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Energetics of the extremely long-living bivalve *Arctica islandica* based on a Dynamic Energy Budget model

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Abstract

The ocean quahog *Arctica islandica* is the longest–living mollusk on Earth with a lifespan of at least 500 years. The slow senescence of this bivalve has promoted a great interest in its metabolic strategy. A dynamic energy budget (DEB) model was applied to describe how this species allocates its energy to maintenance, growth, maturation, and reproduction in a variable environment. We studied the relationship between *A. islandica* growth, lifespan, and food availability at eight different locations in the North Atlantic Ocean. Our results indicate that *A. islandica's* extreme longevity arises from its low somatic maintenance cost $[\dot{p}_M]$ and low ageing acceleration $\ddot{h}_a$, but there was not a direct relationship between food availability and lifespan in these *A. islandica* locations. Monkey Bank (North Sea), Iceland, and Ingøya (northern Norway) had the highest food availability estimates of all the localities but did not have the lowest longevities, in contrast to the theory of caloric restriction.

Keywords

Ocean quahog, growth, metabolism, ageing, food conditions, temperature, Dynamic Energy Budget (DEB) Theory

1. Introduction

The slow-growing bivalve *Arctica islandica* is one of the longest-living organisms on Earth, with a life span of up to five centuries (Wanamaker et al., 2008; Butler et al., 2013). This species has a decrease in growth after the first ~20 years of its life (Ropes, 1985; Kilada et al., 2007; Begum et al., 2009), exhibiting, as adults, one of the slowest growth rates reported among bivalves (values even < 0.05 mm per year; Thompson et al., 1980a; Murawski et al., 1982; Kennish et al., 1994; Wanamaker et al., 2008; Mette et al., 2016). *A. islandica* is widely distributed on both sides of the North Atlantic, where its populations exhibit geographical differences in shell shape, color, and growth rate (Ropes, 1985; Witbaard and Duineveld, 1990; Witbaard et al., 1999; Dahlgren et al., 2000). Moreover, *A. islandica* populations vary greatly in their maximum lifespan, from ~40 years in Kiel Bight (Germany) to 507 in Iceland (Philip and Abele, 2010; Begum et al., 2010; Butler et al., 2013). Most genetic and physiological studies indicate that such variations in growth and life span reflect a response to local environmental conditions rather than being a result of genetic differences (Witbaard et al., 1996; Dahlgren et al., 2000; Schöne et al., 2003; Witbaard et al., 2003; Holmes et al., 2003; Begum, 2009; Strahl and Abele, 2010). Previous studies on *A. islandica* showed that gaping activity, shell growth, and tissue growth were closely correlated with food availability and, to a lesser degree, with temperature (Ballesta-Artero et al. 2017, 2018). Limited food availability in winter (seasonal caloric restriction) and associated deep-burrowing and metabolic depression (Philipp and Abele, 2010; Ballesta-Artero et al., 2017) may be the keys to understanding this organism's long lifespan.

Here, we use the Dynamic Energy Budget (DEB) theory to investigate whether variations in *A. islandica* growth and energy allocation can be explained in terms of environmental factors (i.e., food and temperature) and if there is an evident relationship between local food conditions and lifespan (theory of caloric restriction, e.g., Sinclair 2005). We compare growth data from eight *A. islandica* locations on the North East Atlantic coast: Ingøya (northern Norway), Iceland, Faroe, Fladen Ground (northern North Sea), Fisher Bank (northern North Sea), Monkey Bank (central North Sea), Silver Pit (southern North Sea), and Kiel Bight (Baltic Sea; Fig. 1).

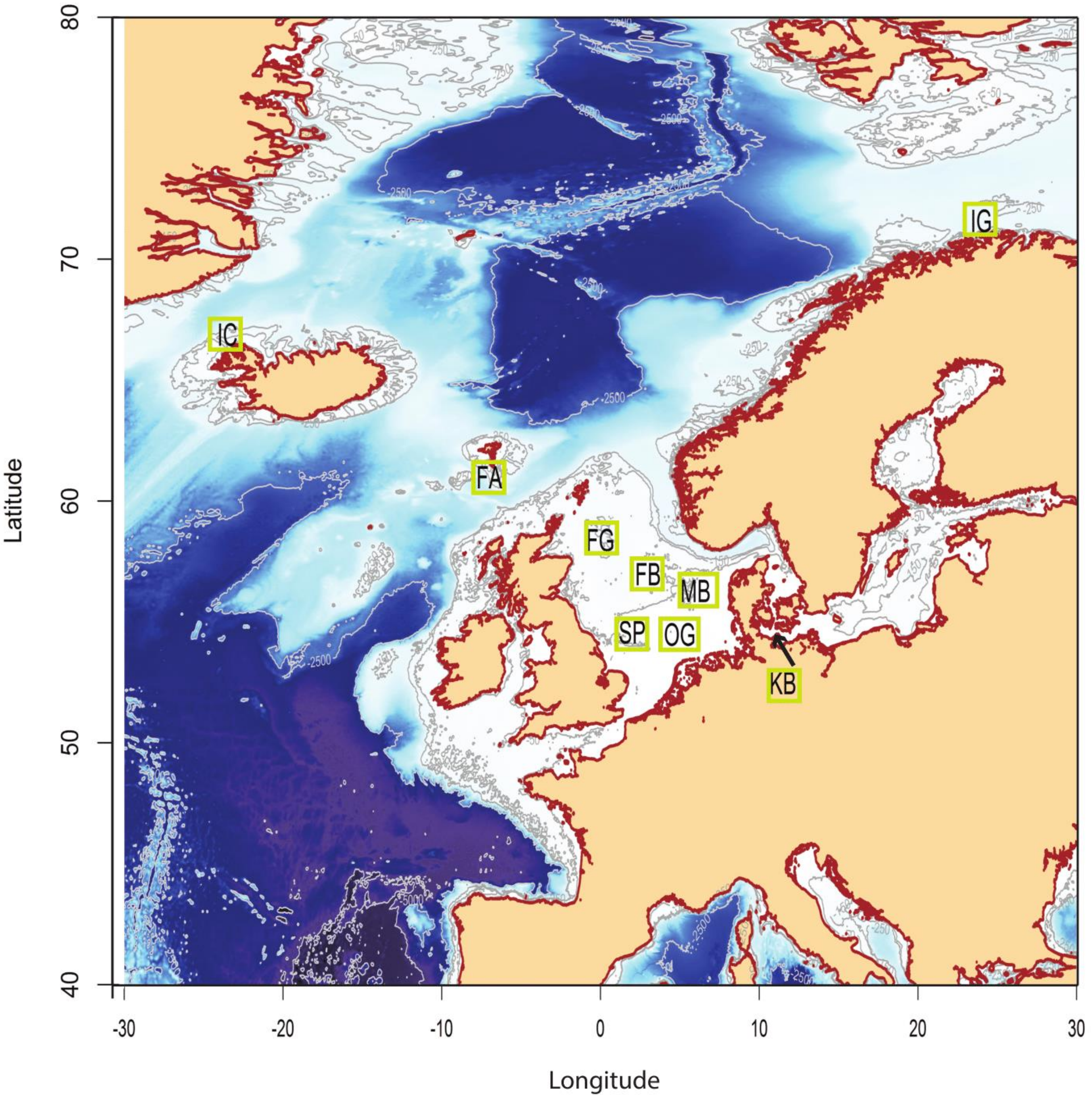

Fig 1: Geographic locations of *Arctica islandica* specimens used in this study: Ingøya (IG), Iceland (IC), Faroe (FA), Fladen Ground (FG), Fisher Bank (FB), Monkey Bank (MB), Silver Pit (SP), Oyster Ground (OG), and Kiel Bight (KB; laboratory specimens). Map colors represent water depth: white, shallower than 250 m and, from clear blue to black, water depths range from 250 to ≥ 5000 m (steps of 250 m).

