Supplementary Material

Exploring the influence of food and temperature on North Sea sandeels using a new dynamic energy budget model

Alan MacDonald[1]**, Douglas C. Speirs**[1]**, Simon P.R. Greenstreet**[2]**, Michael R. Heath**[1]

[1]Department of Mathematics & Statistics, University of Strathclyde, Glasgow, UK

[2]Marine Scotland Science, Marine Laboratory, Aberdeen, UK

***Correspondence:**
Alan MacDonald

Department of Mathematics & Statistics, University of Strathclyde, Glasgow, UK, alan.macdonald@strath.ac.uk

Keywords: growth$_1$, model$_2$, reserve$_3$, energy$_4$, *A. marinus*$_5$, energy$_6$, copepod$_7$

APPENDIX A

ESTIMATING THE EFFECT OF BODY SIZE AND TEMPERATURE ON SANDEEL METABOLISM

A. hexapterus respiration rate data is used to parameterize our model of metabolism (Quinn and Schneider, 1991). Our model requires data on body weight, temperature and oxygen consumption rates during summer and winter, which is only available for the closely related species, *A. hexapterus* (Quinn and Schneider, 1991).

The effect of body mass on *A. marinus* overwintering metabolism has not been quantified in the literature. However, Quinn and Schneider (1991) measured the respiration rates of *A. hexapterus* of different weights at 12ºC (Figure A5). The range of body weights is sufficient to estimate a scaling exponent for metabolism. A respiration rate model of the form: Respiration rate$(\mu l\ 0_2\ h^{-1}) = aw^r$ was fitted to *A. hexapterus* oxygen consumption data using non-linear least squares ($R^2 = 0.84$, $p<0.001$, Figure A5).

$$\text{Respiration rate}(\mu\text{l}\ 0_2\ \text{h}^{-1}) = 110.05w^{0.645} \tag{A1}$$

Quinn and Schneider (1991) estimated the effect of temperature on feeding and overwintering *A. hexapterus*. The Q10 for feeding and overwintering *A. hexapterus* is 1.8 and 1.46, respectively (Quinn and Schneider, 1991). We reviewed Q10s for metabolism in other fish, which show species typically have a Q10 close to 2 (Clarke and Johnston, 1999).

ESTIMATING $\mathbf{M_f}$ and $\mathbf{M_o}$

The response of metabolism to temperature and body size has been estimated. The final step in deriving equations for metabolism is to estimate the metabolic cost rate scales M_f and M_o (equations A49 & A56 in Appendix F). Estimating these coefficients requires data on body weight, temperature and oxygen consumption rates. Oxygen consumption data for summer and winter acclimatized *A. hexapterus* is used (Table A1). First, oxygen consumption rates OCR (μl 0_2 $g^{-1}\mathrm{h}^{-1}$) are converted into energy depletion rates E (kJ d^{-1}) Thus,

$$E = 24 * 10^{-6} * A * B * w * OCR \tag{A2}$$

$$E = 24 * 10^{-6} * 1.43 * 14 * 3 * OCR$$

$$E = 0.00144 * OCR$$

where A is the number of grams of oxygen gas required to make 1 litre of oxygen gas, B is a general oxycaloric coefficient (J mg^{-1}) (van Deurs et al., 2011), w is the wet weight of animals in respiration experiments (g) and OCR is oxygen consumption rate (μl 0_2 $\mathrm{g}^{-1}\mathrm{h}^{-1}$). Derived energy depletion rates are shown in (Table A1).

Thus, to calculate the summer metabolic cost rate M_f, nonlinear regression is used to solve

$$M_{feed} = M_f \; 1.8^{T/10} \; 3^{0.645} \tag{A3}$$

with summer energy depletion rates (M_{feed}) given in Table A1. Equation A3 represents the standard metabolic rate of feeding sandeels, since the animals in the respiration experiments were completely inactive (Quinn and Schneider, 1991).

The winter metabolic cost rate M_o is calculated in a similar way

$$\mathrm{M_{ov}} = \mathrm{M_o}\ 1.46^{T/10}\ 3^{0.645} \tag{A4}$$

with winter energy depletion rates (M_{ov}) given in Table A1. Modelled metabolic costs of summer and winter acclimatised animals at 12ºC are illustrated in Figure A6.

TABLE. A1. Laboratory derived *A. hexapterus* oxygen consumption rates ($\mu\mathrm{l}\ \mathrm{O_2}\ \mathrm{g^{-1}}\ \mathrm{h^{-1}}$) (from Quinn and Schneider, 1991) and modelled energy depletion rates ($\mathrm{kJ\ d^{-1}}$) (this study) according to season and temperature. Oxygen consumption rates are adjusted to a standard body weight of 3 g.

Season	Temperature (ºC)	Oxygen Consumption ($\mu\mathrm{l}\ \mathrm{O_2}\ \mathrm{g^{-1}}\ \mathrm{h^{-1}}$)	Energy depletion rate ($\mathrm{kJ\ d^{-1}}$)
Summer	5	38.4	0.0553
	12	57.9	0.0834
Winter	5	29.3	0.0422
	12	38.3	0.0552

APPENDIX B

INGESTION

Body size has a critical influence on ingestion rate. Larger sandeels swim faster than smaller individuals and so encounter more prey items. Further, the guts of larger individuals can hold more prey items than smaller sandeels. All of this is represented by S^q in equation A5. Temperature also increases ingestion rate ($Q_{10,U}^{T/10}$ in equation A5). We assume ingestion rate follows a type III response. Ingestion rate (kJ day^{-1}) during a search time (t_S, days) is

$$I = (a_L\, t_S n_L^2 E_L^2 + a_S\, t_S n_S^2 E_S^2 + a_B\, t_S n_B^2 E_B^2) S^q Q_{10,U}^{T/10} \tag{A5}$$

where a_L, a_S and a_B are attack rates ($\frac{1}{kJ^q \text{ days}}$), n_L, n_S and n_B are the number of prey and E_L, E_S and E_B is prey energy (kJ).

No quantitative information exists on the effect of sandeel body size on search rate, so the choice of scaling exponent is tricky. A common theoretical assumption is that search rate should scale with the surface area of the individual. A scaling of $q = 2/3$ is adopted, a value commonly found for fish species.

Search time t_S is found by subtracting the total time handling prey (days) from the total time foraging (days)

$$t_S = P_d - (a_L t_S n_L^2 h_L + a_S t_S n_S^2 h_S + a_B t_S n_B^2 h_B) S^q \tag{A6}$$

Rearranging for t_S,

$$t_S = \frac{P_d}{1 + (a_L n_L^2 h_L + a_S\, n_S^2 h_S + a_B n_B^2 h_B) S^q Q_{10,U}^{T/10}} \tag{A7}$$

Writing prey energy concentration as $F_i = n_i E_i$, we see that ingestion rate (kJ day^{-1}) is

$$I = P_d \frac{(a_L F_L^2 + a_S F_S^2 + a_B F_B^2) S^q Q_{10,U}^{T/10}}{1 + (a_L n_L^2 h_L + a_S\, n_S^2 h_S + a_B n_B^2 h_B) S^q Q_{10,U}^{T/10}} \tag{A8}$$

One might expect the two handling times to be different since adult *Calanus* are an order of magnitude larger than adult calanoid copepods of other species. Modelled handling time will likely increase with increasing copepod weight and energy. Handling time in our model is positively related to copepod weight and energy. Hence, $h_i = \phi\, w_i\, E_i = \phi \frac{E_i^2}{Ed_i}$ where ϕ is a variable.

$$I = P_d \frac{(a_L F_L^2 + a_S F_S^2 + a_B F_B^2) S^q Q_{10,U}^{T/10}}{1 + \left(a_L n_L^2 \phi \frac{E_L^2}{Ed_L} + a_S\, n_S^2 \phi \frac{E_S^2}{Ed_S} + a_B n_B^2 \phi \frac{E_B^2}{Ed_B} \right) S^q Q_{10,U}^{T/10}} \tag{A9}$$

Thus,

$$I = P_d \frac{\frac{1}{\phi} (a_L F_L^2 + a_S F_S^2 + a_B F_B^2) S^q Q_{10,U}^{T/10}}{\frac{1}{\phi} + \left(\frac{a_L F_L^2}{Ed_L} + \frac{a_S F_S^2}{Ed_S} + \frac{a_B F_B^2}{Ed_B} \right) S^q Q_{10,U}^{T/10}} \tag{A10}$$

We assume a constant concentration of other prey F_B. Therefore, $a_B F_B^2 = B$.

