winter feeding activity. Above L_{th} there is a surplus of energy which is available for reproductive investment (*dark grey* area)

In the present study, we developed a bioenergetic model of energy expenditure in overwintering sandeels. The model is parameterised based on measurements of standard metabolic rate (SMR) conducted on buried sandeels over the course of a week, and we explicitly test whether depression of metabolism occurs on a time scale of months by validating the model in a long-term overwintering experiment. Initial attempts to transport high quality samples of live *A. marinus* from off-shore areas in the North Sea to the laboratory failed. SMR measurements and validation experiments were therefore conducted on *A. tobianus* (a close relative of *A. marinus*), which were available from a nearby shore and thus easily transported to the lab. We then estimated ΔE_{ow} and $R_{\max}$ for various fish lengths using the bioenergetic model and data from Hislop et al. (1991), respectively, and from these estimates we derived L_{th} for *A. marinus* in the North Sea under the assumption that SMR of *A. tobianus* can be applied to *A. marinus*.

Lastly, we investigated the following predictions using field-based observations of size at maturation and total body energy in December and February: (1) *A. marinus* smaller than L_{th} must be engaged in winter feeding activity to account for the energy deficit between reserve size and the energetic cost of overwintering, and (2) size at first maturation should be larger than L_{th}, since only then are energy reserves sufficient to accommodate both the metabolic cost of overwintering and reproductive investments.

Materials and methods

Bioenergetic model (ΔE)

Assuming that the routine metabolic rate of an overwintering sandeel resembles SMR (gonadal development not included), the rate at which energy reserves are depleted [J ind^{-1} h^{-1}] can be expressed as:

$$\mathrm{SMR}(w,T) = S_0 w^n f(T), \tag{1}$$

where w is fish wet weight [g], n the allometric scaling exponent of metabolism ($n \sim 0.8$, Clarke and Johnston 1999), and $f(T)$ the temperature dependency of SMR [J g^{-1} h^{-1}]. $S_0 = w_e^{1-n}$, where w_e is the mean wet weight of fish used in the respirometry experiments ensuring that SMR(w_e, T) = w_e $f(T)$. With this gross rate of reserve-depletion [J ind^{-1} h^{-1}] during overwintering, we can calculate the energetic cost of overwintering [J ind^{-1}] from time 0 to t for an individual:

$$\Delta E(t, T_t; \Delta t, w_0) = -\sum_{t=0}^{t/\Delta t} \mathrm{SMR}(w_t, T_t)\Delta\tau, \tag{2}$$

where T_t is the temperature [$^{\mathrm{o}}$C] at time t, Δt is the duration of the period for which we want to calculate ΔE, $\Delta\tau$ is the time step in hours (we used 24 h time-steps), and w_0 is the weight of the sandeel at $t = 0$ [g]. The wet weight at time step t is calculated from the previous time step as:

$$w_t = \begin{cases} w_0 & \text{for } t = 0 \\ w_{t-1} - E_d^{-1}\mathrm{SMR}(w_{t-1}, T_{t-1})\Delta\tau & \text{else} \end{cases}, \tag{3}$$

where E_d is the energy density of energy reserves [J g^{-1} wet weight].