A standard DEB model describes how an organism uses food to live in a changing environment (Kooijman, 2010). Using a DEB model, processes such as maintenance, growth, and reproduction are quantified as energy and mass fluxes (Fig. 2; for more details see supplementary material Box A.1, Van der Meer, 2006 and Kooijman, 2010). So far, DEB models have been successfully used to describe the energy allocation of 1250 species (AmP 2018). The strength of the DEB theory is that differences between species are reflected in the differences between parameters values (Van der Veer et al., 2001; Sousa et al., 2008; Freitas et al., 2009; Kooijman, 2010).

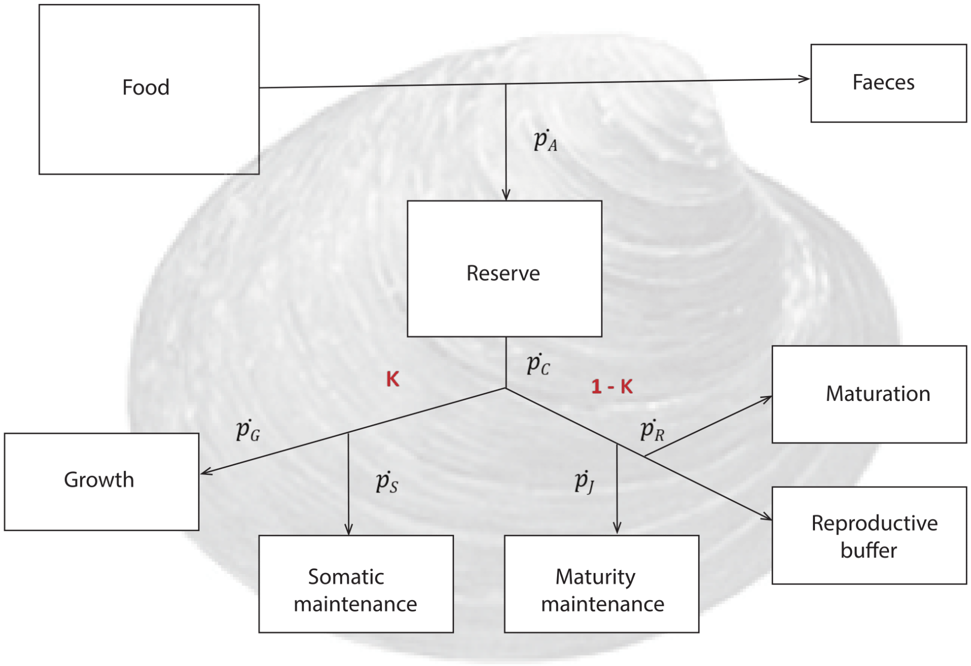

Fig. 2: Representation of the main metabolic processes in DEB theory (Kooijman 2010). There are six energy fluxes: assimilation ($\dot{p}_A$), mobilization ($\dot{p}_C$), somatic maintenance ($\dot{p}_S$), growth ($\dot{p}_G$), maturity maintenance ($\dot{p}_J$), and maturation + reproduction ($\dot{p}_R$). NOTE: The parameter κ (red kappa) is the fraction of the mobilized energy allocated to growth and somatic maintenance. The remaining portion 1-κ is the fraction allocated to maturity maintenance and to maturation (for juveniles) or reproduction (for adults). See supplementary material for equations.

In this study, we use DEB modeling to (1) describe the energetics of the long-living bivalve *A. islandica*, (2) predict the food conditions that might explain the observed growth patterns in eight North Atlantic locations and to see whether these predictions correlate with local primary productivity estimates, and (3) investigate characteristics regarding its unique ageing. We compare the estimates of all DEB parameters for *A. islandica* with those of 1250 other species (AmP 2018) and explore which parameters relate to ageing. Additionally, we examine whether differences in longevity among *A. islandica* localities coincide with local food conditions (theory of caloric restriction).

2. Methods

2.1 DEB model

DEB theory describes an organism's energy use with the state variables structural volume V (cm^3), reserves E (J), maturity E_H (J), and reproduction buffer E_R (J) (see equations in supplementary material Box A.1). It also distinguishes three different life stages: embryo (no food is ingested), juvenile (eats but does not reproduce), and adult (eats and reproduces). At each life stage transition, which occurs when a specific level of maturity is reached, a metabolic switch takes place. For instance, puberty is the moment when energy allocation to maturation is redirected to reproduction (Kooijman, 2010). The ages at which switches are triggered depend on past food intake and may differ among individuals (Kooijman, 2010). The state variables are related to direct measurements such as length and body weight. We assumed that shell length is proportional to structural length (through the shape factor δ_M), while reserve, structure, and reproductive buffer contribute to body mass (for more details, see Van der Meer, 2006; Kooijman, 2010; Lika et al., 2011).

The dynamics of the state variables are determined by six energy fluxes: assimilation ($\dot{p}_A$), mobilization ($\dot{p}_C$), somatic maintenance ($\dot{p}_S$), growth ($\dot{p}_G$), maturity maintenance ($\dot{p}_J$), and maturation + reproduction ($\dot{p}_R$; Fig. 2, see equations in supplementary material Box A.1). First, ingested food is assimilated by the organism (assuming a fixed efficiency) and subsequently incorporated into a reserve pool from which energy is mobilized and allocated on the basis of the κ-rule. The κ-rule states that a fixed fraction (κ) of the energy is allocated to growth and somatic maintenance, and the remaining portion (1-κ) is used for maturity maintenance and maturation (for juveniles) or reproduction (for adults; Fig. 2). All metabolic rates are also dependent on temperature through the Arrhenius rule (supplementary material Box A.2).

Mass invested in reproduction accumulates inside a reproduction buffer which is emptied at spawning events. However, not much is known about when exactly spawning occurs for *A. islandica* nor what actually triggers it (Thompson et al., 1980b; Thorarinsdottir and Steingrimsson, 2000; Ballesta-Artero et al. in preparation). Due to the lack of detailed information on reproduction for the species, we included gonad-free dry mass as function of length in order to estimate this species DEB model parameter values. Species-specific reproduction buffer handling rules need to be developed in order to specify the accumulation time of reproductive material in the body before spawning (see e.g. Gourault et al 2018, this special issue). This fell outside the scope of the current study.

DEB theory considers that some taxa, such as bivalves, exhibit an acceleration of metabolism during their life cycle that results in higher metabolic rates than the 'normal' expected trajectory for the standard species (Kooijman, 2014). Bivalve larval stages have a very different morphology compared to the subsequent juvenile and adult stages. These planktonic larval stages develop slower than the benthic juvenile and adult stages (Kooijman, 2014). Metabolism accelerates after the first feeding and/or settlement. This type of acceleration is represented by a one-parameter extension of the standard DEB model (Kooijman, 2010, 2014). The differential equations that describe the dynamics of the state variables are provided in the supplementary material Box A.1; the associated DEB parameters are given in Table 1.

