Polar Biol (2017) 40:2429–2433
https://doi.org/10.1007/s00300-017-2154-8

SHORT NOTE

# Comment on the ecophysiology of the Greenland shark, *Somniosus microcephalus*

**Starrlight Augustine**[1] · **Konstadia Lika**[2] · **Sebastiaan A. L. M. Kooijman**[3]

Received: 23 March 2017 / Revised: 11 June 2017 / Accepted: 27 June 2017 / Published online: 5 July 2017

**Abstract** The recent finding that the Greenland shark, *Somniosus microcephalus*, reaches a life-span of almost 4 centuries and attains sexual maturity around 1.5 centuries, made us wonder what metabolic differences were responsible for these seemingly extreme values, compared to the related and better known spurdog *Squalus acanthias*. We studied this in the context of the dynamic energy budget (DEB) theory for metabolic organisation, which was applied to some 700 animal species from all large phyla and all chordate orders. The referenced data, estimated parameters and implied properties for all these species are published in the online Add-my-Pet collection, which provides a frame of reference for metabolic and life history properties. Given the few known data on *S. microcephalus*, we were able to estimate ageing parameters and gestation time, by application of the standard DEB model. We inferred that a recently estimated life-span of 392 years is probably too short for life at 2 °C, rather than too long. The ageing acceleration is only slightly smaller than that of the spurdog, and the gestation time is very likely between 8 and 18 years with the implication of around 200–700 pups per life-time. The low body temperature and high maximum reserve density of *S. microcephalus* could be identified as the causes of its long life-span. We see the latter cause as an adaptation to a life in the deep sea sporadically preying on big carcasses, where it is necessary to survive long spells of starvation. This application of the standard DEB model shows that it can be applied in situations where few data are available and how implied properties (gestation) can be used to constrain parameter values. The methods used here could be further developed by fisheries biologists working with deep sea species for which very little is known.

**Keywords** *Somniosus microcephalus* · *Squalus acanthias* · life-span · gestation time · maintenance rate · reserve density · add-my-pet · Dynamic energy budget (DEB) theory

## Introduction

Dynamic energy budget (DEB) theory specifies commonalities underlying uptake and use of substrates for all organisms. Over the last 7 years, the standard DEB model has been applied to animal species for all large phyla and all chordate orders with a mean relative error of less than 0.1 for thousands of data sets. The data and the resulting parameter estimates for 695 species at 2017/06/10 are compiled in the ever expanding online data base: Add-my-Pet AmP (2017). Kooijman and Lika (2014) compare the various fish taxa on the basis of DEB models. That the standard DEB model can capture both pre- and post-natal growth for sharks is demonstrated in Kooijman (2014) for the milk shark *Rhizoprionodon acutus*.

The recent finding that the Greenland shark, *Somniosus microcephalus*, could reach a life-span of 392 years (Nielsen et al. 2016), give or take 120 years, inspired us to see what the application of the standard DEB model could

✉ Starrlight Augustine
sta@akvaplan.niva.no

Sebastiaan A. L. M. Kooijman
bas.kooijman@vu.nl

[1] Akvaplan-niva, Fram High North Research Centre for Climate & Environment, 9296 Tromsø, Norway

[2] Department of Biology, University of Crete, 70013 Heraklion, Greece

[3] VU University Amsterdam, Amsterdam, The Netherlands

tell us about the ageing rate and see how exceptional this remarkable life-span actually is, with respect to other sharks in AmP (2017).

In the following sections, we will first describe data for *S. microcephalus*, the model we used and the parameter estimation method. Then we will present results and discuss them with respect to DEB parameters of a closely related shark, the spurdog *Squalus acanthias*.

## Materials and methods

### Data and pseudo-data

We collected the following data from the literature: time since birth at maturity is 156 years (Nielsen et al. 2016), length at birth is 40 cm (MacNeil et al. 2012), maximum length is 640 cm (Bigelow and Schroeder 1948 in MacNeil et al. 2012), maximum litter size is 10 pups for a 500-cm-long female (Koefoed 1957). The length at maturation was taken to be 480 cm after (MacNeil et al. 2012).