Measuring SMR at different temperatures

The study animals (*A. tobianus*, mean wet weight = 4.7 g, SD = 0.68) were caught by seine in a bay in east Denmark (56$^{\mathrm{o}}$N, 12$^{\mathrm{o}}$E) and kept for c. 6 months prior to the experiment in round 1,660 L holding tanks with 10°C fully oxygenated and recirculated water and a salinity of 30. A 10 cm layer of sand on the bottom of the tanks allowed the sandeels to maintain their natural burying behaviour and they were fed frozen artemia once every week day. The SMR temperature function, $f(T)$ in Eq. 1, was derived from measurements of oxygen consumption of buried *A. tobianus* [mg O$_2$ g^{-1} h^{-1}] at different temperatures using closed circuit respirometry (e.g. Behrens and Steffensen 2007). The respirometer was custom-made from acrylic glass and with a water volume of 6.48 L and contained rinsed and burned sand distributed over the bottom (450°C for 6 h). To ensure a stable temperature within the respirometer, it was submerged into a large tube which received water from one of the holding tanks. The water recirculation system of the laboratory facility supplied water at both 5°C and 10°C. By manually adjusting the water inflow of 5°C and 10°C, any water temperature between these temperatures could be maintained. To achieve water temperatures above 10°C, a heating element attached to a thermostat was used. Prior to initiation of a trial, ten sandeels (starved for c. 72 h prior to each trial) were selected randomly from the holding tank and placed in the respirometry chamber, which was subsequently kept in darkness. Visual inspections twice a day confirmed that the sandeels were buried in the sand. Each trial lasted for 5 days. Throughout this period, the respirometer alternated between being flushed with oxygen-saturated water for periods of 20 min, and being closed for 2 h periods. The rather long closed circuit interval was necessary due to relatively low ratio of fish to water volume in the chamber, which again was a compromise between precision of measurements and allowing the fish to move freely in the sand. The flushing/measuring periods were automated by connecting a timer to a pump attached on the chamber inlet. For continuous measurements of oxygen and temperature, water from the respirometer was pumped through a silicone tube and over an oxygen probe connected to a WTW microprocessor oximeter (Oxi 340i) after which the water was returned to the respirometer. The rate of oxygen consumption was calculated from the slopes of the oxygen decrease during the closed circuit intervals. No UV sterilizer was used, however, by the end of each trial the fish were carefully removed and the background oxygen consumption was measured. The entire experiment consisted of twelve trials, each of which was carried out at a temperature between 5.3 and 18.3°C. For each of the twelve trials, we calculated the mean oxygen consumption rate during the last three closed circuit intervals and subtracted the corresponding measurements of background oxygen consumption. These oxygen consumption rates were subsequently used to derive $f(T)$ for Eq. 1 after translating oxygen consumption into rate of energy expenditure [J g^{-1} h^{-1}] using a general oxycaloric coefficient of 14 J mg^{-1} O$_2$ (Brett 1973).

Validation of model

Two separate long-term experiments were executed in the laboratory (VAL-1 and VAL-2) to validate the bioenergetic model. During these experiments, we deprived *A. tobianus* of food, which after c. one week induced an overwintering-like behaviour where all fish remained permanently submerged in the sand. Experiments ran for 131 and 298 days. It should be emphasised that long periods of starvation are a natural component of the life-cycle of sandeels and hence do not cause unnatural distress. VAL-1 was conducted at 10°C in three 2.5-L containers containing a c. 15-cm thick layer of sand and constantly recirculated and fully oxygenated water. Five small sandeels were taken from a holding tank in the laboratory (also 10°C) and placed in each container (mean fish wet weight 1.37 g, SD = 0.18). Containers were inspected twice a week to ensure that fish remained buried. VAL-2 was conducted with larger sandeels (mean fish wet weight 4.06 g, SD = 0.58) in a video-monitored 1,600-L holding tank containing a c. 10 cm layer of sand, recirculated and fully oxygenated water, and variable water temperature (100 days of 5°C, 14 days of 14°C and 184 days of 10°C). The variable temperature of VAL-2 was not meant to resemble natural conditions, but was part of an attempt to trigger the fish to end the induced overwintering-like behaviour, but the attempt was not successful. A sample of fish ($n = 9$ in VAL-1 and $n = 6$ in VAL-2) were collected on the first (baseline conditions) and last day (final conditions) of the experiment, killed by a blow to the head, and stored at −80°C. Length, wet weight, and dry weight (drying at 60°C for 48 h) were measured and total body energy was determined by bomb calorimetry in an IKA C-7000 bomb calorimeter. There were no signs of spawning or developing gonads in any of the fish. Lastly, validation of the bioenergetic model was carried out by comparing model predictions (ΔE), for VAL-1 and VAL-2, respectively, to the observed change in total body energy (mean body energy on the first day minus mean body energy on the final day of each experiment).

Energy reserves and body weight prior to overwintering ($R_{\max}$ and $w_{\max}$) and water temperature (T_t)

Total body energy of *A. marinus* in the North Sea reaches a maximum in August and a minimum in April where average total body energy is 53% of total average body energy in August (Hislop et al. 1991). Assuming that sandeels have empty reserves in April and full reserves in August, the potential energy reserves prior to overwintering can be estimated from:

$$R_{\max} = (1 - 0.53) \times (0.0041L^{3.66}) = 0.00193L^{3.66}, \qquad (4)$$

where the last parenthesis represents total body energy in august [KJ ind^{-1}] as a function of fish length [cm]. The parameterisation is based on data from Table 2 (August) in Hislop et al. (1991).