Assuming that maximum ingestion rate (I_{max}) is reached for extremely large prey concentrations,

$$\frac{E_d P_d}{\phi} = I_{max} \tag{A11}$$

where prey energy density E_d is

$$E_d = \frac{Ed_L\, a_L\, F_L^2 + Ed_S\, a_S\, F_S^2 + Ed_B\, B}{a_L\, F_L^2 + \ a_S\, F_S^2 + B} \tag{A12}$$

$$I = P_d \frac{\frac{I_{max}}{E_d P_d} (a_L F_L^2 + a_S F_S^2 + B) S^q Q_{10,U}^{T/10}}{\frac{I_{max}}{E_d P_d} + \left(\frac{a_L F_L^2}{Ed_L} + \frac{a_S F_S^2}{Ed_S} + \frac{a_B F_B^2}{Ed_B} \right) S^q Q_{10,U}^{T/10}} \tag{A13}$$

Three biological factors determine sandeel maximum ingestion rate. These are the rate at which food leaves the stomach (referred to as the digestion rate), the maximum stomach capacity, and the reserve ratio. The latter influences maximum ingestion rate because sandeels appear to increase their consumption rates if condition falls below a threshold value. Referred to as compensatory growth, this phenomenon is an adaptation to highly variable food availability, and has been demonstrated in a number of species (Christensen and McLean, 1998; Jobling and Johansen, 1999; Xie, 2001). The fact that sandeels grow very rapidly over a extremely short time after emerging from the overwintering period suggests a compensatory growth response.

Hence, maximum ingestion rate can be expressed in terms of a digestion rate Q (day^{-1}), maximum stomach weight SW_{max}(g), and function of reserve ratio $\Lambda\ (\rho)$

$$I_{max} = P_d\ \Lambda\ (\rho)\ Q\ SW_{max} \tag{A14}$$

Where

$$\Lambda = \begin{cases} \lambda, if\ \rho < \tau \\ 1, \text{otherwise} \end{cases} \tag{A15}$$

Hence, sandeels increase their maximum ingestion rate if the reserve ratio falls below a critical threshold τ. This threshold, referred to as the 'hungry threshold', is treated as a fitting parameter (see Appendix D). When this happens, maximum ingestion rate is multiplied by a term λ. Hence, the maximum ingestion rate of a sandeel with reserve ratio less than τ is therefore greater than that of a sandeel with identical structural weight and reserve ratio greater than τ. Note that τ is

Digestion rate is a function of temperature T (ºC) and prey energy density Ed (kJ (g WW)$^{-1}$).

From van Deurs et al. (2015), sandeel digestion rate Q (day^{-1}) is

$$Q = \frac{3.696}{E_d} e^{0.054\,T} \tag{A16}$$

It should be noted this is the gastric evacuation rate and not the true digestion rate. However, both rates should be similar due to sandeel's ability to rapidly digest prey (Christensen, 2010).

Using data on the relationship between length and maximum stomach weight (Figure A7), estimated from supplementary material in Van Deurs et al. (2010),

$$SW_{max}(g) = 0.000436\ L^3 \tag{A17}$$

The maximum energy ingested is found my multiplying maximum stomach weight (g) by prey energy density E_d

$$SW_{max}(kJ) = 0.000436\ E_d\ L^3 \tag{A18}$$

Next, length is expressed in terms of structural energy (see Appendix C),

$$SW_{max}(kJ) = 0.000436\ E_d \left(\frac{S}{0.00465}\right) \tag{A19}$$

$$SW_{max}(kJ) = 0.0937\ E_d\ S$$

$$I_{max} = \mathrm{P_d}\, \Lambda(\rho)\, Q\, SW_{max} \tag{A20}$$

$$I_{max} = \mathrm{P_d}\, \Lambda(\rho)\, \frac{3.696}{E_d}\, e^{0.054\,T}\, 0.0937\, E_d\, S$$

$$I_{max} = \mathrm{P_d}\, \Lambda(\rho)\, 0.346\, e^{0.054\,T} S$$

The temperature effect term $e^{0.054\,T}$ is rewritten as $Q_{10,U}^{T/10}$. Hence, maximum ingestion rate (kJ d^{-1}) is expressed as

$$I_{max} = P_d\, \Lambda(\rho)\, 0.346\, 1.72^{T/10} S \tag{A21}$$

Therefore, Ingestion rate is written as

$$I = P_d \frac{\frac{0.346\ \Lambda(\rho)}{E_d}\left(a_L F_L^2 + a_S F_S^2 + B\right)}{\frac{0.346\ \Lambda(\rho)\ S^{1-q}}{E_d} + \left(\frac{a_L F_L^2}{Ed_L} + \frac{a_S F_S^2}{Ed_S} + \frac{a_B F_B^2}{Ed_B}\right)}\ 1.72^{T/10} S \tag{A22}$$

APPENDIX C

THE RELATION OF STRUCTURE AND RESERVE ENERGY TO LENGTH AND WEIGHT

The model is run using reserve and structural energy of 0-group and age 1 fish in summer as initial conditions. Each cohort consists of a group of individuals, each characterized by a unique structural and reserve energy, and abundance. Sandeel energy data is required to fit our model and estimate unknown parameters. Ideally, this test data would be field measurements of sandeel energy content between 2000 and 2008 in our study area (Figure 1). Unfortunately these data are not available, so a different approach is needed. First, structural, reserve and gonad energy content is related to length and weight using empirically derived relationships. The model is then validated against sandeel length and weight. Estimates of sandeel length and weight were derived from Firth of Forth field data.

First, length and weight of individual sandeels was estimated (Figures A3). This was carried out using the following method: For each survey, probability distributions of ages for each 5 mm length class were estimated using the continuation-ratio logit method (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). Changes in distribution of age at a given length, as a function of length, were estimated using Generalized Linear Modelling. Fitting was performed using Maximum Likelihood code (Stari et al., 2010) developed for the R statistical environment (R development Core Team, 2014). The resultant probability matrices of age-given-length were multiplied by abundance-at-length to give matrices of abundanceat- age-and-length. That is, for a given age and cohort, each length carried an associated abundance. The next step was to associate a weight with each individual. For each cohort, otolith data was used to estimate the probability of weight given age and length.

Reserve, structural and gonad energy is converted into wet weight using two steps. First, R, S and G are converted to dry weight using dry weight energy densities. Then, reserve, structural and gonad dry weight is converted into wet weight using conversion factors.

$$W = \frac{R_{dry}}{E_r} R + \frac{S_{dry}}{E_s} S + \frac{G_{dry}}{E_g} G \tag{A23}$$

R_{dry}, $S_{dry}$and G_{dry} is the ratio of wet weight to dry weight for reserve, structural and gonad tissue. E_r, E_s, E_g are energy densities for reserve, structural and gonad dry weight. By definition, structure cannot decrease. Consequently, structure is a proxy for length. Several DEB models (Broekhuizen et al., 1994; Jones et al., 2002) assume this relationship takes the form:

$$L = \left(\frac{S}{\alpha}\right)^{1/\beta} \tag{A24}$$

where α and β are the length-structure scale and the length-structure exponent, respectively. Modelled sandeels are assumed to be isomorphic so they retain the same shape as they grow. Thus, $\beta = 3$ in equation A24. Isomorphism is common assumption in DEB models, having been assumed for countless species (Kooijman, 2010). Wet weight can be separated into 2 components: water (w) and dry weight DW. Dry weight can be broken down further into reserve dry weight (R_{dry}), structural dry weight (S_{dry}) and gonad dry weight (G_{dry})

$$\begin{aligned} W &= w + DW \\ &= w + R_{dry} + S_{dry} + G_{dry} \\ &= w + \frac{R}{E_r} + \frac{S}{E_s} + \frac{G}{E_g} \end{aligned} \tag{A25}$$

The ultimate aim is to rewrite equation A25 purely in terms of reserve, structural and gonad energy. Thus, water weight must be expressed in terms of energy, and the energy densities of reserve, structural and gonad dry weight have to be determined. To aid the estimation of parameters, let us imagine an immature sandeel, i.e. $G_{dry} = 0$.

$$W = w + R_{dry} + S_{dry} \tag{A26}$$

Sandeel dry weight is composed almost entirely of fat, protein and ash. However, the contribution of these three elements to reserve, structure and gonad tissue is likely to vary. Reserves, the parts that a sandeel will use to burn energy will likely contain a higher fat content than structural tissue, which is primarily comprised of skeletal tissue and organs. The first step in doing this is to express water weight (w) in terms of reserve dry weight (R_{dry}). This is done by assuming that R_{dry} is proportional to sandeel fat weight F. Then fat is expressed as a function of wet weight.