In addition, we include length–weight relationships reported in Leclerc et al. (2012), Nielsen et al. (2014) and length after 16 years from a unique case of recapturing a tagged animal (Hansen 1963 in MacNeil et al. 2012). The gender of the recaptured animal is not known.

We estimate parameters for females, but males are smaller and are thought to mature at a smaller size. Length at maturity for females is reported to range between 355 and 480 cm according to MacNeil et al. (2012). The authors suggest that males mature at 260 cm. 447 cm is the observed length of one mature female in Nielsen et al. (2014). Yano et al. (2007) expect a length at maturity of 450 cm for females and 300 cm for males.

We refer to MacNeil et al. (2012) for a full discussion of what is known in the literature on the reproductive biology of this species. They conclude that length at birth must be between 40 and 90 cm.

We assumed that the typical temperature is 2 °C. Gestation time and litter interval are unknown.

To make sure that all parameters can be estimated, we added pseudo-data, see Lika et al. (2011), with reduced weight coefficients, see subsection on parameter estimation. The values, which turn out to be typical for many animal species, were energy conductance $\dot{v} = 0.02$ cm $\mathrm{d}^{-1}$, allocation fraction $\kappa = 0.8$, reproduction efficiency $\kappa_R = 0.95$, growth efficiency $\kappa_G = 0.8$ (based on dry/wet weight ratio of 0.2), maturity maintenance rate coefficient $\dot{k}_J = 0.002$ $\mathrm{d}^{-1}$, specific somatic maintenance $[\dot{p}_M] = 18$ J $\mathrm{d}^{-1}\mathrm{cm}^{-3}$. We checked that the values for the pseudo-data $\kappa$, $\dot{v}$ and $[\dot{p}_M]$ affected the resulting parameter estimates only little. We refer the reader to the downloadable code to see how exactly the values for the pseudo-data contribute to the resulting parameter estimates, but we believe that our choices are realistic.

### Standard DEB model

The standard DEB model, see Kooijman (2010), that we fitted to data is as follows: Three life stages are delineated: embryo (which does not eat), juvenile (which does not allocate to reproduction) and adult. The transition events, called birth and puberty, respectively, depend on maturity (=level of complexity), which has no matter or energy, and only the embryo and juvenile increase their maturity, adults don't. Metabolic rates depend on temperature according to the Arrhenius rule. The body of the individual consists of reserve and structure in terms of matter, and of maturity and damage by ageing in terms of quality. The adult also has a reproduction buffer that is continuously filled by reserve allocation to reproduction and emptied at events by production of one or more eggs (and/or sperm). Food, reserve and structure are assumed to have a constant chemical composition and thermodynamic properties, a property called strong homeostasis.

Food uptake is proportional to (structural) surface area. The individual either searches for food or processes it, while the processing time is independent of food availability. These three rules fully specify food uptake as function of food availability.

Food is converted to reserve; reserve is mobilised for metabolic use at a rate such that weak homeostasis is preserved: reserve density, defined as the ratio between reserve and structure, remains constant in juveniles and adults if (and only if) food availability remains constant. This property fully specifies reserve mobilisation.

A fixed fraction, called $\kappa$, of mobilised reserve is allocated to somatic maintenance plus growth of structure, the combination of endpoints that is called soma, the rest is allocated to maturity maintenance plus maturation in the embryo and juvenile, or deposited in a reproduction buffer in the adult. Somatic maintenance is proportional to the amount of structure, maturity maintenance to the level of maturity. Maturity is quantified as the cumulative amount of reserve that was invested into maturity.

The embryo starts as a blob of reserve, with zero structure, maturity and damage by ageing. The initial amount of reserve of an egg is such that the reserve density at birth equals that of the mother at egg laying, a property called maternal effect.