To estimate the metabolic cost of a full overwintering period from Eq. 2, total body wet weight prior to overwintering ($w_0 = w_{\max}$) is needed along with water temperature. Based on data in Appendix 1 of Electronic supplementary material (June) in Hislop et al. (1991) and Table 2 (August) in Hislop et al. (1991), we derived a relationship between wet weight [g] prior to overwintering and total fish length [cm]:

$$w_{\max} = 0.0019L^{3.21} \qquad (5)$$

Bottom temperature profiles for Dogger Bank (2°E, 55°N) and Fisher Bank (7°E, 57°N), two areas important to the central North Sea sandeel fishery, were taken from the NORWECOM model (Skogen et al. 1995). Temperatures are monthly mean values averaged over the years from 2000 to 2007 (Fig. 2).

Field observations of size at maturation and total body energy in December and February

Size at maturation, represented by the proportion of mature sandeels in each centimetre length group, was determined based on 1763 specimens of *A. marinus* sampled in December 2006 and December 2007 (between December 5th and 17th) from various sampling stations between 0°E–8°E and 54°N–58°N. Sampling was carried out with a modified scallop dredge (catching only buried sandeels) as part of a routine sampling programme at the National Institute of Aquatic Resources (DTU Aqua).

During the same surveys, another 728 sandeels were sampled from six selected stations. Those six stations were revisited in February 2007 and 2008 (between February 12th and February 20th). From each station, fifty sandeels, distributed equally over half-centimetre groups, were analysed with respect to total length [mm], age (based on number of winter-rings in otoliths), and body weight [g] (both wet weight and dry weight; dried at 60°C for 48 h).

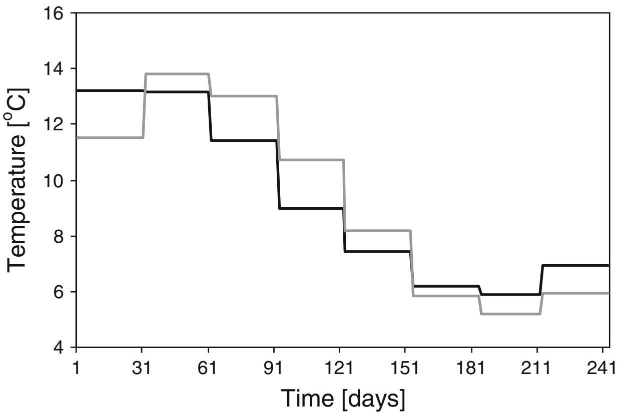

Fig. 2 Monthly mean bottom temperature (averaged in the period 2000–2007) during the overwintering period of *A. marinus* (starting on August 1st) presented for two areas important to the central North Sea sandeel fishery (*black*: Dogger Bank (2°E, 55°N); *grey*: Fisher Bank (7°E, 57°N)). Data are monthly means from the NORWECOM model

Dry weight (w_{dry} [g]) was translated into total body energy (E [KJ ind^{-1}]) based on a linear regression model fitted to bomb calorimetry data ($r^2 = 0.995$) from the experiment described above:

$$E = 23.4 w_{\mathrm{dry}} - 1.4 \tag{6}$$

Data from both December and February were then divided into seven size-intervals: 6–6.9, 7–7.9, 8–8.9, 9–9.9, 10–10.9, 11–13.9, and 14–17 cm. Mean total body energy and mean wet weight for each size-interval and sampling month was derived by fitting a linear regression model for each size-interval: $Y = aX + b$, where Y is either total body energy or wet weight and X is the length of the fish in mm, and subsequently calculating Y for each size-interval by inserting the mid-point of the respective size-interval into the regression model. Lastly, the observed change in energy (ΔE_{obs}) was calculated for each size-interval as the difference in mean total body energy between December and February. We will subsequently be referring to the size-intervals as size-classes and use the midpoints of the intervals.