2.2 Data

We estimated *A. islandica* DEB parameters primarily using our own field and laboratory datasets. We included information from the literature only for the so-called zero-variate data (Table 2). This is a minimum set of relatively simple species-specific biological scalars, such as age at birth or ultimate shell length. The *A. islandica* univariate data, set of pairs of values for an independent and associated dependent variable, are length-weight and age-length-time data. They originate from:

- A laboratory growth experiment with juveniles of *A. islandica* reared at 3 different temperatures (3, 8, 13 °C) at high food conditions (~15 x 10^6 cells/L; Ballesta-Artero et al., 2018)

- A sample taken from a wild population from Ingøya (northern Norway). Mette et al. (2016) provided age-length data, and length- gonad-free dry weight data were obtained from our own dissections (Ballesta-Artero et al. in prep).
- Seven different North Atlantic locations: Iceland, Faroe, Fladen Ground , Fisher Bank, Monkey Bank, Silver Pit, and Kiel Bight (Witbaard et al., 1999; Fig. 2, Table 3). Samples taken by Witbaard et al. (1999) provided age-length data. For the Iceland population, growth measurements were also obtained from Schöne et al. (2005). This data included a very old specimen, whereas Witbaard et al. (1999) only covered a limited set of age classes (< 50 years old).

2.3 Food availability

A. islandica is a filter-feeding bivalve that feeds on the available phytoplankton at the sea bottom. According to DEB theory, the ingestion rate of an organism is proportional to the scaled functional response *'f'*, which is related to the food density (X) by a Holling type II curve. That is:

$$f = \frac{\mathrm{X}}{\mathrm{X} + X_K}$$

where X_K is the half-saturation parameter. f varies between 0 and 1, i.e., from starvation to *ad libitum* feeding conditions. In our study, exact food conditions of the fieldwork locations were unknown thus f of each population was assumed constant over time (i.e., $X_t = X$, where t is time), and estimated from the data. We also estimated the f for the laboratory experiment.

Primary productivity (or phytoplankton production) is highly variable in time and space due to factors such temperature, light, and nutrient supply (Skogen et al., 2007). Different models and *in situ* records have been used to calculate primary productivity in the North Atlantic (Joint and Pomroy, 1993; Skogen and Moll, 2000; Skogen et al., 2007; Capuzzo et al., 2017). Primary productivity estimates vary considerably among studies (Table 3). We used an average value of the various available estimates (Joint and Pomroy, 1993; Skogen and Moll, 2000; Skogen et al., 2007; Steingrund and Gaard, 2005; Astthorsson et al., 2007; and Capuzzo et al., 2017) and compared it to our estimated scaled functional response (Table 3).

2.4 Parameter estimation

We used an improved version of the co-variation method for parameter estimation (Lika et al., 2011), presented in detail in the online AmP manual (DEB Wiki; Marques et al., 2018a, b). Code, data, and results can be downloaded from the add-my-pet collection (AmP 2018). Estimated parameters are listed in Table 1, and are stored in AmP as version 2018/09/03: https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Arctica_islandica/Arctica_islandica_res.html

The overall goodness of fit was measured with the mean relative error (MRE), which can vary between 0 and ∞, and the symmetric mean squared error (SMSE), varying between 0 and 1, for the univariate data, and with the relative error (RE) for all zero-variate data (see Marques et al. 2018a for equations). The relative error is a ratio of the absolute error of a measurement to the measurement being taken.

Table 1: DEB parameter values for *Arctica islandica* at reference temperature 20 °C. AmP, version 3rd September 2018, https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/

Symbol	Value	Unit	Definition
$\{\dot{p}_{Am}\}$	16.87*	J cm^{-2} d^{-1}	Maximum surface area-specific assimilation rate
$[\dot{p}_M]$	3.818	J cm^{-3} d^{-1}	Volume-specific maintenance costs
$\dot{v}$	0.04105*	cm d^{-1}	Energy conductance
$[E_G]$	2365	J cm^{-3}	Volume-specific costs of growth
κ	0.4733	-	Allocation fraction to soma
E_H^b	0.0129	J	Maturity threshold at birth
E_H^j	0.1697	J	Maturity threshold at metamorphosis
E_H^p	30450	J	Maturity threshold at puberty
δ_M	0.3700	-	Shape factor laboratory
δ_{Mb}	0.4404	-	Shape factor field
z	2.092	-	Zoom factor
$\ddot{h}_a$	2.031^{-12}	d^{-2}	Weibull ageing acceleration
T_A	8000	K	Arrhenius temperature
s_M	2.358	-	Acceleration factor
$\dot{k}_\mathrm{j}$	0.0005	d^{-1}	Maturity maintenance rate coefficient
f	see Table 3	-	Scaled functional response

NOTE: * values before acceleration, see supplementary material Box A.1 for explanation

3. Results and Discussion

3.1 *DEB parameters and predicted values*

We estimated DEB model parameters and scaled functional responses from all data simultaneously using the technique of fitting multiple models to multiple data as described in Marques et al., (2018b), this issue. The overall goodness of fit of the model was: the MRE 0.254 and the SMSE 0.204. The relative error for all zero variate data was less or equal to 20% except for the length at metamorphosis, which had a RE of 2.8 (Table 2). Overall, the predicted lengths did not fit as well as the predicted rates, times, and weights. This result is not unexpected due the variability in morphology among locations and individuals. The maximum length (11.2 cm) was underestimated when compared to the 14-cm shell length given by Ropes (1985), although it still falls well within the range of published values (9-14 cm, Sager and Sammler, 1983; Begum et al., 2010).

The site-specific empirically reconstructed growth curves were generally well captured by the DEB model assuming a constant food level over time (Fig. 3). The mean relative error between the data and model was between 0.08 and 0.30. The largest discrepancy between the model and data was found for the Ingøya population, and the underlying cause is not yet clear. The Ingøya population showed a sudden transition from rapid to slow growth, which seems to coincide with the juvenile-adult transition. Holmes et al. (2003) suggests that the reason why growth slows during ontogeny is that the allocation to growth and somatic maintenance is suddenly reduced after sexual maturation. According to the DEB theory, growth and maturation are parallel process that do not directly compete with each other for resources (the kappa rule).

The duration of the egg and larval stages were well captured by the model (Table 2). *A. islandica* needs 4 days to birth (from embryo to larvae), and 28 days to metamorphosis (from planktonic larvae to benthonic juvenile or spat). According to the constructed DEB model, the species reaches maturity at an age of ~5.8 years old (2121 days at 13 ° C) when shell length is ~5cm (Table 2). Better knowledge concerning the weight at metamorphosis would help determine how accurate the DEB model is since morphology at metamorphosis might be more variable than in the later juvenile and adult stages. Meanwhile, the predicted dry weight at metamorphosis at *ad libitum* food is 7 µg. An advantage of a modelling framework like DEB is that unknown quantities can be predicted and then subsequently tested. The duration and timing of key events like first feeding, metamorphosis, and reproduction are well captured by the model.