Sandeels accumulate a considerable amount of fat prior to the overwintering period, suggesting fat is a critical part of reserve energy (Winslade, 1974). Reserve energy is assumed to be proportional to fat content. Hence,

$$F = a\, R_{dry} \tag{A27}$$

Fat replaces water between April and August; fat content declines once sandeels begin overwintering in August (Hislop et al., 1991). Fat and water content are inextricably linked in pelagic fish (Iles and Wood, 1965; Wallace and Hulme, 1977; Dubreuil and Petitgas, 2009). There is a significant relationship between sandeel fat and water content (Fat content (% wet weight) = - 0.777 x Water content (% wet weight) + 64.094, $R^2 = 0.9$, N = 143, P < 0.001, Hislop et al., 1991). Combining this relationship with the assumption that reserve weight is proportional to fat content, water content is expressed as

$$w = 0.825\, W - 1.287\, F \tag{A28}$$

$$w = 0.825\, W - 1.287\, a\, R_{dry}$$

where $\gamma = 0.825$ is the maximum proportion of water in a sandeel and b = 1.287 is the water weight lost (g) when a sandeel gains a gram of fat.

Substituting this into equation A25 yields

$$W = 0.825\, W - 1.287\, a\, R_{dry} + R_{dry} + S_{dry} \tag{A29}$$

The minimum possible weight of an immature individual is structural dry weight (S_{dry}) and water. Setting R_{dry} to be zero in equation A29 yields a minimum wet weight in terms of structural dry weight

$$W_{min} = 5.711\, S_{dry} \tag{A30}$$

The corollary is that the proportion of water in a sandeel cannot exceed 83 percent. Equation A29 can be rewritten as

$$W = 0.825\,W - 1.287\,a\,R_{dry} + R_{dry} + \alpha L^3 \tag{A31}$$

Now, the wet weight of a sandeel can be written as

$$W = 5.711\big((DW - \alpha L^3)(1 - 1.287a) + \alpha L^3\big) \tag{A32}$$

Sandeel energy content is determined by fat and protein. Fat and protein have energy densities of 39.6 and 23.7 kJ g^{-1}, respectively (Crisp, 1971). Using these values for energy density of fat (g) and protein (g) the energy content (kJ) of a sandeel can be written as

$$E = 39.6\,Fat + 23.7\,Protein \tag{A33}$$

$$E = 39.6\,a\,R_{dry} + 23.7\,(R_{dry} + S_{dry} - a\,R_{dry} - Ash)$$

Now, ash content is related to reserve energy, structural energy and wet weight. *A.hexapterus* data is used to relate ash dry weight to water content (Figure A8).

There is a strong linear relationship between the percentage of ash in dry weight and percentage of water in wet weight (Equation A34).

$$Ash\ (\%\ DW) = -49.778\,DW + 0.808\,w\ (\%\ WW) \tag{A34}$$

Hence, ash (g) is written as

$$Ash = -0.498\, DW + 0.808 \frac{w}{W} DW \tag{A35}$$

where ash_x= 0.498 and ash_y= 0.808. Using this information in equation A33, the energy content of a sandeel is written as

$$\begin{aligned} E &= 39.6\, a\, R_{dry} + 23.7(R_{dry} + S_{dry} - a\, R_{dry} - Ash) \qquad \text{(A36)} \\ &= 39.6\, a\, R_{dry} + 23.7\, \left(DW - a\, R_{dry} - \left(-0.498\, DW + 0.808\, \frac{w}{W} DW\right)\right) \\ &= 39.6\, a\, R_{dry} + 23.7\, \Bigg(R_{dry} + S_{dry} - a\, R_{dry} \\ &\qquad - \Bigg(-0.498\, (R_{dry} + S_{dry}) \\ &\qquad + 0.808 \left(\frac{0.825\, W - 1.287\, a\, R_{dry}}{W} \right) (R_{dry} + S_{dry}) \Bigg) \Bigg) \end{aligned}$$

Empirical data is used to estimate unknown parameters a and α in equations A32 and A36. Doing this requires information on sandeel dry weight, wet weight, length and energy content. This collection of data is available for *A. marinus* (Appendix I, Hislop et al., 1991), however, it is not suitable for our purpose. There are two reasons for this. First, length was grouped into .5 cm classes, which is too imprecise. Second, estimates are mean values of a group of individuals, not a single individual. Fortunately, higher precision data is available from experiments on *A. tobianus* energy content (Figure A9). Values for a and α are found by minimising the overall square relative error between predicted and observed energy content (kJ) and wet weight (g). Figure A10 illustrates the quality of fits to energy and weight data. Finally, wet weight (g) is obtained in terms of R_{dry} and S_{dry},

$$W = 3\, R_{dry} + 5.7\, S_{dry} \tag{A37}$$

Hence, every gram of reserve dry weight represents 3 grams of wet weight. Similarly, every gram of structural dry weight represents 5.7 grams of wet weight. Length is written as a function of structural weight,

$$L = 5.989\, S^{1/3} \tag{A38}$$

Total energy content (kJ) of a sandeel is obtained in terms of R_{dry} and S_{dry},

$$E = \left(25.6 + 9.14\left(\frac{R_{dry} + S_{dry}}{W}\right)\right)R_{dry} + 19.7\, S_{dry} \tag{A39}$$

Note the $R_{dry}\, S_{dry}$ term is grouped into reserve energy, since the energy density of structure is assumed to be fixed. Thus, the estimated structural energy density is 19.7 kJ g^{-1}, which assuming little fat content, and negligible mineral mass, is 17% ash and 83% protein. Note that reserve energy density E_r is dependent on the ratio of dry weight to wet weight, i.e. sandeels with a high water content will have less energy per unit gram in the reserve mass.

APPENDIX D

TABLE. A2. Model parameters. Where possible, parameters where either taken or derived from the literature. Many model equations have parameters that can be estimated using empirical data from the literature. These are referred to as ‘derived’. For example, the metabolic rate exponent r is estimated using data on oxygen consumption rates of animals of different weights in Quinn and Schneider (1991). ‘Chosen’ parameters were assigned appropriately based on knowledge of sandeel biology and ecology. For example, the overwintering end date is April 1st based on observations that sandeels end overwintering between March and the end of April (Reeves, 1994). A sensitivity analysis showed that uncertainty in the chosen parameters where no information exists in the literature (e.g. G_{dry}) does not have a significant effect on model results. Remaining parameters were found by selecting the set of parameters (Ω) that minimized the error between observed and modeled length, weight, reserve ratio and abundance at survey date.