Results

Parameterisation and validation of model

The SMR temperature function, $f(T)$, was derived from measurements of oxygen consumption of buried *A. tobianus* (Fig. 3). A linear fit, $f(T) = 0.08T - 0.25$, explained data significantly better than the best curvilinear fit, $f(T) = 0.11e^{0.14T}$, which we tested in a multiple regression model on the form: $f(T) = e^{aT} + bT + c$. Furthermore, visual inspection of Fig. 3 clearly illustrates that the curvilinear fit underestimates SMR for intermediate temperatures. Oxygen levels in the chamber dropped 5–35% over the 2 h measuring period depending on temperature. The r^2 values calculated for the linear regressions fitted to the rate of oxygen decline was on average 0.98 (SD = 0.015, $n = 36$, minimum value = 0.93). Data from the bomb calorimetry experiment provided a way of approximating the energy density of reserves: $E_d = (\Delta E/\Delta w_{\mathrm{dry}})/(\Delta w/\Delta w_{\mathrm{dry}}) = 8.6 \cdot 10^3$, where ΔE is mean total body energy before the starvation period minus mean total body energy observed after the starvation period, and likewise for Δw and Δw_{dry}. The estimate is a mean between large fish from VAL-2 ($E_d = 9.1 \cdot 10^3$) and small fish from VAL-1 ($E_d = 8.2 \cdot 10^3$) (the difference between small and large fish was due to smaller delta $w/\Delta w_{\mathrm{dry}}$ for the large fish). With this parameterisation of Eq. 2, we predicted ΔE for each of the validation experiments, VAL-1 and VAL-2, and compared the values to the observed change in total body energy. ΔE deviated from observed ΔE by only 6 and 0.7% in VAL-1 and VAL-2, respectively (Table 1). Due to technical problems, three fish from the baseline-sample of VAL-1 were lost (n in this sample was therefore reduced from 9 to 6).

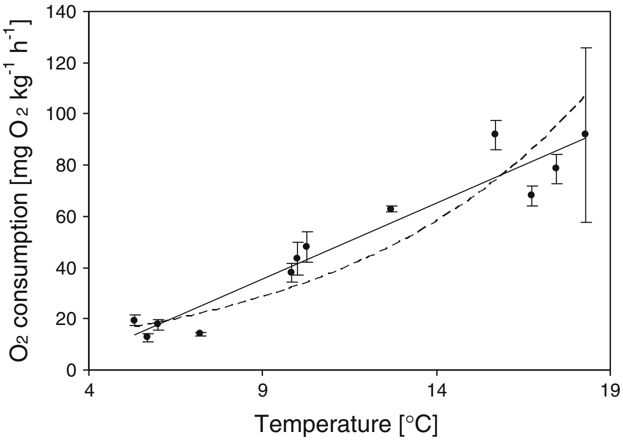

Fig. 3 Measurements of oxygen consumption of buried *A. tobianus*. Each data point in the graph represents a mean of three repeated measurements (*whiskers* represents standard deviations). Linear relationship: $y = aT - b$ (*solid line*). Curvilinear fit: $y = ae^{bT}$ (*dashed line*)

Calculating the critical threshold size

According to the definition given in the introduction (Fig. 1), the length at which $R_{\max}$ minus ΔE_{ow} equals zero corresponds to L_{th}. The energetic cost of a full overwintering period, lasting from August to April ($\Delta E_{\mathrm{ow}} = \Delta E_{8\ \mathrm{months}}$), was calculated for each size-class using Eq. 2. As input to Eq. 2 we used $\Delta t = 242$ days (1st August to 1st April), $w_0 = w_{\max}$ (Eq. 5), and $T(t)$ = monthly means between Dogger Bank and Fisher Bank from August to April (Fig. 2). Calculated values of $\Delta E_{8\ \mathrm{months}}$ and R_{max} for each size-class are presented in Table 2. The deviation between $R_{\max}$ and $\Delta E_{8\ \mathrm{months}}$ ($R_{\max}$ minus $\Delta E_{8\ \mathrm{months}}$) increased gradually with fish length and shifted from negative values to positive values around size-class 9.5 cm (Fig. 4, grey bars).

L_{th} depends partly on the environmental temperature in the overwintering habitat and the assumption made about duration of a full-scale overwintering period. An elevation of the temperature profile by 1°C throughout the overwintering period resulted in an increase in L_{th} of roughly 1 cm. Likewise, an increase in the duration of the overwintering period by 1 month resulted in an increase in L_{th} of roughly 0.5 cm. The precise magnitude of the response to changes in the duration of the overwintering period was dependent on the temperature, with a larger response towards higher temperatures (Fig. 5).