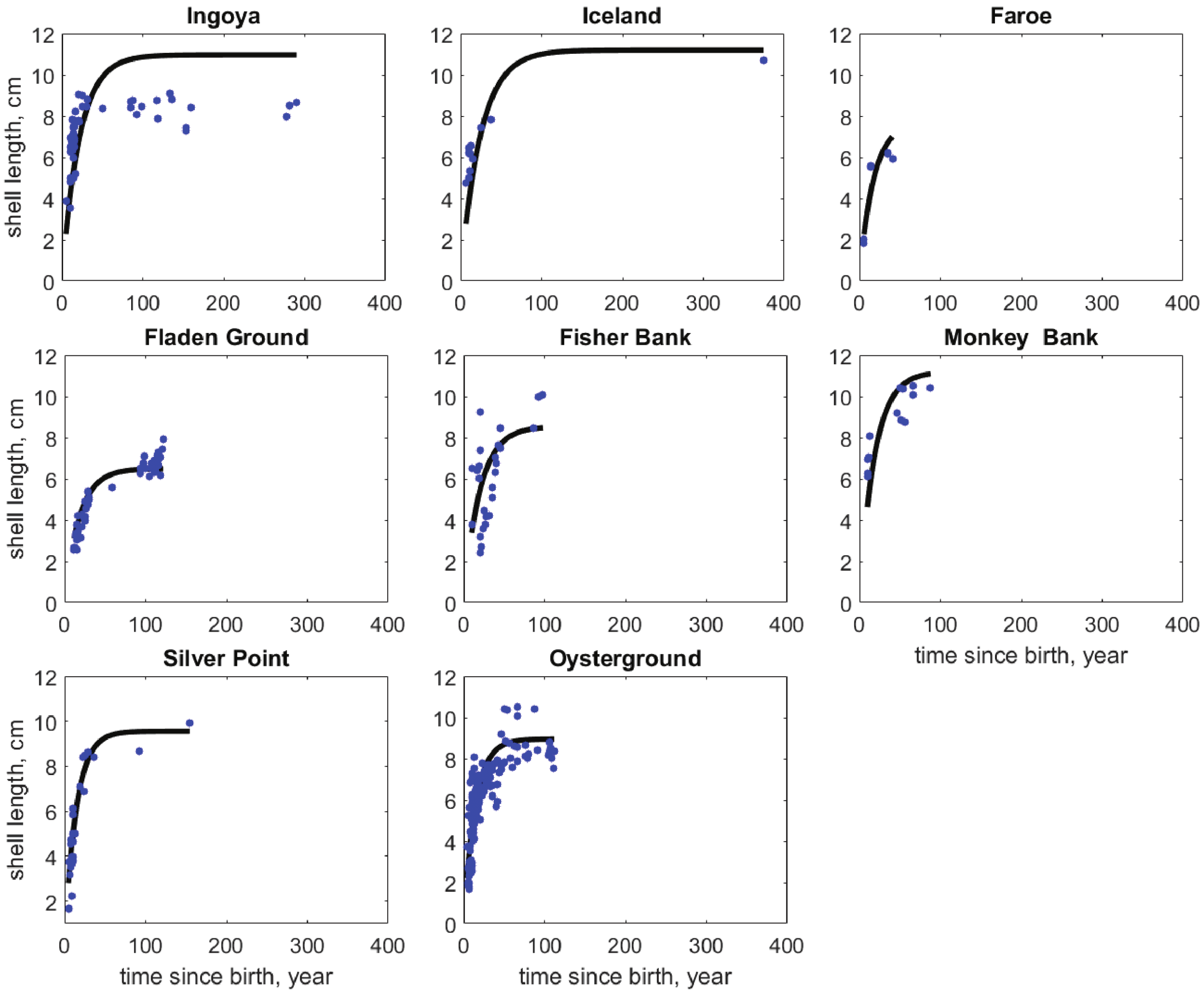

Fig. 3: *Arctica islandica* growth curves at different North Atlantic locations. Points indicate observed data and lines indicate model predictions

Unexpectedly, we needed to use two shape factors (δ_M) to get a good fit for the growth of the laboratory specimens and the field populations at the same time (Table 1). We think this was due to the fact that the specimens from the laboratory were juveniles (not adults as in the field locations) and, furthermore, come from a location (Kiel Bight, Germany) where uniquely stressful local environmental conditions (low salinity and high temperature, Zettler at al., 2001) contribute to particular shape features. Moreover, weights in combination with lengths were available for both laboratory specimens as well as field populations, meaning that there was enough information to estimate both shape coefficients.

Table 2: Comparison of observed and model predicted zero-variate data (temperature dependent data): maximum reproductive rate, age, length, and weight at different life stages. RE: Relative error.

Data	Observed	Predicted	(RE)	Unit	Description	Ref.
a_b	4	4.247	0.062	d	Age at birth	Lutz et al., 1982
t_j	34	27.52	0.191	d	Time since birth at metamorphosis	Lutz et al., 1982
t_p	2190	2121	0.031	d	Time since birth at puberty	Thompson et al., 1980b
a_m	1.85E+05	1.85E+05	0.000	d	Life span	Butler et al., 2013
L_J	0.024	0.091	2.787	cm	Shell length at metamorphosis	Lutz et al., 1982
L_P	4	4.686	0.172	cm	Shell length at puberty	Thompson et al. 1980b
L_i	14	11.2	0.200	cm	Ultimate shell length	Ropes, 1985
W_w^0	0.01375	0.013	0.070	mg	Wet weight of an egg.	Oertzen, 1972
W_w^p	0.98	0.948	0.028	g	Dry weight at puberty	Ballesta-Artero in prep.
R_L	1096	1122	0.023	egg/d	Reproduction rate at 5-cm	Oertzen, 1972

When compared to the rest of species from the DEB collection, *A. islandica* seems to have a low allocation fraction to soma (κ = 0.47; Fig. 4a), a low volume specific somatic maintenance ($[\dot{p}_M]$ =3.82; Fig. 4b), and an average energy conductance ($\dot{v} = 0.0968$, values post-metamorphosis; Fig. 4c).

The allocation fraction to soma (κ = 0.47) is lower than the median value of the 1250 species in AmP at 3rd September 2018 (0.89, Fig. 4a). The distribution of kappa values follows a beta distribution with surprising accuracy, both for bivalves and for all species together (see Lika et al. 2018, this special issue). The estimated κ of 0.47 is close to the value that maximizes reproductive output of an organism, estimated to be around 0.45 (Lika and Kooijman, 2003).

This suggests that *A. islandica*'s metabolism prioritizes reproductive output. A 5-cm *A. islandica* specimen produces ~400,000 eggs per year (Oertzen, 1972), equating to a reproduction rate of 1096 eggs d^{-1} (predicted 1124 eggs) for an individual of that size at a temperature of 10 °C (see comparison of *A. islandica* reproduction rate with other mollusks species in supplementary material Box A.3). Using the parameters obtained here (Table 1), the expected reproduction rate for an individual of maximum size is 4508.83 d^{-1}, with a cumulative reproductive output (number of eggs) of 78 $x10^7$ eggs (~896 g dry weight) over its entire life time (at high food and typical temperature of 6 °C). These findings assume that *A. islandica* reproduces during its entire adult life without signs of reproductive senescence, in accordance with observational studies (Thompson et al., 1980b; Thorarinsdottir and Steingrimsson, 2000).

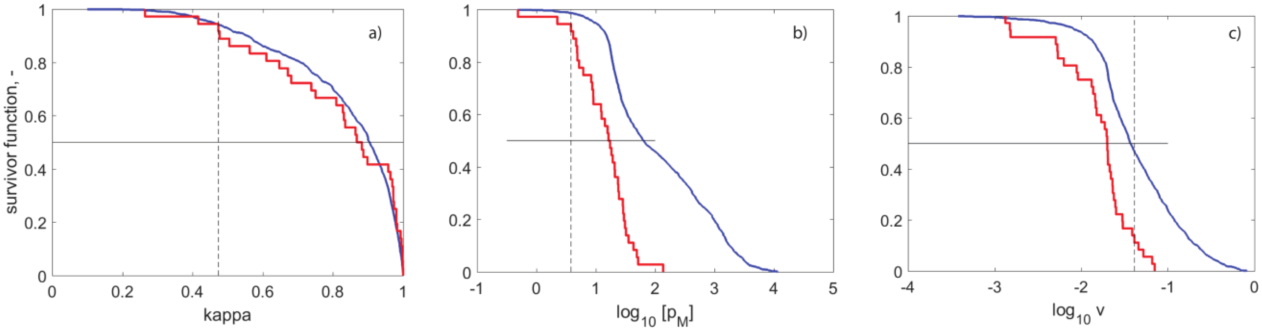

Fig. 4: Survival functions (fraction of species that has a value larger than the x-axis) for all species in the DEB collection (blue curve), and all bivalves (red curve). Horizontal solid line shows the median. The estimated value for *A. islandica* is indicated by the dashed vertical line. a) Allocation fraction to soma κ; b) volume-specific maintenance cost $[\dot{p}_M]$; c) energy conductance $\dot{v}$ (post-metamorphosis).