Parameter	Description	Value	Units	Source	Species
Conversion factors					
R_{dry}	Reserve dry to wet weight conversion factor	2.99	g WW g DW^{-1}	Derived	*A.marinus, A.hexapterus, A.tobianus*
S_{dry}	Structure dry to wet weight conversion factor	5.71	g WW g DW^{-1}	Derived	*A.marinus, A.hexapterus, A.tobianus*
G_{dry}	Gonad dry to wet weight conversion factor	5.71	g WW g DW^{-1}	Chosen	—
β	Length-structure exponent	3	—	Kooijman (2010)	—
α	Length-structure scale	0.000236	g cm$^{-\beta}$	Derived	*A.marinus, A.hexapterus, A.tobianus*
Energy densities					
E_f	Energy density of fat	39.6	kJ g^{-1}	Crisp (1971)	—
E_p	Energy density of protein	23.7	kJ g^{-1}	Crisp (1971)	—
E_r	Reserve energy density	28	kJ g^{-1}	Derived	*A.marinus, A.hexapterus, A.tobianus*
E_s	Structure energy density	19.7	kJ g^{-1}	Derived	*A.marinus, A.hexapterus, A.tobianus*

E_g	Gonad energy density	19.7	kJ g^{-1}	Chosen	
Ed_L	Large copepod energy density	5.6	kJ g^{-1}	van Deurs et al. (2015)	
Ed_S	Small copepod energy density	3.2	kJ g^{-1}	van Deurs et al. (2015)	
Feeding					
ϵ	Assimilation efficiency	0.82 + 0.0076 T	—	Gilman (1994)	*A .dubius*
p	Maximum ingestion rate exponent	1	—	Derived	*A. tobianus*
q	Search rate exponent	0.67	—	Chosen	—
$Q_{10,U}$	Ingestion rate Q10	1.72	—	Derived	*A. tobianus*
I_0	Ingestion scale	0.346	$\text{kJ}^{1-p}\ \text{d}^{-1}$	Derived	*A. tobianus*
λ	Hungry ingestion scaling factor	2	—	Miglavs and Jobling (1989)	Arctic charr *Salvelinus alpinus*
τ	Hungry threshold	3.99	—	Fitted	—
a_L	Large copepod encounter rate	3.0434	$\text{kJ}^{-\text{q}}\ \text{days}^{-1}$	Fitted	—
a_S	Small copepod encounter rate	0.5340152	$\text{kJ}^{-\text{q}}\ \text{days}^{-1}$	Fitted	—
B	Other prey	0.1468888	$\frac{\text{kJ}^2\ \text{m}^{-6}}{\text{kJ}^{\text{q}}\ \text{days}}$	Fitted	—
E_B	Other prey energy density	4.352669	kJ g^{-1}	Fitted	—
Metabolism					
$Q_{10,Mo}$	Q10 for winter metabolism	1.46	—	Quinn and Schneider (1991)	*A.hexapterus*
$Q_{10,Mf}$	Q10 for summer metabolism	1.8	—	Quinn and Schneider (1991)	*A.hexapterus*
r	Metabolic rate exponent	0.645	—	Derived from Quinn and Schneider (1991)	*A.hexapterus*
M_o	Overwinter metabolic cost rate scale	0.01722		Derived from Quinn and Schneider (1991)	*A.hexapterus*
M_f	Summer metabolic cost rate scale	0.02025882		Derived from Quinn and Schneider (1991)	*A.hexapterus*
Overwintering					

OV_1	Overwinter threshold parameter	25.81315		Fitted	—
OV_2	Overwinter threshold parameter	0.1067149		Fitted	—
OV_3	Overwinter threshold parameter	0.2508339		Fitted	—
OV_{END}	Julian day of overwintering exit	92	—	Chosen	—
Survival					
σ_1	Survival parameter 1	18.98968	—	Fitted	—
σ_2	Survival parameter 2	0.6978547	—	Fitted	—
Allocation					
S_1	Structural allocation constant	86.91716	—	Fitted	—
S_2	Structural allocation exponent	18.04641	—	Fitted	—
G_1	Gonadal allocation constant	-4.846421	—	Fitted	—
G_2	Gonadal allocation exponent	16.60141	—	Fitted	—
ρ_ω	Allocation switch width	1127.035	—	Fitted	—
ρ_0	Defended reserve ratio	0.9303551	—	Fitted	—
Fat					
γ	Maximum proportion of water (wet weight)	0.825	—	Derived	*A.marinus*
b	Water lost (g) for every gram of fat	1.287	—	Derived	*A.marinus*
a	Proportion of reserves that are fat	0.371	—	Derived	*A.marinus, A.hexapterus, A.tobianus*
Ash					
ash_x	Ash parameter 1	0.498	—	Derived	*A. hexapterus*
ash_y	Ash parameter 2	0.808	—	Derived	*A. hexapterus*
Abundance					
$N_{0,2000}$	0-group abundance in 2000	$10^{11.667022}$	—	Fitted	—
$N_{0,2001}$	0-group abundance in 2001	$10^{11.250303}$	—	Fitted	—

$N_{0,2002}$	0-group abundance in 2002	$10^{11.397335}$	—	Fitted	—
$N_{0,2003}$	0-group abundance in 2003	$10^{10.315859}$	—	Fitted	—
$N_{0,2005}$	0-group abundance in 2005	$10^{11.727198}$	—	Fitted	—
$N_{0,2006}$	0-group abundance in 2006	$10^{11.850109}$	—	Fitted	—
μ_{2000}	daily (annual) survival rate for 2000 cohort	0.9957 (0.2088)	day^{-1}	Fitted	—
μ_{2001}	daily (annual) survival rate for 2001 cohort	0.9973 (0.3693)	day^{-1}	Fitted	—
μ_{2002}	daily (annual) survival rate for 2002 cohort	0.9963 (0.25959)	day^{-1}	Fitted	—
μ_{2003}	daily (annual) survival rate for 2003 cohort	0.9966 (0.2856)	day^{-1}	Fitted	—
μ_{2005}	daily (annual) survival rate for 2005 cohort	0.9984 (0.56258)	day^{-1}	Fitted	—
μ_{2006}	daily (annual) survival rate for 2006 cohort	0.98595 (0.0057)	day^{-1}	Fitted	—

APPENDIX E

TABLE. A3. Length-weight relationships for *A. dubius, A. hexapterus, A. marinus, A. personatus* and *A. tobianus* of the form $W = a\,L^b$.

Species	a	b	Month	Year	Location	5 cm	10 cm	15 cm	20 cm	Source
A. dubius	0.005420	2.72	Spring	1986-1988	Gulf of Maine	0.43	2.86	8.62	18.85	Nelson and Ross (1991)
	0.002999163	2.93	Spring		Georges bank (spring)	0.33	2.55	8.35	19.40	
	0.0008830798	3.39	Summer		Georges bank (summer)	0.21	2.17	8.57	22.72	
	0.0012705740	3.26	Autumn		Georges bank (autumn)	0.24	2.32	8.69	22.22	
	0.0059292550	2.66	Spring		Southern New England (spring)	0.43	2.74	8.06	17.34	
	0.0011830420	3.30	Spring		Middle Atlantic (spring)	0.24	2.37	9.02	23.32	

	0.0007852356	3.50	Autumn		Middle Atlantic (autumn)	0.22	2.49	10.32	28.26	
A. hexapterus	0.0021379620	3.17	June	1996,1997	Alaska	0.35	3.16	11.43	28.46	Robards et al. (1999)
	0.0022387220	3.19	August			0.38	3.47	12.64	31.64	
	0.0063095720	2.72	October			0.50	3.31	9.98	21.82	
A. marinus	0.0026266027	3.09	June	2000	Firth of Forth	0.38	3.24	11.35	27.63	This work
	0.0018783011	3.07	March	2001		0.26	2.19	7.57	18.29	
	0.0041648881	2.90	June	2001		0.44	3.31	10.74	24.74	
	0.0008568574	3.46	October	2001		0.22	2.47	10.04	27.17	
	0.0018336215	3.06	March	2002		0.25	2.11	7.28	17.56	
	0.0014626338	3.31	June	2002		0.30	3.01	11.54	29.95	
	0.0010593220	3.38	October	2002		0.25	2.56	10.09	26.71	

	0.0017268847	3.10	March	2003		0.25	2.19	7.69	18.77	
	0.0024661197	3.10	June	2003		0.36	3.08	10.81	26.35	
	0.0014812690	3.25	October	2003		0.28	2.65	9.89	25.20	
	0.0019965780	3.04	March	2004		0.27	2.21	7.59	18.22	
	0.0017412346	3.17	September	2004		0.29	2.60	9.43	23.51	
	0.0009975049	3.38	November	2010		0.23	2.40	9.46	25.03	
	0.0029508268	2.90	March	2011		0.31	2.33	7.55	17.37	
	0.0042000000	2.87	NA	NA	Shetland	0.43	3.14	10.05	22.97	Baistrocchi (2003)
	0.0012000000	3.32	NA	NA	SpeyBay	0.25	2.52	9.71	25.26	
	0.0020000000	3.11	NA	NA	WeeBankie	0.30	2.59	9.17	22.45	
	0.0014860000	3.18	April	2007	Faroe Islands	0.25	2.25	8.19	20.45	Eliasen (2013)
	0.002379000	3.09		2008		0.34	2.92	10.23	24.89	