The bioenergetic model used operates in discrete time-steps in order to account for month-to-month variation in temperature. However, the model can be written as a single

Table 1 Observed and predicted energy depletion in sandeel (*A. tobianus*) during two laboratory experiments where buried sandeels were food deprived (VAL-1 and VAL-2)

	Duration and temperature (days and °C)	Initial wet weight (g ind^{-1})	Initial energy content (KJ ind^{-1})	Final energy content (KJ ind^{-1})	Observed energy depletion (KJ ind^{-1})	Predicted energy depletion (ΔE [KJ ind^{-1}])	Deviation (%)
1	131d at 10°C	1.37 (SD = 0.18, $n = 9$)	6.66 (SD = 1.08, $n = 6$)	3.98 (SD = 0.49, $n = 9$)	2.68 (40%)	2.85	6
2	100d at 5°C 14d at 14°C 184d at 10°C	4.06 (SD = 0.58, $n = 6$)	24.60 (SD = 3.81, $n = 6$)	12.87 (SD = 2.43, $n = 6$)	11.73 (48%)	11.65	0.7

The change in body energy was predicted using Eq. 2 (predicted energy depletion) based on duration of the experiments, temperature, and initial fish weight. The predicted values were then compared to the observed mean change in body energy (observed energy depletion = initial energy content − final energy content), and the percentage deviation between the predicted and observed values were calculated

Table 2 Data used to generate the grey and black bars in Fig. 4

Size-class (cm)	$R_{\max}$ (KJ ind^{-1})	Predicted cost of overwintering (8 months) ($\Delta E_{8\text{ months}}$ [KJ ind^{-1}])	Predicted cost of overwintering between mid December 11th and February 16th ($\Delta E_{2\text{ months}}$ [KJ ind^{-1}])	Observed change in total body energy between December 11th and February 16th (ΔE_{obs} [KJ ind^{-1}])
6.5	1.83	2.93	0.59	0.33
7.5	3.0	3.99	0.81	−0.05
8.5	4.89	5.39	1.10	−0.47
9.5	7.34	7.22	1.47	−1.18
10.5	10.59	9.50	1.94	−2.06
12.5	20.07	15.58	3.17	−4.56
15.5	44.13	29.21	5.57	−12.16

Column two and three present the calculated maximum reserve size ($R_{\max}$) and predicted (Eq. 2) total energetic costs of overwintering ($\Delta E_{8\text{ months}}$) for various size-classes of sandeels. Column four and five presents the predicted (Eq. 2) and observed (field data) cost of overwintering between February 11th and December 16th ($\Delta E_{2\text{ months}}$ and ΔE_{obs})

equation in which L_{th} can be isolated if a constant temperature profile is used (online resources). As this analytical equation does not require any programming, it is a simple tool for making, for example, first hand estimates of L_{th}. Lastly, it is important to emphasise that L_{th} is the critical threshold size for fish that have acquired maximal realisable energy reserves before winter.

Field observations of reduction in body energy during winter and size at maturation

There were no mature sandeels in the size-classes 6.5, 7.5, 8.5, and 9.5. At larger size, maturation frequency increased gradually from around 15% for size-class 10.5 to more than 90% for size-class 15.5 (Fig. 4, white bars). Based on Eq. 2, we calculated the metabolic cost of overwintering from December 11th till February 16th ($\Delta E_{2\text{ months}}$) (input to Eq. 2: $\Delta t = 66$, w_0 = weights observed in the December samples). The values of $\Delta E_{2\text{ months}}$ together with the field observations of change in total body energy between December 11 and February 16 (ΔE_{obs}) are presented in Table 2. The deviation between the observed and predicted values (ΔE_{obs} minus $\Delta E_{2\text{ months}}$) increased gradually with the size of the fish and shifted from negative values to positive values around size-class 9.5 cm (Fig. 4, black bars).

In order to address the basic assumption that sandeels in general reach (or get close to) $R_{\max}$ prior to overwintering and that neither 1986, 2006 or 2007 represent exceptions to this, we estimated total body energy of a 9.5 cm sandeel in August 2006 and 2007. This was done by adding the energetic cost of overwintering between August and December (using Eq. 2) to the mean body energy observed in December 2006 and 2007, and subsequently comparing these values to the corresponding August value in the 1986 data from Hislop et al. (1991). The data from Hislop et al. (1991) and the calculations for 2006 and 2007 were comparable (~15 kJ) thus supporting the basic assumption.