The ageing module assumes that the formation of damage inducing compounds, e.g. modified mitochondrial DNA, is proportional to dioxygen consumption. These damage inducing compounds produce damage compounds, e.g. modified proteins, and the hazard rate for ageing is taken proportional to the density of damage compounds. Dioxygen consumption is obtained by closing the mass balance for the 4 most abundant chemical elements, C, H, O and N, given that food and dioxygen are consumed and feaces, carbon dioxide, water and ammonia are produced.

## Parameter estimation

The parameter estimation is presented in detail at the online AmP manual (http://www.debtheory.org/wiki/) and summarised here. All parameters were estimated from all $n$ available data sets simultaneously on the basis of the minimisation of the loss function $F = \sum_{i=1}^{n} \sum_{j=1}^{n_i} w_{ij} \frac{(d_{ij} - p_{ij})^2}{d_i^2 + p_i^2}$ (paper in preparation), where data set $i$ has $n_i$ data points, $w_{ij}$'s are weight coefficients, $d_{ij}$'s are data points, $p_{ij}$'s are predicted values, $d_i = n_i^{-1} \sum_{j=1}^{n_i} d_{ij}$ is the mean value for dataset $i$, $p_i = n_i^{-1} \sum_{j=1}^{n_i} p_{ij}$ is the mean predicted value for dataset $i$. We used the Nead-Melder simplex method, to find the minimum and the parameter estimated, using a filter that prevents that trials for parameter values are outside the boundaries of the physically allowed values, see Lika et al. (2014). The weight coefficients $w_{ij}$ for data points were set to $n_i^{-1}$, but those for the pseudo-data points energy conductance $\dot{v}$, reproduction efficiency $\kappa_R$, specific somatic maintenance $[\dot{p}_M]$ and maturity maintenance rate coefficient $\dot{k}_J$ were set to 0.1 and that for growth efficiency $\kappa_G$ to 20.

All code, data and results are downloadable from http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Somniosus_microcephalus_res.html, which allows, in combination with the freely downloadable DEBtool at http://www.bio.vu.nl/thb/deb/deblab/, to repeat all our computations, down to the tiniest detail. This also holds for the spurdog what we use for comparison. We present the resulting parameters and discuss the findings in the following section.

## Results and discussion

### Litter interval

We estimated the DEB parameters on the assumption that the litter interval was 1, 2, etc years, and then saw what the expected gestation times were, see Table 1. A decreasing energy allocation to reproduction (i.e. the fraction of mobilised energy not allocated to soma) affects ontogeny, including embryo development, the reason being that this also decreases the amount of energy allocated to development in embryos.

Given 10 pups per litter, the larger the assumed interlitter interval, the larger the gestation time and allocation fraction to soma. Given that the gestation time must be smaller than the litter interval in this ovoviviparous shark, we can conclude that the gestation time is at least 8 years, which amounts to a maximum life-time reproductive output of 707 pups per female (at 2 °C), if ageing would be the only cause of death. In practice it will be much less.

We accurately predict growth of the tagged individual who was recaptured 16 years later in MacNeil et al. (2012), and estimate that the scaled function response $f = 0.46$, meaning that food intake was about half the maximum possible one for an individual of that size; $f = 0$ means no food, and $f = 1$ means *ad libitum* feeding. These DEB parameters imply that the annual growth rate is 1.5 cm year$^{-1}$ for a 260-cm shark that is living at $f = 0.6$ and 2.9 cm year$^{-1}$ at $f = 1$ .

### Metabolism

"The ecological significance of Greenland shark cannot be fully evaluated without estimates of shark abundance and an understanding of metabolic expenditures" (Nielsen et al. 2014). We cannot agree more, which is why we performed this study.