	0									
	0.0015380000	3.22		2009		0.27	2.54	9.35	23.60	
	0.0017710000	3.09		2010		0.25	2.16	7.53	18.30	
A. personatus	0.0024220000	3.23			Ise Bay, Japan	0.44	4.11	15.24	38.59	Tomiyama and Yanagibashi (2004)
A. tobianus	0.0001472000	4.21			Laboratory acclimatised (caught in North Sea)	0.13	2.41	13.30	44.69	Unpublished data (Van Deurs, 2011)

APPENDIX F

TECHNICAL DESCRIPTION

State variables

The model described in this paper is a group of 3 nonlinear ODEs used to model length, weight and energy dynamics of individual sandeels. The model is fitted to length and weight observations of sandeels off the Scottish east coast between 2000 and 2008 (56^{o} 00N and 56^{o} 30N and longitudes 003^{o} 00W and 001^{o} 00W, Figure 1). Only postmetamorphic sandeels are modelled; egg and larval stages are omitted. Each individual is grouped according to reserve, structural and gonad energy, overwintering status (whether they are overwintering or feeding) and maturity status. Model ODEs are solved using the Euler method with discrete daily time steps. We use deep and surface models to describe the energy dynamics of overwintering and feeding sandeels, respectively.

Model ODEs

Only postmetamorphic sandeels are modelled; egg and larval stages are omitted. The model is split into two post larval components, immature and mature sandeels. Individuals are modelled in terms of structural mass, reserve mass and gonad mass. Sandeels incur two types of mortality in our model – starvation and background. The former occurs when sandeels exhaust energy reserves while the latter covers all causes of mortality except starvation.

A key model assumption is that sandeel energy is largely comprised of reserve energy, structural energy and gonad energy. First, sandeels mobilize energy reserves to survive a long overwintering period, suggesting reserves are a key component (Winslade, 1974; van Deurs et al., 2011). Second, sandeel gonads constitute approximately a third of total body mass, suggesting considerable energy in gonad formation (Gauld and Hutcheon, 1990). Last, structure represents the skeleton among other vital parts, which form a large part of the body.

An important concept in the model is energy allocation. Allocation to structure is length-dependent due to the different energy dynamics of small and large sandeels, which prioritize growth and gonad production, respectively. The aim of the model is to model energy dynamics of sandeel cohorts. The abundance of different size classes of age 0 and age 1 individuals can be estimated (see methods). Therefore, the decision was made to begin model simulations using these field estimates of energy content and abundance. Tracking changes in individual energy content and the distribution across cohorts will therefore be informative of the influence of environmental drivers. This model was then parameterised and tested using field data (see section on 'Parameter estimation and model implementation'.).

Individual sandeels are modelled in terms of energy content of structure (S), reserves (R) and gonads (G), with kilojoules as a unit of energy. The rate of change of R, S and G is modelled separately using 3 ordinary differential equations.

The metabolic cost of sustaining the life of an individual is prioritised over growth and reproduction. Therefore, energy allocation to gonad and structure should only occur after metabolic costs are covered. This is modelled using the following assumptions: 1. All assimilated energy enters reserves. 2. Metabolic costs are subtracted from reserves. 3. Once metabolic costs have been paid a fraction of remaining assimilated energy is allocated to structure and gonads.

The rate of change of reserve energy is given by:

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} - \frac{dG}{dt} \tag{A40}$$

Where A is the rate at which an animal assimilates energy (kJ d^{-1}) and M is the rate at which animals lose energy to metabolism (kJ d^{-1}).

The rate of change of structural energy is given by:

$$\frac{dS}{dt} = C(\rho, S)\ [A - M]^{+} \tag{A41}$$

where ρ is the sandeel reserve ratio, $C(\rho, S)$ is the fraction of assimilated energy remaining after metabolism that is used to form structure and $[X]^{+}$denotes $max(0, X)$.

$C(\rho, S)$ takes the form:

$$C(\rho, S) = \begin{cases} f(S_1 - S_2\, log(S)), if\ \rho > \rho_0 + \rho_\omega \\ f\left(\dfrac{S_1 - S_2\, log(S)\,[\rho - \rho_0]^+}{\rho_\omega}\right) \text{ otherwise} \end{cases} \tag{A42}$$

where S_1 and S_2 are constants for the maximum proportion of energy allocated to structure, ρ_0 is the defended reserve ratio and ρ_ω is the allocation switch width. The function $f(\cdot)$ constrains energy allocation $C(\rho, S)$ between 0 and 1, thus $f(X) = max(0, min(1, X))$.

The rate of change of gonad energy is given by:

$$\frac{dG}{dt} = G(\rho, S)\, R \tag{A43}$$

where $G(\rho, S)$ is the fraction of reserve energy directed to gonads.

$G(\rho, S)$ takes the form:

$$G(\rho, S) = \begin{cases} f(G_1 + G_2\, log(S)), if\ \rho > \rho_0 + \rho_\omega \\ f\left(\dfrac{G_1 + G_2\, log(S)\,[\rho - \rho_0]^+}{\rho_\omega}\right), if\ \rho \leq \rho_0 + \rho_\omega \\ 0, \text{otherwise} \end{cases} \tag{A44}$$

where G_1 and G_2 are constants for the maximum proportion of energy allocated to gonads.

Overwintering timing

An individuals feeding/overwintering status OV_{state} is tracked by

$$OV_{state} = \begin{cases} 1, if \text{ overwintering} \\ 0, if \text{ feeding} \end{cases} \tag{A45}$$

If $OV_{state} = 0$, that is, animals are feeding, we check if the condition for overwintering is satisfied.

Modelled individuals begin overwintering once the reserve ratio $\frac{R}{S+G}$ exceeds a critical value OV_{thresh}.

$$OV_{thresh} = \frac{OV_1 - OV_2 d}{S^{OV_3}} \tag{A46}$$

where d is Julian day, OV_1 is the overwinter threshold intercept (kJ^{OV_3}), OV_2 is the overwinter threshold slope (kJ^{OV_3}d^{-1}) and OV_3 (> 0) is the overwinter threshold length-dependent exponent.

The term S^{OV_3} in equation 46 reflects the need of smaller fish to attain a higher reserve ratio than larger fish before overwintering. OV_{thresh} is a decreasing function of time because the reserves necessary to begin overwintering in July exceed those required to begin overwintering in December.

If $OV_{state} = 1$, that is, animals are overwintering, we check if the condition for overwintering is satisfied

$$\mathrm{d} > OV_{END} \tag{A47}$$

where OV_{END} is the Julian day of the end of overwintering.

Deep model

Overwintering animals are inactive and so deplete energy at a rate equivalent to the standard metabolic rate. No structural allocation occurs, however some reserve energy is allocated towards forming gonads during a period of time.

$$\frac{dR}{dt} = -M - \frac{dG}{dt} \tag{A48}$$

$$\frac{dS}{dt} = 0$$

$$\frac{dG}{dt} = G(\rho, S)\ R$$

Metabolism

$$M_{ov} = \text{standard metabolic rate} \tag{A49}$$

$$M_{ov} = M_o Q_{10,M_o}^{T/10} w^r$$

$$M_{ov} = M_o\ Q_{10,M_o}^{T/10}\ (\frac{R_{dry}}{E_R}R + \frac{S_{dry}}{E_S}S + \frac{G_{dry}}{E_G}G)^r$$

where M_o is the metabolic cost rate scale in winter (kJ $g^r d^{-1}$) and $Q_{10,M_f}^{T/10}$ is the Q10 for winter metabolism.

Conservation of mass

To conserve mass we update equations representing energy densities and dry-wet ratios.

The reserve dry weight DW_R (g) is

$$DW_R = \frac{R}{E_R^*} - \frac{1}{E_G}\frac{dG}{dt} \tag{A50}$$

We update the dynamical equations governing reserve and gonad energy (equation 48).