Discussion

In this study, we used the unique overwintering and burying behaviour of sandeels to estimate the basic

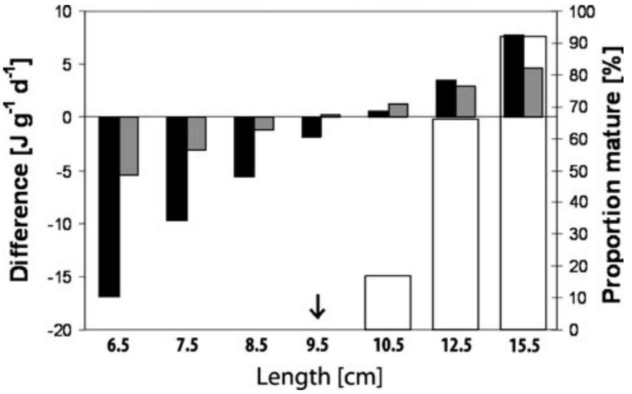

Fig. 4 Estimation of critical threshold size (L_{th}) and comparison with field observations. *Grey bars*: Maximum energy reserves (R_{max}) minus metabolic cost of overwintering ($\Delta E_{8\ months}$), standardised to J per gram per day. L_{th} is the length at which $R_{max} - \Delta E_{8\ months} = 0$ (Fig. 1). *Black bars*: Observed energy usage for sandeels in the field (ΔE_{obs}) minus model prediction of standard metabolic cost ($\Delta E_{2\ months}$), standardised to J per gram fish per day. $\Delta E_{obs} - \Delta E_{2\ months}$ should be zero if the fish were overwintering. If $\Delta E_{obs} - \Delta E_{2\ months}$ is different from zero, it indicates that the fish were engaged in activities such as feeding (if <0) or developing gonads (if >0) (Fig. 1). White bars: Frequency of mature sandeels caught in the North Sea in December. Estimated L_{th} is indicated by *arrow*. Raw values of R_{max}, $\Delta E_{8\ months}$, ΔE_{obs}, and $\Delta E_{2\ months}$ are provided in Table 2

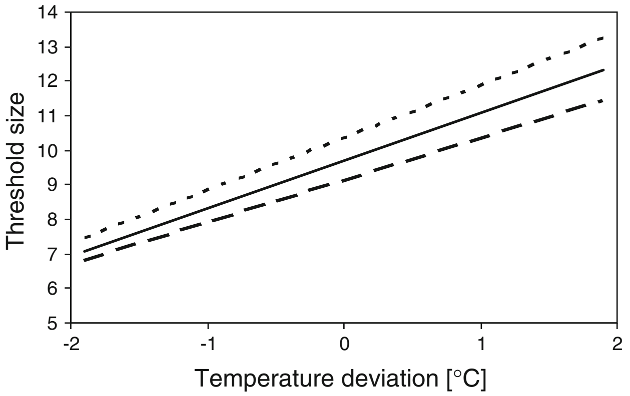

Fig. 5 The critical threshold size L_{th} [cm] for sandeels as a function of temperature for three different lengths of overwintering: 7 months (*dashed*), 8 months (*solid*) and 9 months (*dotted*). *Horizontal axis* shows temperature deviation from the mean temperature profile applied in Fig. 4, where e.g. 1°C deviation implies that the temperature was raised by 1°C in all months