Metabolism affects ageing, as discussed in the subsection on the standard DEB model. The mean life-span at abundant food is approximately (Kooijman 2010, Section 6.1.1)

$$1.62 \left( \frac{\kappa \{\dot{p}_{Am}\}}{\ddot{h}_a \dot{v} [\dot{p}_M]} \right)^{1/3} = 1.62 \left( \frac{L_m}{\ddot{h}_a \dot{v}} \right)^{1/3}$$

with ageing acceleration $\ddot{h}_a$, energy conductance $\dot{v}$, volume-specific somatic maintenance rate $[\dot{p}_M]$, allocation fraction to soma $\kappa$ and surface area-specific maximum assimilation rate $\{\dot{p}_{Am}\}$, maximum structural length $L_m$, (see Lika et al. 2011, Table 1, for an in depth description of these DEB the parameters). We compare *S. microcephalus* with *S. acanthias*, on the basis of parameters at a reference temperature of 20 °C, using an Arrhenius temperature of 8 kK, which is a typical value for many species. This better known order member of 12 kg has a life-span of 80 years at 9 °C, which translates to 160 years at 2 °C.

Table 2 shows that the specific somatic maintenance and the allocation fraction to soma are quite similar for both species, implying that the difference in specific maximum assimilation directly relates to difference in maximum structural length. The allocation fraction $\kappa$ of mobilised reserve to soma quantifies the allocation to somatic maintenance plus growth, relative to that to maturity maintenance and maturation (before puberty) or reproduction (after puberty). Since birth occurs when maturity hits a threshold parameter, an increase in $\kappa$ results in a longer waiting time to reach that threshold, hence, elongates the gestation time.

**Table 1** Estimates (assuming a length at birth of 40 cm) for the gestation time at 2 °C and allocation fraction to soma, for different values of the inter-litter interval and the resulting mean relative error (MRE) of data predictions for *Somniosus microcephalus*

| Llitter interval (year) | Gestation time (year) | Allocation fraction | MRE |
|---|---|---|---|
| 1 | 7.24 | 0.53 | 0.082 |
| 2 | 7.77 | 0.65 | 0.066 |
| 5 | 7.97 | 0.80 | 0.064 |
| 8 | 8.03 | 0.87 | 0.065 |
| 9 | 8.05 | 0.89 | 0.065 |
| 10 | 8.06 | 0.90 | 0.065 |
| 15 | 8.11 | 0.93 | 0.066 |

**Table 2** Parameter estimates for *Somniosus microcephalus* and *Squalus acanthias* at 20 °C, using an Arrhenius temperature of 8 kK

| Species | Ageing acceleration $\ddot{h}_a$ (d$^{-1}$) | Spec. somatic maintenance $[\dot{p}_\text{M}]$ (J d$^{-1}$ cm$^{-3}$) | Energy conductance $\dot{v}$ (cm d$^{-1}$) | Allocation fraction $\kappa$ | Spec. max. assim. rate $\{\dot{p}_\text{Am}\}$(J d$^{-1}$ cm$^{-2}$) |
|---|---|---|---|---|---|
| *S. microcephalus* | $8.041 \times 10^{-10}$ | 19 | 0.02 | 0.89 | 1350 |
| *S. acanthias* | $2.076 \times 10^{-9}$ | 34 | 0.03 | 0.85 | 559 |

Moreover, we see that ageing accelerations are quite similar, implying that the difference in life-span is mainly due to the difference in maximum reserve density (i.e. reserve per structure), $[E_m] = \{\dot{p}_\text{Am}\}\dot{v}^{-1}$, which is the ratio of the specific maximum acceleration (i.e. input to reserve) and the energy conductance (i.e. drain of reserve), amounting to 57 and 20 kJ cm$^{-3}$ for *S. microcephalus* and *S. acanthias*, respectively. So the Greenland shark has 2.8 times more reserve capacity than the spurdog, meaning that it can survive starvation roughly three times as long at the same temperature. The formula for the expected life-span, as shown in the section on metabolism, tells us that this trait has the side effect that the Greenland shark can live twice as long, as far as ageing is concerned. A conclusion that is not that self-evident without application of the theory.