The new reserve energy density E_R^* (kJ g^{-1}) is

$$E_R^* = \frac{R}{DW_R} \tag{A51}$$

and the new ratio of wet to dry reserve weight R_{dry}^* is

$$R_{dry}^* = \frac{W - \frac{G_{dry}}{E_G} G - \frac{S_{dry}}{E_S} S}{R / E_R^*} \tag{A52}$$

Gonad Allocation

Maturation occurs in July and a single batch of eggs is layed in winter (Bergstad et al., 2001; Boulcott et al., 2007). *A.marinus* are capital breeders, meaning energy stores gained during the summer feeding period are used to form gonads (Macer, 1966; Boulcott and Wright, 2008). Modelled gonad energy allocation therefore begins on 1st November, since field data shows a substantial increase in gonad size after October (Bergstad et al., 2001). Gonad formation efficiency is assumed to be 100%. $G(\rho, S)$ increases with length and the reserve ratio, reflecting the fact that larger fish invest more energy in gonad production (Figure A1). Mean spawning day in the northwestern North Sea between 2000 and 2009 is 21st January (MacDonald, 2017).

$G(\rho, S)$ takes the form:

$$G(\rho, S) = \begin{cases} f(G_1 + G_2\, log(S)), if\ \rho > \rho_0 + \rho_\omega \text{ and Date } = \text{ 1st November} \\ f\left(\frac{G_1 + G_2\, log(S)\, [\rho - \rho_0]^+}{\rho_\omega}\right), if\ \rho \le \rho_0 + \rho_\omega \text{ and Date } = \text{ 1st November} \\ 0, \text{otherwise} \end{cases} \tag{A53}$$

where G_1 and G_2 are constants for the maximum proportion of energy allocated to gonads.

Surface model

Feeding animals use assimilated food to build structure. No gonad allocation occurs during the feeding season.

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} \qquad \text{(A54)}$$

$$\frac{dS}{dt} = C(\rho, S)\ [A - M]^{+}$$

$$\frac{dG}{dt} = 0$$

Assimilation

Assimilation rate A (kJ d^{-1})is written as

$$A = \epsilon\, P_d \frac{\frac{\mathrm{I}_0\ \Lambda(\rho)}{E_d}\left(a_L F_L^2 + a_S F_S^2 + a_B F_B^2\right)}{\frac{\mathrm{I}_0\ \Lambda(\rho)\ S^{1-q}}{E_d} + \left(\frac{a_L F_L^2}{Ed_L} + \frac{a_S F_S^2}{Ed_S} + \frac{a_B F_B^2}{Ed_B}\right)}\ {Q_{10,U}}^{T/10} S \qquad \text{(A55)}$$

Where ϵ is assimilation efficiency, I_0 is the ingestion scale, ($\mathrm{kJ}^{1-p}\ \mathrm{d}^{-1}$), $\Lambda(\rho)$ is the starvation response factor, E_d is the average prey energy density (kJ g^{-1}), a_L, a_S and a_B are attack rates on large and small copepods and other prey, respectively ($\frac{1}{kJ^q\ \mathrm{days}}$), Ed_L, Ed_S and Ed_B are energy densities of large and small copepods, and other prey (kJ g^{-1}), q is the search rate exponent and $Q_{10,U}$ is the ingestion rate Q10.

Metabolism

Metabolism M (kJ d^{-1}) of feeding animals is the sum of standard metabolic rate and activity costs:

$$M_{feed} = \text{standard metabolic rate } + \text{ activity} \tag{A56}$$

$$M_{feed} = M_f Q_{10,M_f}^{T/10} w^r + P_d M_f Q_{10,M_f}^{T/10} w^r$$

$$M_{feed} = (1 + P_d)(M_f Q_{10,M_f}^{T/10} w^r)$$

$$M_{feed} = (1 + P_d)\left(M_f Q_{10,M_f}^{T/10} \left(\frac{R_{dry}}{E_R} R + \frac{S_{dry}}{E_S} S + \frac{G_{dry}}{E_G} G\right)^r\right)$$

where M_f is the metabolic cost rate scale during the feeding season (kJ $g^r d^{-1}$). $Q_{10,M_f}^{T/10}$ is the Q10 for feeding metabolism, r is the metabolic rate exponent. Parameter values are derived using experimental data (see Appendix A). The term P_d in equation 56 represents the proportion of the day with daylight. R_{dry}, $S_{dry}$and G_{dry} are dry-wet weight conversion factors for reserve, structural and gonad tissue. E_R, E_S And E_G are energy densities of reserve, structural and gonad dry tissue.

Structural allocation

Animals assimilate energy A (kJ) and lose M (kJ) to metabolism. We refer to the remaining energy $(A - M)$ as the net assimilation.

Individuals allocate a fraction $C(\rho, S)$ of net assimilation to structure.

$\mathrm{C}(\rho, \mathrm{S})$ takes the form:

$$C(\rho, S) = \begin{cases} f(S_1 - S_2\, log(S)), if\ \rho > \rho_0 + \rho_\omega \\ f\left(\dfrac{S_1 - S_2\, log(S)\,[\rho - \rho_0]^+}{\rho_\omega}\right) \text{ otherwise} \end{cases} \tag{A57}$$

where S_1 and S_2 are constants for the maximum proportion of energy allocated to structure, ρ_0 is the defended reserve ratio and ρ_ω is the allocation switch width. The function $f(\cdot)$ constrains energy allocation $C(\rho, S)$ between 0 and 1, thus $f(X) = max(0, min(1, X))$.

Conservation of mass

To conserve mass we update equations representing energy densities and dry-wet ratios.

We assume the new reserve dry weight DW_R(g) is

$$DW_R = \frac{1}{E_R^*}R + \frac{1}{E_R}\frac{dR}{dt} \tag{A58}$$

We then update the dynamical equations (equations 1,2 & 3).

The new reserve energy E_R^* (kJ g^{-1}) is written as

$$E_R^* = \frac{R}{DW_R} \tag{A59}$$

and the new ratio of wet to dry reserve weight is

$$R_{dry}^* = \frac{W - \frac{G_{dry}}{E_G}G - \frac{S_{dry}}{E_S}S}{R/E_R^*} \tag{A60}$$

Starvation mortality

Modelled sandeels incur condition-dependent starvation mortality. While a sandeel with no energy reserves is likely to suffer mortality, starvation may start to occur once the reserve ratio falls below a critical value. Starvation is regarded as a probabilistic process, so a given fraction of the population is removed. Hence the probability of a sandeel with reserve ratio ρ surviving starvation on any given day is

$$\xi_S = \frac{1}{1 + e^{-\sigma_1(\rho - \sigma_2)}} \tag{A61}$$

where σ_1 is the starvation response shape parameter and σ_2 represents the reserve ratio at 50% survival.

Natural mortality

Modelled sandeels incur a constant background mortality over their lifetime. We define the probability of an individual with reserve ratio ρ surviving background mortality on a given day by

$$\xi_N = \mu \tag{A62}$$

APPENDIX G

PARAMETER SENSITIVITY

A one-at-a-time sensitivity analysis was performed to determine the sensitivity of model parameters. This was done to determine what parameters are sensitive and to check if model robustness to changes in parameter values. To do this, each parameter was varied by 10% and changes in mean weight and starvation mortality of the 2000 cohort were tracked until immediately prior to spawning at age 4. Then, predicted cohort mean weight and starvation mortality was compared to modelled values at age 4. See table A2 for parameter details. Note that R_{dry}, S_{dry}, E_s and E_r are determined by γ, a, b, E_f, E_p, ash_x and ash_y and so are excluded from the sensitivity analysis.

Figures A11 and A12 illustrate that modelled sandeel growth and survival is most sensitive to the maximum proportion of water in a sandeel, the timing of overwintering entry and overwinter metabolism. Other parameters that have a demonstrable effect on growth and survival are ash_y, ϵ, β

and a. These parameters determine relationships between ash and water content, assimilation efficiency, length-structure exponent and the proportion of reserves that are fat, respectively. Note that an increase in weight does not necessarily translate to an increase in survival. For instance, a 10% decrease in the defended reserve ratio (ρ_0) increases weight but decreases survival. This is because when the reserve ratio threshold at which sandeels cease structural growth investment is lowered, individuals increase size but have inadequate reserves to survive winter.

APPENDIX H

Field data indicates postmetamophic sandeels feed primarily on the dominant calanoid copepods; *Calanus, Pseudocalanus, Temora, Centropages, Acartia, Paracalanus, Oithona and Microcalanus* (Macer, 1966; van Deurs et al., 2013, 2014, 2015), ignoring nauplii (van Deurs et al., 2013, 2014, 2015).