energetic cost of overwintering by use of a bioenergetic model. By calculating the energetic cost of overwintering for various size-classes, and subsequently relating these values to maximum energy reserves, we were able to estimate the critical threshold size in terms of length (L_{th}) for *A. marinus* in the North Sea to ~9.5 cm. Furthermore, the rate of energy use during winter, as observed in the field, closely resembled SMR near the estimated L_{th}, while the rate of energy use exceeded SMR for fish larger than L_{th}, indicating that only fish larger than L_{th} were allocating energy to gonadal development. This interpretation of the results was further supported by field data revealing that the smallest maturing individuals were slightly larger than L_{th}. At the other end of the size-range, the smallest of the fish depleted energy reserves at a mean rate considerably lower than SMR, indicating that fish smaller than L_{th} were acquiring energy from feeding. This perception is further supported by the literature, in which juvenile *A. marinus* remaining in the pelagic as late as in December has been reported several times (Macer 1966; Reeves 1994; Kvist et al. 2001). Previous fish studies emphasising the bioenergetic constraints in life-history traits of high latitude species has shown that: (1) juvenile growth rates and sex determination of Atlantic silversides (*Menidia menidia*) have evolved in response to a selection pressure imposed by size-dependent energy depletion and latitudinal gradients in the length of the growing season (e.g. Conover 1992; Schultz et al. 1998, 2002), (2) the time constraint imposed by size-selective winter mortality promotes high risk-high gain foraging behaviour and fast growth in juvenile largemouth bass (*Micropterus salmoides*) and rainbow trout (*Oncorhynchus mykiss*) (Schindler 1999; Garvey and Marschall 2003; Biro et al. 2005), and (3) the northern distributional limit for yellow perch (*Perca flavescens*), Eurasian perch (*P. fluviatilis*), smallmouth bass (*M. dolomieui*), and largemouth bass (*M. salmoides*) are determined by the ability of the young of the year to complete a minimum amount of growth during a growth season that shortens towards higher latitudes (Shuter and Post 1990; Fullerton et al. 2000). While all of the above mentioned studies imply the existence of a critical threshold size, none of these studies actually estimated the threshold size. Furthermore, while the energetic requirements of overwintering are known to affect size at first reproduction in temperate non-migrating bird species (Downhower 1976), the present study is the first to link allometric scaling of metabolism to maturation size and overwintering strategy of fish.

Our results show that L_{th} is positively correlated with water temperature and that maturation should be postponed until after L_{th} has been reached. We therefore expect that size at maturation should respond to differences in water temperature in a situation where it is close to L_{th}. Size at maturation for *A. marinus* varied considerably among three study locations in the North Sea, Fisker Bank, Dogger Bank, and Firth of Forth (Boulcott et al. 2007). Fish on Fisker Bank matured both later in life and at larger size compared to the other areas. Fisker Bank is highly influenced by the coastal water system and the water column stability is weak, which results in relatively high bottom temperatures in summer and fall. The influence of different site temperatures combined with L_{th} may therefore explain the observed pattern of size at maturation. Even small changes in temperature can have major impact on local sandeel populations: intra-annual variation in winter mortality is partly explained by intra-annual variation in average seabed temperatures of less than 1°C in south-eastern Scotland (Greenstreet et al. 2010).

Reaction norm theory predicts that when growth conditions are poor, size at maturation decreases (Plaistow et al. 2004). However, when size at maturation approaches L_{th} this effect on the reaction norm may be countered by natural selection against individuals that mature at sizes below L_{th}. We suggest that this counter-effect may have influenced the size at 50% maturity for North Sea herring (*Clupea harengus*) both before and after the severe stock decline (Engelhard and Heino 2004). Before the decline, spawning stock biomass was large, and consequently intra-specific competition for resources was presumably intense. In the overexploitation period, the spawning stock biomass was reduced by a factor of ten, and the mean size at maturation increased in accordance with the typical norm of reaction. However, inter-annual variability also increased considerably in the period of low stock sizes, with size at maturation occasionally being as low as but never lower than in the pre-overexploitation period. If size at maturation was close to L_{th} during the pre-overexploitation period, the previously mentioned counter-effect would explain why variability in size at maturation was reduced during this period.

Comatose-like conditions, impairment of sensory performance, and anaerobic metabolism (the latter only found in the crucian carp *Carassius carassius*) have been observed in a few fish species when exposed to severe hypoxic environments (e.g. Ultsch 1989; Nilsson and Renshaw 2004). However, even though sandeels bury into anoxic sediment and stay there for extended periods, they sustain their oxygen requirements by sucking down oxygenated water from above the sediment surface (Behrens et al. 2007). We also considered the possibility that sandeels benefit from absorbing some of the naturally occurring toxic hydrogen sulphide in the sediment. This toxic compound inhibits the enzyme cytochrome oxidase, resulting in depressed aerobic metabolism (e.g. Doeller 1995). However, as shown in Behrens et al. (2007) buried sandeels are enveloped by relatively oxygen rich water leaving the gills. This is because only a fraction of the oxygen is being removed when the water passes over the gills. The Antarctic *Notothenia coriiceps* enters a comatose-like state after exposure to extremely low temperatures (~2°C) (Campbell et al. 2008). In contrast to *N. coriiceps* sandeels in the present study appeared to be perfectly agile and showed no signs of impaired sensory reactions when disturbed after being buried for several weeks at 5°C or even months at 10°C (the bottom temperature in the North Sea rarely falls below 5°C). This together with the consistency between predictions from our bioenergetic model and measurements of the reduction in energy content of long-term buried sandeels in the laboratory (Val-1 and Val-2) leads us to conclude that comatose or advanced metabolic depression does not occur in over-wintering sandeels, and that large energy reserves and reduced activity are sufficient to cope with long periods of starvation.