The specific reserve capacity $[E_m] = \frac{\{\dot{p}_{Am}\}}{\dot{v}}$ (J/cm^3) quantifies the capacity of organisms to adapt to fluctuations in food availability. *A. islandica* resides in strongly variable (seasonal) environments and survives long periods of starvation (Taylor, 1976; Ballesta-Artero et al., 2017, 2018). We hypothesized, therefore, that the species might have an exceptionally high reserve capacity. In Fig. 5a, the maximum reserve density as function of structural size is presented for all bivalves in the DEB collection. The estimated reserve capacity value for *A. islandica* is not exceptionally high. On the contrary, it is on the lower end of the range of values for that size class. The energy conductance $\dot{v}$ is close to the median value for all DEB collection species (Fig.

4c, Fig. 5b). This suggests that low volume-specific somatic maintenance $[\dot{p}_M]$ rather than a low value of $\dot{v}$ may be the reason for *A. islandica*'s prolonged survival during starvation (Fig. 4b). Our findings of a low maintenance costs for *A. islandica* is in agreement with earlier studies of the species (Begum et al., 2009, 2010).

The DEB modelling framework developed in this study not only allows the estimation of DEB parameters from data, but also provides a framework to assess how these parameters relate to those of bivalves in general, providing first steps in the direction of understanding selection pressure of adapting to particular environments.

3.2 *DEB parameters and ageing*

To explore which DEB parameters could be related to the unique ageing of *A.islandica*, a comparison was made with 69 mollusk species (37 bivalves; Fig. 5a-h). We present the parameters as a function of the ultimate structural length to correct for size. For most parameters examined, *A. islandica* had values within the range of other bivalves, though visually at the edge (Fig. 5a-h). Only its ageing acceleration factor ($\ddot{h}_a$; Fig 5e) strongly deviated, being the lowest of all the mollusks within the DEB collection (AmP, 2018). *Tridacta gigas* (the giant clam) had parameters values that were more outside the norm than those of *A. islandica*.

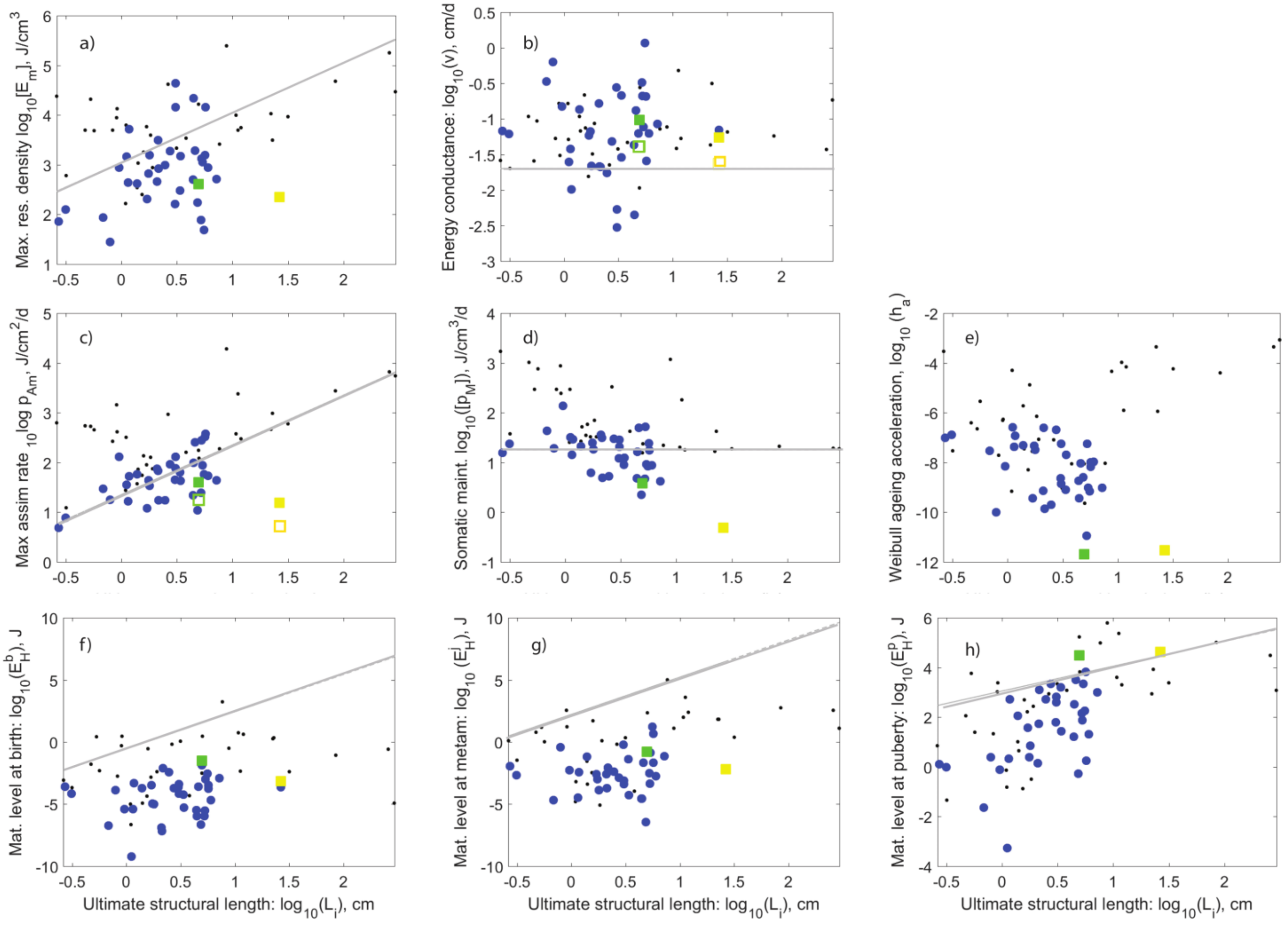

Fig. 5: Comparison of DEB parameters as functions of ultimate structural length in mollusks. Small (black) dots: All Mollusca; large (blue) dots: only Bivalvia; green square: *A. islandica*; and yellow square: *T. gigas* (full square before metamorphosis, empty square after metamorphosis). Grey line: expectation of the DEB generalized animal. The parameters are: a) maximum energy density (E_m), b) energy conductance ($\dot{v}$), c) maximum specific assimilation $\{\dot{p}_{Am}\}$, d) specific somatic maintenance cost $[\dot{p}_M]$, e) ageing acceleration ($\ddot{h}_a$) , f) maturity at birth (E_H^b), g) maturity at metamorphosis (E_H^j), and f) maturity at puberty (E_H^p)