TABLE. A4. Energy content of large copepods. Prosome lengths (PL) of adult *C. finmarchicus* and *C. helgolandicus* were available from field data in Jonasdottir et al. (2005). C6 male *C. helgolandicus* PL was assumed to be equal to C6 female *C. helgolandicus* PL. Other prosome lengths were derived from using the relationship between temperature and PL for *C. finmarchicus* in Campbell et al. (2001), assuming a temperature of 10 ^{o}C, which is the 10-year average surface temperature from Stonehaven. Copepod energy content was estimated in the following way: First, copepod prosome length was converted to wet weight (van Deurs et al., 2015),

$$W_c = 5\left(\frac{10^{3.13\,log_{10}(1000\,PL)-8.18}}{10^6}\right) \tag{A63}$$

Next, wet weight was converted into energy content. This was done by multiplying wet weight by an energy density for large copepods. van Deurs et al. (2013) derived energy densities for large copepods (> 1.3 mm) from data on the monthly energy content of four North Sea copepod species in spring (Corner and O'Hara, 1986). An energy density of 5.6 kJ g^{-1} was assumed for large copepods.

Genus	Species	Stage	Length (mm)	Energy (J)
Calanus	*C. finmarchicus*	C6 Female	2.66	9.706
		C6 Male	2.61	9.146
		C5	2.33	6.412
	C. helgolandicus	C6 Female	2.53	8.297
		C6 Male	2.53	8.297
		C5	2.33	6.412
	Unidentified	C6 Female	2.6	9.037
		C6 Male	2.57	8.715
		C5	2.33	6.412
		C4	1.81	2.909

		C3	1.35	1.162

TABLE. A5. Energy content of small copepods. *Calanus* prosome lengths were derived from using the relationship between temperature and PL for *C. finmarchicus* in Campbell et al. (2001), assuming a temperature of 10 ^{o}C, which is the 10-year average surface temperature from Stonehaven. *Pseudocalanus* PL was taken from Lynch *et al*. (2001). *Temora* and *Centropages* PL was taken from Hirst et al. (1999). *Acartia* PL was taken from Leandro et al. (2006). *Paracalanus* PL was taken from Davis (1984). Due to the lack of *Oithona* and *Microcalanus* data, we assume a similar stage-specific energy content to *Centropages*. Copepod energy content was estimated in the following way: First, copepod prosome length was converted to wet weight (equation A63,van Deurs et al., 2015). Next, wet weight was converted into energy content. This was done by multiplying wet weight by an energy density for small copepods. van Deurs et al. (2013) derived an energy densitty for small copepods (< 1.3 mm) from data on the monthly energy content of four North Sea copepod species in spring (Corner and O'Hara, 1986). An energy density of 3.2 kJ g^{-1} was assumed for small copepods.

Genus	Species	Stage	Length (mm)	Energy (J)
Calanus	Unidentified	C2	1.04	0.293
		C1	0.74	0.101
Pseudocalanus	*Pseudocalanus minutus elongatus*	C6 Female	1	0.26
		C6 Male	1	0.26
		C5 Female	0.88	0.174
		C5 Male	0.88	0.174

		C4	0.73	0.097
		C3	0.62	0.05812
		C2	0.52	0.03351
		C1	0.42	0.01717
Temora	*Temora longicornis*	C6 Female	0.76	0.1099
		C6 Male	0.68	0.0776
		C5 Female	0.64	0.06419
		C5 Male	0.58	0.04717
		C5	0.61	0.05523
		C4	0.51	0.03154
		C3	0.44	0.01987
		C2	0.4	0.01474
		C1	0.34	0.008864
Centropages	*Centropages hamatus*	C5 Female	0.64	0.06419

		C6 Female	0.85	0.156
		C5 Male	0.68	0.0776
		C6 Male	0.8	0.1291
		C5	0.66	0.07068
		C4	0.55	0.03994
		C3	0.45	0.02131
		C2	0.37	0.01155
		C1	0.31	0.006639
	Centropages typicus	C6 Female	0.85	0.156
		C6 Male	0.8	0.1291
		C5	0.66	0.07068
		C4	0.55	0.03994
		C3	0.45	0.02131
		C2	0.37	0.01155

		C1	0.31	0.006639
Acartia	*Acartia clausii*	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
		C5 Female	0.79	0.1241
		C5 Male	0.77	0.1145
		C5	0.78	0.1192
		C4	0.66	0.07068
		C3	0.56	0.04226
		C2	0.46	0.02283
		C1	0.37	0.01155
	Acartia longiremis	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
	Acartia discaudata	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156

	Acartia bilosa	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
Paracalanus	*Paracalanus parvus*	C6 Female	0.74	0.1011
		C6 Male	0.74	0.1011
		C5 Female	0.62	0.05812
		C5 Male	0.62	0.05812
		C5	0.62	0.05812
		C4	0.52	0.03351
		C3	0.41	0.01593
		C2	0.36	0.0106
		C1	0.28	0.004828
Oithona		C6 Female		0.156
		C6 Male		0.1291
		C4,C5		0.05531

		C3		0.02131
		C2 C1		0.01155 0.006639
Microcalanus	*Microcalanus pusillus*	C6 Female		0.156
		C6 Male		0.1291
		C5		0.07068
		C4		0.03994
		C3		0.02131
		C2		0.01155
		C1		0.006639

REFERENCES

Baistrocchi, A. (2003). Modelling the spatial dynamics of sandeels in the western North Sea. M.Sc. thesis, University of Strathclyde, Glasgow, Scotland, UK.

Bergstad, O.A., Høines, Å.S., and Krüger-Johnsen, E.M. (2001). Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. *Aquatic Living Resources* 14, 293-301.

Boulcott, P., and Wright, P.J. (2008). Critical timing for reproductive allocation in a capital breeder: evidence from sandeels. *Aquatic Biology* 3, 31-40.

Boulcott, P., Wright, P.J., Gibb, F.M., Jensen, H., and, Gibb, I.M. (2007). Regional variation in maturation of sandeels in the North Sea. *ICES Journal of Marine Science* 64, 369-376.

Broekhuizen, N., Gurney, W.S.C., Jones, A. and Bryant, A.D. (1994). Modelling compensatory growth. *Functional Ecology* 8, 770-782.

Campbell, R.G., Wagner, M.M, Teegarden, G.J., Boudreau, C.A., and Durbin, E.G. (2001). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series 221, 161-183.

Christensen, S., and McLean, E. (1998). Compensatory growth in Mozambique tilapia (*Oreochromis mossambicus),* fed a sub-optimal diet. *Ribarstvo* 56, 3-19.

Christensen, V. (2010). Behavior of Sandeels Feeding on Herring Larvae. *The Open Fish Science Journal* 3, 164-168.

Clarke, A., and Johnston, N.M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* 68, 893-905.

Corner, E. and O'Hara, S. (1986). The biological chemistry of marine copepods. Oxford University Press, New York, 1-59.

Crisp, D.J. (1971) Energy flow measurements. In: Holme NA, McIntyre AD (eds) IBP handbook, Vol 16. Blackwell Scientific Publications, Oxford, p 197–279.

Davis, C.S. (1984). Predatory control of copepod seasonal cycles on Georges Bank. *Marine Biology* 82, 31-40.

Dubreuil, J., and Petitgas, P. 2009: Energy density of anchovy *Engraulis encrasicolus* in the Bay of Biscay. *Journal of Fish Biology* 74, 521-534.

Eliasen, K. (2013). Sandeel, Ammodytes spp., as a link between climate and higher trophic levels on the Faroe shelf. PhD thesis, Aarhus University.

Gauld, J.A. and Hutcheon, J.R. (1990). Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* Raitt, in the north-western North Sea. *Journal of Fish Biology* 36, 611-613.

Gilman, S.L. (1994). An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977-1986. *Fishery Bulletin* 92(3), 647-654.

Hirst, A.G., Sheader, M., and Williams, J. (1999). Annual pattern of calanoid copepod abundance, prosome length and minor role in pelagic carbon flux in the Solent, UK. *Marine Ecology Progress Series* 177, 133-146.

Hislop, J.R.G., Harris, M.P., and Smith, J.G.M. (1991). Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology* 224, 501-517.