The constructed model relies on the assumption that SMR of *A. tobianus* is similar to that of its close relative *A. marinus*. This assumption was necessary since initial attempts to transport samples of live *A. marinus* from offshore areas in the North Sea to the laboratory failed. However, differences in SMR are more closely related to body shape and behaviour than to phylogenetic relationship (Clarke and Johnston 1999), and since *A. marinus* and *A. tobianus* are nearly identical in terms of body shape and behaviour the assumption is reasonable.

In the present study, a linear relationship between SMR and temperature ($\mathrm{SMR} = aT + b$) outperformed the traditionally applied curvilinear relationship (Jobling 1994). As we did not measure waste products during the closed circuit intervals, we can not eliminate the possibility that accumulation of i.e. ammonia or $\mathrm{CO_2}$ influenced oxygen consumption. However, if measured oxygen consumption was significantly affected by accumulation of waste products, one would expect to see non-linear slopes of the oxygen consumption. This was not seen and there was no tendency towards increasingly non-linear relationships at high temperatures. Furthermore, SMR of buried *A. tobianus* at 10°C has previously been measured to 34.5 ($\pm$2.1, $n = 3$) and 36.0 ($\pm$3, $n = 3$) mg $\mathrm{O_2}$ $\mathrm{kg^{-1}}$ $\mathrm{h^{-1}}$ (Behrens et al. 2007), which is not far from the 39 mg $\mathrm{O_2}$ $\mathrm{kg^{-1}}$ $\mathrm{h^{-1}}$ obtained from our calculations (linear model at 10°C) and thus verifies the precision of the SMR measuring procedure applied.

Energy depletion in the VAL-1 validation experiment was slightly overestimated by the model. This may be due to the use of a metabolic size-scaling exponent of 0.8, which is a crude mean value for fish in general (Clarke and Johnston 1999). Metabolic exponents have been reported in the range from 0.65 to 0.9 (Jobling 1994; Clarke and Johnston 1999). An alternative explanation for the over-estimation may lie in the applied oxycaloric coefficient of 14 J $\mathrm{mg^{-1}}$ $\mathrm{O_2}$. The oxycaloric coefficient depends on the respiratory substrate and is slightly less for proteins than for lipids (Jobling 1994). Therefore, if the small sandeels used in VAL-1 utilised proteins as respiratory substrate to a larger degree than the larger sandeels in VAL-2 this would have caused the predicted energy depletion in VAL-1 to be slightly overestimated.

Estimates of L_{th} proved to be a useful way of studying the mechanisms underlying the physiological link between winter conditions and the timing of maturation and adoption of an overwintering behaviour. Furthermore, L_{th} may affect natural mortality rates. For example in years of poor growth conditions, part of the population may not reach L_{th}, which would either: (1) force the fish to turn to compensatory winter feeding activity, resulting in a prolonged exposure to predation, or (2) cause increased starvation mortality in the population. It is well established that timing and duration of annual increases in zooplankton production is tightly coupled to climate variability (e.g. Sharples et al. 2006), and population dynamics of fish are directly determined by parameters such as mortality, growth rates, and size at maturation. Hence, our results suggest that L_{th} represents a physiological link between climatic variability and population dynamics of zooplanktivorous fishes, and may provide a useful way of predicting consequences of global warming scenarios.

While this work focused on the iteroparous and non-migratory *A. marinus*, other life history strategies have evolved in response to long winters, i.e. as exemplified by the Arctic semelparous migratory capelin (*Mallotus villosus*) (Behrens et al. 2006; Christiansen et al. 2008). The next step towards understanding the full implications of L_{th} could, therefore, be to explore alternative strategies in a framework of a fitness-based life-cycle optimality model (e.g. Fiksen and Carlotti 1998; Garvey et al. 2004).

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