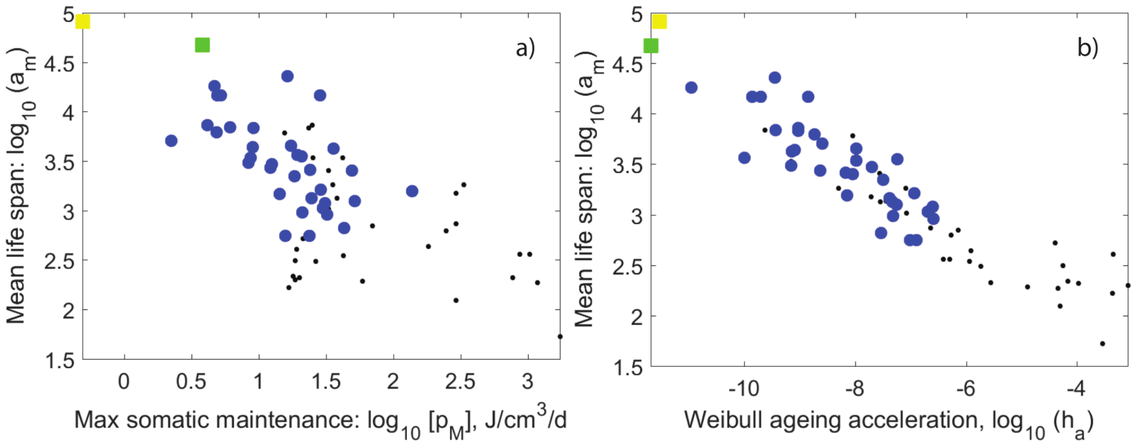

Fig. 6: Mean life span (at abundant food) as function of a) maximum somatic maintenance ($[\dot{\mathrm{p}}_\mathrm{M}]$, J/cm^3/d), and b) ageing acceleration $\ddot{h}_a$. Small (black) dots: Mollusca; large (blue) dots: Bivalvia; green square: *A. islandica*; and yellow square: *T. gigas*. Values are calculated at reference temperature (20 °C).

Next, we investigated how life span is calculated under the DEB theory. According to Kooijman (2010), the mean life span of a species at abundant food conditions can be approximated by:

$$1.62\left(\frac{\kappa\{\dot{p}_{Am}\}s_{\mathcal{M}}}{\ddot{h}_a\dot{v}[\dot{p}_M]}\right)^{1/3}$$ (see supplementary material Box A.4 for more details)

We see from this expression that the maximum specific assimilation $\{\dot{p}_{Am}\}$, energy conductance $\dot{v}$, specific somatic maintenance $[\dot{p}_M]$, and ageing acceleration $\ddot{h}_a$, are involved in determining longevity. *A. islandica* has one of the lowest $[\dot{p}_M]$ and highest mean life span of all mollusks within the DEB collection at the typical temperature for each species (Fig. 5d; AmP 2018). When we computed the mean life span at abundant food of all species at the same reference temperature (20°C), the tropical species *T. gigas* , however, had higher mean life span than *A. islandica*'s (223 vs. 129 years, respectively; Fig. 6a).The same happened with the parameter ageing acceleration (Fig. 6b) . It appeared that mean life span scales negatively with maintenance $[\dot{p}_M]$ and ageing acceleration $\ddot{h}_a$ (Fig. 6a, b). Our data suggest that the extreme longevity of both species is related to the low value of these two parameters (Fig. 6a, b).

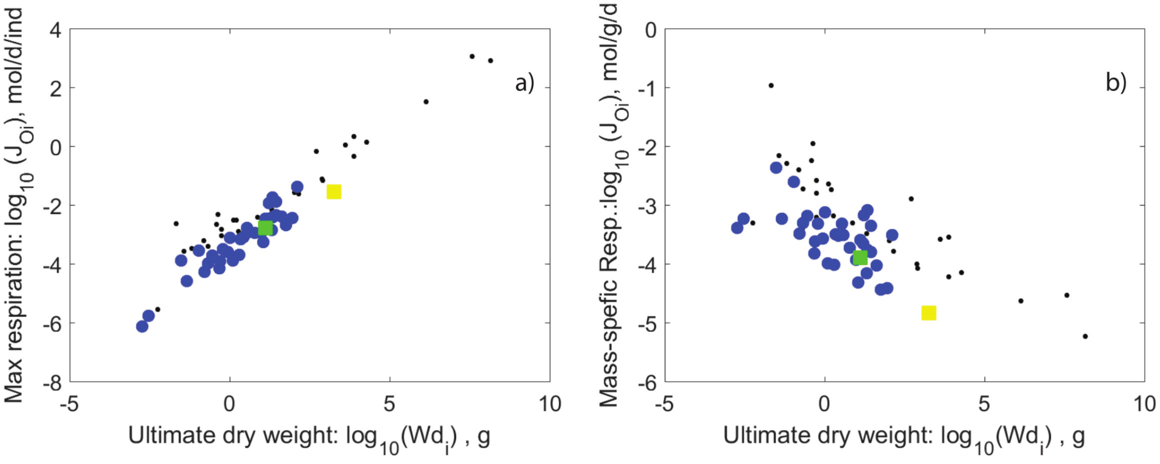

Fig. 7: a) Maximum respiration rate as function of ultimate dry weight (weight at ultimate length) b) mass-specific oxygen consumption of a fully grown individual. Small (black) dots: Mollusca; large (blue) dots: Bivalvia; green square: *A. islandica*; and yellow square: *T. gigas*. NOTE: Values at the reference temperature (20 °C) for each species. The equations to calculate respiration are fully specified in Augustine et al. 2014 (Appendix A.2).

Begum et al. (2009) found that the weight-specific respiration of *A. islandica* was significantly below the average of 59 bivalve species (when compared at the same temperature). Within the DEB framework, the general pattern across species is that respiration of fully grown individuals increases with maximum body weight with a scaling coefficient around 0.75 (Fig. 7a). This implies that mass-specific respiration of adult individuals is negatively related to the maximum body weight with a scaling coefficient around -0.25 (Fig. 7b). In line with the finding of Begum et al. (2009), we found that the expected respiration of fully grown *A. islandica* was lower than the mean for bivalves of the same size (Fig. 7a, b). Begum et al. (2009) also stated that individuals of *A. islandica* of almost the same size, but of quite different ages, had on average the same respiration, indicating that aging in itself does not play a role on the respiration of the species (at least the first 100 year of its life; Begum et al., 2009). However, ageing had a negative effect on respiration in shorter lived bivalves such as *Mytilus edulis* (Begum et al., 2009).

3.3 *Scaled functional responses*

3.3.1 Laboratory data

The DEB scaled functional response *(f) f*or the highest food level within the laboratory growth experiment (Ballesta-Artero et al., 2018) had a value of 0.79 (Table 3). For the estimation of *A. islandica* DEB parameters, we only included laboratory growth data which were derived at the highest food level (Ballesta-Artero et al., 2018). Medium food level data were not included because growth was not statistically different from growth at the highest food level (Ballesta-Artero et al., 2018).

At first, we included all the food treatments (high, medium, low, and no food ([15, 5, 0.5, ~0 x 10^6 cells/L], respectively) from Ballesta-Artero et al. (2018) into the AmP estimation procedure. After a number of unsuccessful attempts, however, to obtain reasonable parameter estimates (due to the very high number of parameters), we decided to only include the data from the high food level for estimating *A. islandica* DEB parameters (see data doi: 10.4121/uuid:39f23dd7-bc2e-495b-a693-4ba70aa5ed75). One likely needs to proceed in a stepwise manner. First: obtain parameters for the standard DEB model under non-starvation conditions. Second: treat those parameters as given and estimate parameters of a starvation module which incorporates assumptions about how the organism responds (e.g. shrinking and/or modulating its maintenance).

It is known that *A. islandica* can reduce its metabolism to 10% of its normal rate (Strahl and Abele, 2010). Thus, it could be interesting to incorporate this behavior into DEB models. For instance, how the specific somatic maintenance $[\dot{p}_M]$, might be modulated during a starvation response. The parameters from this study will be helpful for that purpose.