The values for allocation fraction $\kappa$ are similar between both species; the main metabolic difference between *S. microcephalus* and *S. acanthias* is the assimilation capacity and the maximum reserve density. The latter might be an adaptation to life in deep water and eating big food items with long spells of fasting.

Notice that, DEB theory assumes that somatic maintenance is only paid for structure, not for reserve, so the weight-specific maintenance for *S. microcephalus* is much smaller than that of *S. acanthias*, since both structure and reserve contribute to body weight.

## Size at birth

Since the few data have no redundancy, inaccuracies in data directly translate into inaccuracies in parameter values. As mentioned before, size at birth might be anywhere between 40 and 90 cm. We re-did all of the estimations assuming a size at birth of 90 cm to see how sensitive the expected gestation times were (not shown). In this case, the allocation fraction to soma is much lower, 0.60 and the expected litter interval is at least 19 years and gestation time would be in the order of 18 years. The expected life-time reproductive output in this case is about 220. Again it will be less in practice because food is probably not *ad libitum* and life-span is not maximum.

There are 24 chondrichthyans in AmP (2017). The frill shark, *Chlamydoselachus anguineus*, holds the record in terms of longest gestation time for sharks: 3.5 years at 4 °C. This is very well captured with the standard DEB model. The Greenland shark beats this record at least by a factor 3, but this estimate is sensitive to the size at birth. An increase in size at birth means an increase in the maturity level at birth and, given the reproduction rate (number of pups per time), an increase in allocation to reproduction, so a decrease in allocation fraction $\kappa$. Since the change in maturity threshold at birth and that in allocation fraction to soma have opposite effects on the gestation time, the result is complex enough to work out the consequences in more detail.

Figure 1 shows the survival functions for allocation fraction to soma $\kappa$, i.e. the fraction of $\kappa$'s that exceeds value $\kappa$, for all 695 animal species in the collection, and that for the 24 chondrichthyans species. The value for $\kappa$ follows a beta distribution among animal species with perplexing accuracy, with a median value of 0.9. Although we don't know why $\kappa$ follows a beta distribution, it shows that the pseudo-data point $\kappa = 0.8$, which was used for all entries, hardly affected the resulting parameter estimates. The median value for the 24 chondrichthyans is somewhat

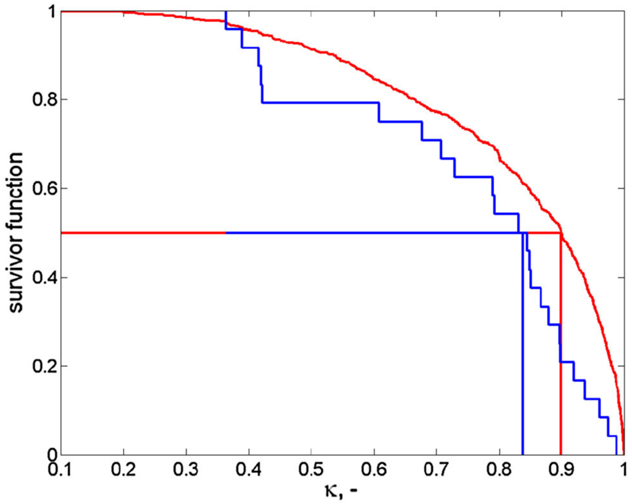

**Fig. 1** Plots of the survivor functions for the allocation fraction to soma, $\kappa$, for all 695 animal species in the AmP collection (*red smooth curve*) and the 24 chondrichthyans (*blue curve* with pronounced steps). The median values are 0.9 for all species and 0.82 for chondrichthyans. (Color figure online)

lower, however, namely $\kappa = 0.82$. This observation is key for a second thought on the 'observed' length at birth, which is an rather unsure data point. A length at birth of 40 cm gave $\kappa = 0.89$ (with gestation time of 8 years), but a length at birth of 90 cm gave $\kappa = 0.6$ (with gestation time of 18 years). It is likely, therefore, that a more typical value for length at birth is somewhere between 40 and 90 cm, giving a likely gestation time between 8 and 18 years.