Iles, T.D., and Wood, R.J. (1965). The fat/water relationship in North Sea herring (*Clupea harengus*), and its possible significance. *Journal of the Marine Biological Association of the UK* 45, 353-366.

Jobling, M. and Johansen, S.J.S. (1999). The lipostat, hyperphagia and catch-up growth. *Aquaculture Research* 30(7), 473-478.

Jonasdottir, S.H., Trung, N.H., Hansen, F., and Gartner, S. (2005). Egg production and hatching success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. Journal of Plankton Research 27(12), 1239-1259.

Jones, W., Gurney, W.S.C., Speirs, D.C., Bacon, P.J., and Youngson, A.F. (2002). Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. *Journal of Animal Ecology* 71, 916-924.

Kooijman, S. A. L. M., 2010: Dynamic energy budget theory for metabolic organisation.

Kvist, T., Gislason, H. and Thyregod, P. (2000). Using continuation-ratio logits to analyze the variation of the age composition of fish catches. Journal of Applied Statistics 27, 303-319.

Leandro, S. M., Queiroga, H., Rodríguez-Graña, L., and Tiselius, P. (2006). Temperature-dependent development and somatic growth in two allopatric populations of *Acartia clausi* (Copepoda: Calanoida). *Marine Ecology Progress Series* 322, 189-197.

Lynch, D. R., Lewis, C.V.W., and Werner, F.E. (2001). Can Georges Bank larval cod survive on a calanoid diet? *Deep Sea Research Part II: Topical Studies in Oceanography* 48, 609-630.

MacDonald, A. (2017). Modelling the impact of environmental change on the physiology and ecology of sandeels. [PhD thesis]. [Glasgow]: University of Strathclyde.

Macer, C.T. (1966). Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Fisheries Investigations, London Series, series 2, volume 24, 1-55.

Miglavs, I., and Jobling, M. (1989). Effects of feeding regime on food consumption, growth rates and tissue nucleic acids in juvenile Arctic charr, *Salvelinm alpinus*, with particular respect to compensatory growth. *Journal of Fish Biology* 34, 947-957.

Nelson, G.A., and Ross, M.R. (1991). Biology and population changes of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. *Journal of Northwest Atlantic Fisheries Science* 11, 11–27.

Quinn, T., and Schneider, D.E. (1991). Respiration of the teleost fish *Ammodytes hexapteru*s in relation to its burrowing behavior. Comparative Biochemistry and Physiology Part A: Physiology 98, 71-75.

R Development Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria www.R-project.org.

Rindorf, A. and Lewy, P. (2001). Analyses of length and age distributions using continuation-ratio logits. Canadian Journal of Fisheries and Aquatic Sciences 58, 1141-1152.

Robards, M.D., Piatt, J.F., and Rose, G.A. (1999). Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska. *Journal of Fish Biology* 54, 1050-1068.

Stari, A., Preedy, K.F., McKenzie, E., Gurney, W.S.C., Heath, M., Kunzlik, P. and Speirs, D.C. (2010). Smooth age length keys: observations and implications for data collection on North Sea haddock. Fisheries Research 105, 2–12.

Tomiyama, M., and Yanagibashi, S. (2004). Effect of temperature, age class, and growth on induction of aestivation in Japanese sandeel (*Ammodytes personatus*) in Ise Bay, central Japan. *Fisheries Oceanography* 13, 81-90.

van Deurs, M., Christensen, A., Frisk, C., Mosegaard, H. (2010). Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective. *Marine Ecology Progress Series* 416, 201-214.

van Deurs, M., Christensen, A. and Rindorf, A. (2013). Patchy zooplankton grazing and high energy conversion efficiency: ecological implications of sandeel behavior and strategy. *Marine Ecology Progress Series* 487, 123-133.

van Deurs, M., Hartvig, M., Steffensen, J.F. (2011). Critical threshold size for overwintering sandeels (*Ammodytes marinus*). *Marine Biology* 158(12), 2755-2764.

van Deurs, M., Jørgensen, C., Fiksen, Ø. (2015). Effects of copepod size on fish growth: a model based on data for North Sea sandeel. *Marine Ecology Progress Series* 520, 235-243.

van Deurs, M., Koski, M. and Rindorf, A. (2014). Does copepod size determine food consumption of particulate feeding fish? ICES Journal of Marine Science 71, 35-43.

Wallace, P.D., and Hulme T.J. (1977). The Fat/Water Relationship in the Mackerel, *Scomber scomber* (L.), Pilchard, *Sardinia pilchardus* (Walbaum) and the Sprat, *Sprattus sprattus* (L.) and the Seasonal Variations in Fat Content by Size and Maturity, vol. 35. MAFF Directorate of Fisheries Research: Lowestoft.

Winslade, P. (1974). Behavioural studies on the lesser sandeel Ammodytes marinus (Raitt) III . The effect of temperature on activity and the environmental control of the annual cycle of activity. Journal of Fish Biology 6, 587-599.

Xie, S. Zhu, X., Cui, Y., Wootton, R.J., Lei, W., and Yang, Y. (2001). Compensatory growth in the gibel carp following feed deprivation: temporal patterns in growth, nutrient deposition, feed intake and body composition. *Journal of Fish Biology* 58(4), 999-1009.

SUPPLEMENTARY MATERIAL FIGURE CAPTIONS

Figure A1: Energy allocation to structure and gonads. The left and right panels show energy allocation to structure, $C(\rho, S)$ and gonads $G(\rho, S)$ respectively. No allocation to structure or gonads occurs below a reserve ratio of ρ_0.

Figure A2: Large and small calanoid copepod energy concentration. A loess smooth (span = 0.04) is fitted to weekly observations (points).

Figure A3: Year-to-year changes in length and weight at age 1 and age 0. Each point represents a group of individuals with equal length and weight. The number of each individual in a length-weight group is indicated by the size of the point. All fish were caught in summer trawl surveys with the exception of 2002 and 2004 where dredge data was used. This is because few age 1 fish were caught by pelagic trawl in 2002, and no trawling is conducted outside the summer months. No summer surveys were undertaken in 2004, therefore the model is run with age 1 fish caught in the spring dredge survey. There is considerable year-to-year variation in sandeel 0-group size. For example, almost 60% of age 0 individuals caught in 2000 had lengths 7, while all sandeels caught in 2005 and 2006 were smaller than 7 cm. All fish were caught in summer trawl surveys.

Figure A4: Length and weight of the average 0-group between 2000-2003 and 2005-2006 off the Firth of Forth. Abundance of each 0-group cohort between 2000-2003 and 2005-2006 was normalised. Then, we combined all length-weight data.

Figure A5: *A. hexapterus* resting oxygen consumption. Oxygen consumption scales with body weight to the power 0.65. Therefore, the relative metabolic rate of a sandeel decreases substantially with weight. Data digitized from figure 1 in Quinn and Schneider (1991).

Figure A6: Modelled seasonal variation in sandeel standard metabolic rate at 12 ^{o}C. Metabolism of feeding sandeels is twice as high as overwintering individuals. Metabolic rates derived from Table 1 in Quinn and Schneider (1991).

Figure A7: Maximum stomach weight in relation to length. A sandeel stomach shows isomorphic growth. Relationship was derived from supplementary material in Van Deurs et al. (2010).

Figure A8: Relationship between water content (\% wet weight) and ash content (\% dry weight) in *A. hexapterus* (Robards et al., 1999) (intercept = -49.77837, slope = 0.80780 , $R^2 = 0.81$, n = 20 , p <1e-10).

Figure A9: Length, wet weight, dry weight and energy content of 27 *A. tobianus* individuals derived from laboratory experiments.

Figure A10: Modelled vs observed energy content and wet weight using equations A32 and A36. The model provides excellent fits to weight and energy data (R^2 = 0.998 and = 0.991, respectively.

Figure A11: One-at-a-time sensitivity analysis of model parameters. Each parameter is adjusted 10% and predicted starvation survival is compared to modelled starvation survival given by the baseline parameterisation.

Figure A12: One-at-a-time sensitivity analysis of model parameters. Each parameter is adjusted 10% and predicted mean weight is compared to modelled mean weight given by the baseline parameterisation. Note that there is no modelled mean weight for the case where is increased by 10%. This is due to 100% starvation mortality.