3.3.2 *Field data*

Monkey Bank, Iceland, and Ingøya had the highest estimated values of scaled functional response *'f'* of all the localities (Table 3). Fladen Ground, in contrast, had the lowest. Our finding are in agreement with the food ranking of populations from Witbaard et al (1999). These rankings are not in agreement with those of average primary productivity estimates (Fig. 8; r=0.6, p-value>0.05). For instance, Silver Pit population had a high *f* but a very low primary productivity (Table 3).

Table 3: Lifespan and scaled functional response estimates for the different locations. Maximum longevity (Long.) recorded indicated higher maximum longevities found in previous studies. Maximum longevity estimated was calculated with DEB parameters (Table 1).

Location	*f*	Prim. Prod mean gC m^{-2} yr^{-1}	Prim. Prod estimates gC m^{-2} yr^{-1}	Long. recorded years	Long. estimated years	T °C	Depth m
Fladen Gr.	0.58	124	110-138 [1, 1985-1994]	122 [7]	449	7.3	140
Faroe	0.69	60	60 [2, 1990-2003]	303 [8]	420	7.9	134-177
Fisher Bank	0.76	140	90-109, 119, 200 [1,3 (1988-1989), 4 (1988-2013)]	98 [7]	476	6.7	61
Lab. Exp.	0.79	-	-	-	-	-	-
Oyster Gr.	0.80	249	126-204, 199, 382 [1,3,4]	112 [7]	340	10	37-41
Silver Pit	0.85	89	97-117, 79, 82 [1,3,4]	155 [7]	343	9.9	40-68
Ingøya	0.98	160	120-200 [5,1981-2004]	290 [9]	507	6.0	10
Iceland	1	250	200-300 [6, 1958-1982]	507 [10]	562	4.7	5-7
Monkey Bank	1	271	171-225, 261, 354 [1,3,4]	88 [7]	439	7.4	52

Note: numbers between square brackets denotes references and years of estimates: [1] Skogen and Moll 2000, [2] Steingrund and Gaard 2005; [3] Joint and Pomroy1993, [4] Capuzzo et al.2017, [5] Skogen et al. (2007), [6] Astthorsson et al. (2007), [7] Witbaard et al. 1996,1999,2003, [8] Bonitz et al. 2018, [9] Mette et al. 2016, [10] . Butler et al., 2013. Comas separate different studies values.

Shell measurements used here came from specimens that were live-collected between 1993 and 2016. In the analyses, we did not make a distinction between the exact periods the animals were sampled. Therefore, part of the discrepancy between food availability estimates could result from multidecadal or higher frequency variations in primary production (see Table 3). Witbaard et al. (1999) demonstrated, however, that the relative differences in growth between localities remain equal when comparing the same or different periods of time, implying that *A. islandica* growth rates reflect long-term systematic differences in site-specific environmental variability.

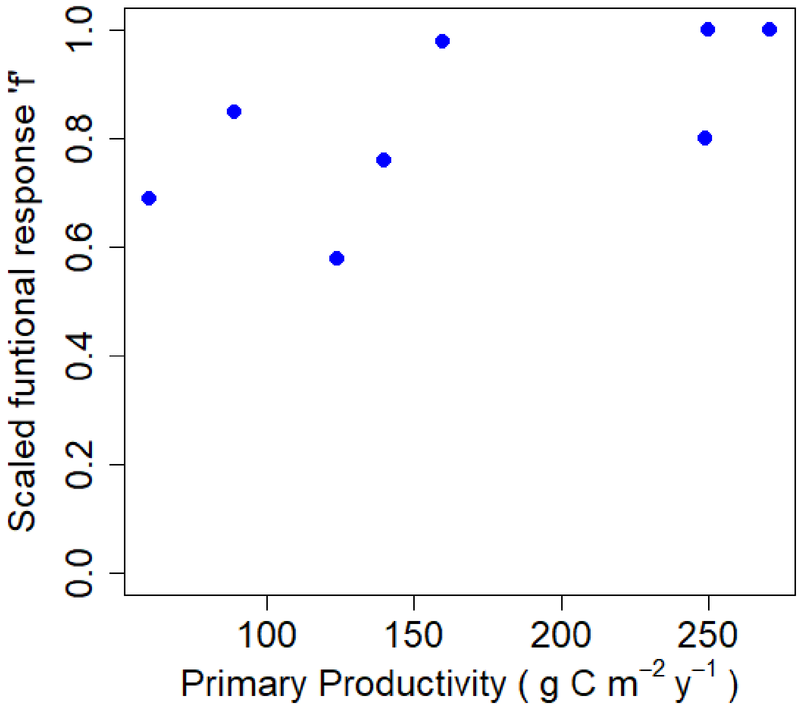

Fig. 8: Scaled functional response as a function of primary production (average of estimates Table 3).

Furthermore, although primary productivity at the surface can be an indicator for food availability at the seafloor, these two measurements may differ substantially (Fig. 8). Depth of the population under study is an important factor to consider (Witbaard and Duineveld, 1990; Witbaard et al., 1999). The deeper a population lives, the longer the time it takes for phytoplankton to sink to the seafloor. During this time, the phytoplankton is grazed by zooplankton and degraded by bacteria. Thus, depth will affect both the quantity and quality of the food available to benthos. Therefore, using the scaled functional response may be a more accurate tool to describe food availability for benthic organisms because it integrates decades and even centuries of information from the benthic zone. Moreover, for some locations, *f* could be the only source of information.

3.3.3 *Lifespan versus food availability*

We investigated the relationship between *A. islandica* lifespan and food availability (*f*) at the different North Atlantic localities, but, did not find a clear trend between these two variables (Table 3). The Iceland and Ingøya localities contain specimens with the highest longevity (≥ 300 years) and exhibit the highest food availability. Yet, the Monkey Bank location, also exhibited one of the highest levels of food availability, whereas the oldest individual recorded was only about 88 years old (Table 3). We must also consider that maximum age observed and recorded could differ from the actual maximum lifespan of a population (Beukema, 1988).

Under DEB theory, lower food levels for a population are associated with longer life-spans of its individuals (at the same temperature; Kooijman 2010). Other studies using various taxa have also reported that caloric restriction increases organism's lifespans, probably due to a reduction in its metabolic rate (Fontana et al., 2010; Moss et al., 2016). Therefore, A. *islandica's* self-induced metabolic rate depression (MRD) periods, varying between 1-30 days (Taylor, 1976, Abele et al., 2008; Ballesta-Artero et al., 2017), may be a factor involved in its extreme longevity. Another factor can be its high antioxidant capacity (Abele et al., 2008), captured in our DEB model by the extremely low ageing acceleration parameter $\ddot{h}_a$ (Fig. 5d), i.e., a low accumulation of the cellular waste that provokes ageing (Kooijman, 2010). Those factors together increase the species longevity because they reduce the generation of reactive oxygen species (ROS), which damages cells structures and deteriorate the physiological functions of the organism (Philipp et al. 2005; Philipp and Abele, 2010). Our data, however, suggest no direct relationship between food availability and longevity of the studied *A. islandica* localities (Table 3).

4. Conclusions

We constructed the first DEB model for the long-living bivalve *Arctica islandica*. Our results indicate that: (1) *A. islandica's* extreme longevity arises from low somatic maintenance costs $[\dot{p}_M]$ and a low ageing acceleration ($\ddot{h}_a$), (2) food availability estimates based on the DEB's scaled functional response may be a more accurate estimates than primary productivity for *A. islandica* localities because it integrates decades, and even centuries, of food information from the benthic zone. Moreover, we could not find a direct relationship between *A. islandica* lifespan and food availability in the studied North Atlantic locations.