After determining that the Greenland shark is among the longest living animals on earth, (Nielsen et al. 2016) state that that their "estimates strongly suggest a precautionary approach to the conservation of the Greenland shark".

It is their new information on the age at maturation (in combination with the existing data) that allowed us to estimate DEB parameters and discover the constraint on the litter-interval. With a gestation time of 8–18 years, a precautionary approach is indeed required. This study is the first that provide estimates of metabolism and reproductive output giving added value to years of dedicated field research. We hope that this will be useful to the community.

This application of the standard DEB model shows that it can be applied in situations where few data are available, see also van der Meer and Kooijman (2014) and how implied properties can be used to constrain parameter values. Parameter estimates for *S. microcephalus* and *S. acanthias*, computational details and code can be found in the add-my-pet collection (AmP 2017)

**Acknowledgements** This work is supported by the Norwegian Research Council Marinforsk program (FREE 255295). The authors thank Gonçalo Marques and Laure Pecquerie for relevant discussions and critical feedback. The authors also thank 2 anonymous reviewers and Roger Nisbet for valuable comments which improved this study.

## References

Add-my-pet collection (2017) http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html. Accessed 10 June 2017

Koefoed E (1957) Notes on the Greenland shark *Acanthorhinus carcharias* (Gunn). 2. a uterine foetus and the uterus from a Greenland shark. Fiskerdir. Skr. Ser. Havunders 11(10):8–12

Kooijman SALM (2010) Dynamic energy budget theory for metabolic organisation, 3rd edn. Cambridge University Press, Cambridge, ISBN 9780521131919

Kooijman SALM (2014) Metabolic acceleration in animal ontogeny: an evolutionary perspective. J Sea Res 94:128–137

Kooijman SALM, Lika K (2014) Comparative energetics of the 5 fish classes on the basis of dynamic energy budgets. J Sea Res 94:19–28

Leclerc LME, Lydersen C, Haug T, Bachmann L, Fisk AT, Kovacs KM (2012) A missing piece in the arctic food web puzzle? Stomach contents of Greenland sharks sampled in Svalbard, Norway. Polar Biol 35(8):1197–1208

Lika K, Augustine S, Pecquerie L, Kooijman SALM (2014) The bijection from data to parameter space with the standard DEB model quantifies the supply-demand spectrum. J Theor Biol 354:35–47

Lika K, Kearney MR, Kooijman SALM (2011) The "covariation method" for estimating the parameters of the standard dynamic energy budget model II: properties and preliminary patterns. J Sea Res 66:278–288

MacNeil MA, McMeans BC, Hussey NE, Vecsei P, Svavarsson J, Kovacs KM, Lydersen C, Treble MA, Skomal GB, Ramsey M, Fisk AT (2012) Biology of the Greenland shark *Somniosus microcephalus*. J Fish Biol 80(5):991–1018

Nielsen J, Hedeholm RB, Heinemeier J, Bushnell PG, Christiansen JS, Olsen J, Ramsey CB, Brill RW, Simon M, Steffensen KF, Steffensen JF (2016) Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). Science 353(6300):702–704

Nielsen J, Hedeholm RB, Simon M, Steffensen JF (2014) Distribution and feeding ecology of the Greenland shark (*Somniosus microcephalus*) in Greenland waters. Polar Biol 37(1):37–46

van der Meer J, Kooijman SALM (2014) Inference on energetics of deep-sea fish that cannot be aged: the case of the hagfish. J Sea Res 94:138–143

Yano K, Stevens JD, Compagno LJV (2007) Distribution, reproduction and feeding of the Greenland shark Somniosus (Somniosus) microcephalus, with notes on two other sleeper sharks, Somniosus (Somniosus) pacificus and Somniosus (Somniosus) antarcticus. J Fish Biol 70(2):374–390