5. Compliance with Ethical Standards

The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Box A. 1: Main equations of the DEB model

The 'abj'- model which is here applied to *A. islandica* is similar to the standard DEB model ('std'), with the exception that metabolic acceleration occurs between birth and metamorphosis. Before and after acceleration, growth is isomorphic. Metamorphosis occurs at maturity level E_H^j (J), which might or might not correspond with changes in morphology. This model is a one-parameter extension of model 'std'. The dynamics of the state variables of the abj-DEB model are specified by the following equations:

$$\frac{d}{dt}E = \dot{p}_A - \dot{p}_C$$

$$\frac{d}{dt}V = \frac{\dot{p}_G}{[E_G]}$$

$$\frac{d}{dt}E_H = \begin{cases} \dot{p}_R & \text{if } E_H < E_H^p \\ 0 & \text{otherwise} \end{cases}$$

$$\frac{d}{dt}E_R = \begin{cases} 0\ if\ E_H < E_H^p \\ \dot{p}_R \quad \text{otherwise} \end{cases}$$

Where $V = L^3$, is the structural volume. The energy fluxes in J/d are given by:

$$\dot{p}_A = \begin{cases} 0 \text{ if } E_H < E_H^b \\ f\ \{\dot{p}_{Am}\}\ \mathcal{M}(V)\ V^{2/3} \text{ otherwise} \end{cases} \qquad f = \frac{\mathrm{X}}{\mathrm{X} + X_K}$$

To account for the effects of food availability, the DEB model uses a scaled version of the Holling's type II functional response, f, where X is the amount of available resources as density (by volume), $X_K$represents the half saturation coefficient (density at which feeding rate is half of its maximum value).

$$\dot{p}_C = E\left(\frac{[E_G]\ \dot{v}\ \mathcal{M}(V)\ \ V^{2/3} + \dot{p}_S}{\kappa\ E + [E_G]\ V}\right)$$

$$\dot{p}_S = [\dot{p}_M]\ V$$

$$\dot{p}_G = \kappa\ \dot{p}_C - \dot{p}_S$$

$$\dot{p}_J = \dot{k}_J E_H$$

$$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$$

$\mathcal{M}(L)$, is the shape correction function by which both $\dot{v}$ and $\{\dot{p}_{Am}\}$ need to be multiplied. During metabolic acceleration the organism changes in shape: surface area grows proportional to volume:

$$\mathcal{M}(V) = 1 \qquad \text{if} \quad E_H < E_H^b \qquad \text{(embryo)}$$
$$\mathcal{M}(V) = \left(\frac{V}{V_b}\right)^{1/3} \quad \text{if} \quad E_H^b \leq E_H < E_H^j \quad \text{(early juvenile)}$$
$$\mathcal{M}(V) = \left(\frac{V_j}{V_b}\right)^{1/3} \quad \text{if} \quad E_H \geq E_H^j \qquad \text{(late juvenile)}$$

Where V_b(cm) and V_j(cm) is the structural volume at birth and metamorphosis respectively. $L = V^{\frac{1}{3}}$ is the structural length which is taken proportional to shell length (see methods section).

All of the model parameters can be found in Table 1 of the manuscript. The acceleration factor, $s_{\mathcal{M}} = \frac{L_j}{L_b}$ is a food dependant quantity and is equal to 2.35 at f=1.

Box A. 2: Temperature dependence of rates

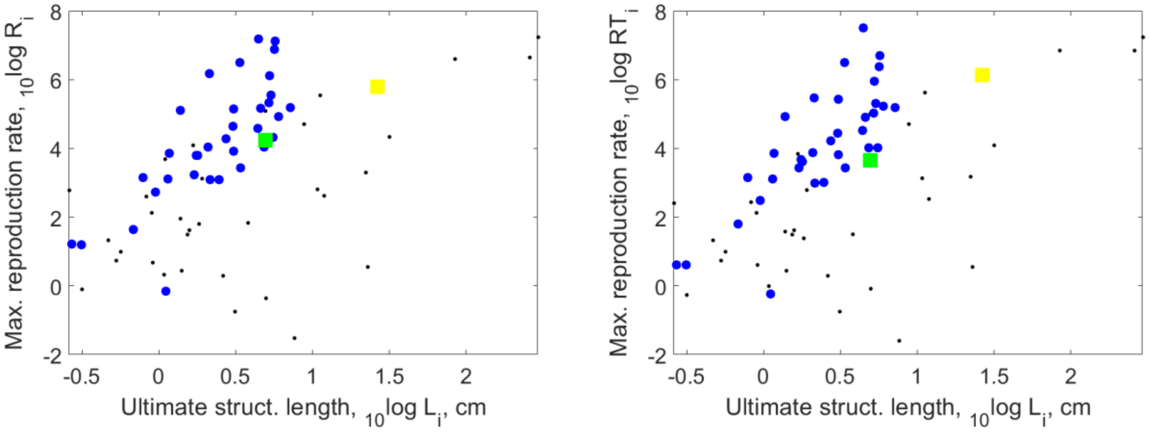
The temperature dependence of rate (and age) constants can be accounted for by multiplying (or dividing) them with a temperature correction factor c_T that can be derived from the Arrhenius relation. The temperature correction is given by:

$$c_T = \left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)$$

All temperatures are given in Kelvin. In this equations, T_{ref} is a reference temperature of 293.15K (20ºC), T is the temperature at which the data was recorded, and T_A is the Arrhenius temperature, which can be estimated if sufficient data is available. In this study we assumed a typical value of 8000 K, as the data were not sufficient to allow estimation.

Box A.3 : *A. islandica* reproductive output

Comparing *A. islandica* reproductive output with other mollusk species from the DEB collection revealed average to high values compare to the rest of species. See plots below:



Plots of maximum reproduction rate as function of size. Left: values are plotted at reference temperature (20 C); right: values are provided at a typical temperature for each species. Small (black) dots: all Mollusca; large (blue) dots: only Bivalvia; green square: *A. islandica*; and yellow square: *T. gigas*

Box A.4 Mean life span

Section 6.1.1 of Kooijman (2010) specifies the mean age at death as : $a_m = \Gamma\left(\frac{4}{3}\right)/\dot{h}_W$ where Γ is the gamma function and $\dot{h}_W = (\frac{\ddot{h}_a e\,\dot{v}}{6\,L})^{1/3}$. e is the scaled reserve density ($e = \frac{E}{V[E_m]}$) and $[E_m] = \frac{\{\dot{p}_{Am}\}}{\dot{v}}$ is the maximum reserve density (J/cm^3). We refer the reader to that chapter for the full derivation and underlying assumptions which is outside the scope of this appendix.

The mean life span at abundant food ($e = 1$) and at maximum size, i.e. $L = L_\infty = \kappa \frac{\{\dot{p}_{Am}\}}{[\dot{p}_M]}\, s_\mathcal{M}$ is derived from this expression:

$$a_m = \frac{\Gamma\left(\frac{4}{3}\right)}{\dot{h}_W} = \Gamma\left(\frac{4}{3}\right)\ \left(\left(\frac{6L}{\ddot{h}_a e\,\dot{v}}\right)^{1/3}\right) \approx 1.62\left(\frac{L}{\ddot{h}_a e\,\dot{v}}\right)^{1/3}$$

$L = L_\infty$ and $e = 1$ is substituted into the expression above which gives:

$$a_m = 1.62\left(\frac{L_\infty}{\ddot{h}_a\,\dot{v}}\right)^{1/3} = 1.62\left(\frac{\kappa\,\{\dot{p}_{Am}\}s_\mathcal{M}}{\ddot{h}_a\,v[\dot{p}_M]}\right)^{1/3}$$