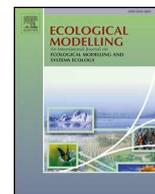




ELSEVIER

Contents lists available at ScienceDirect

## Ecological Modelling

journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)

# Can DEB models infer metabolic differences between intertidal and subtidal morphotypes of the Antarctic limpet *Nacella concinna* (Strebel, 1908)?

Charlène Guillaumot<sup>a,b,\*</sup>, Thomas Saucède<sup>b</sup>, Simon A. Morley<sup>c</sup>, Starrlight Augustine<sup>d</sup>,  
Bruno Danis<sup>a</sup>, Sebastiaan Kooijman<sup>e</sup>

<sup>a</sup> Laboratoire de Biologie Marine, Université Libre de Bruxelles, Avenue F.D.Roosevelt, 50. CP 160/15. 1050 BRUXELLES, BELGIUM

<sup>b</sup> UMR 6282 Biogéosciences, Univ. Bourgogne Franche-Comté, CNRS, EPHE, 6 bd Gabriel F-21000 Dijon, France

<sup>c</sup> British Antarctic Survey, Natural Environment Research Council, Cambridge, CB30ET UK

<sup>d</sup> Kvaplan-Niva, Fram High North Research Centre for Climate and the Environment, 9296 Tromsø, Norway

<sup>e</sup> Department of Theoretical Biology, VU University Amsterdam, de Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

## ARTICLE INFO

## Keywords:

ecological modelling  
Southern Ocean  
marine benthic species  
model relevance  
model accuracy

## ABSTRACT

Studying the influence of changing environmental conditions on Antarctic marine benthic invertebrates is strongly constrained by limited access to the region, which poses difficulties to performing long-term experimental studies. Ecological modelling has been increasingly used as a potential alternative to assess the impact of such changes on species distribution or physiological performance.

Among ecological models, the Dynamic Energy Budget (DEB) approach represents each individual through four energetic compartments (i.e. reserve, structure, maturation and reproduction) from which energy is allocated in contrasting proportions according to different life stages and to two forcing environmental factors (food resources and temperature).

In this study, the example of an abundant coastal limpet, *Nacella concinna* (Strebel 1908), was studied. The species is known to have intertidal and subtidal morphotypes, genetically similar but physiologically and morphologically contrasting.

The objectives of this paper are (1) to evaluate the potential of the DEB approach, and assess whether a DEB model can be separately built for the intertidal and subtidal morphotypes, based on a field experiment and data from literature and (2) to analyse whether models are contrasting enough to reflect the known physiological and morphological differences between the morphotypes.

We found only minor differences in temperature-corrected parameter values between both populations, meaning that the observed differences can be only explained by differences in environmental conditions (i.e. DEB considered variables, food resources and temperature, but also other variables not considered by DEB). Despite the known morphological difference between the populations, the difference in shape coefficients was small.

This study shows that even with the amount of data so far available in the literature, DEB models can already be applied to some Southern Ocean case studies, but, more data are required to accurately model the physiological and morphological differences between individuals.

## 1. Introduction

Antarctic regions have faced strong environmental change since the twentieth century (recently reviewed in [Henley et al. 2019](#)), with a strong warming in some regions, such as in the Western Antarctic Peninsula ([King et al. 2003](#), [Vaughan et al. 2003](#), [Meredith and King 2005](#)), leading to important shifts in sea ice regimes and seasonality, including the duration and extent of sea ice cover

([Stammerjohn et al. 2012](#), [Turner et al. 2016](#), [Schofield et al. 2017](#)). The increase in the rate of glacier melting has been reported as a cause of important disturbance of the physical (currents, salinities) and biological environment (phytoplankton blooms, communities) ([Meredith and King 2005](#), [Schloss et al. 2012](#), [Bers et al. 2013](#)). Such changes have a direct impact on marine communities and particularly in coastal marine areas (both intertidal and subtidal) ([Barnes and Peck 2008](#), [Smale and Barnes 2008](#), [Barnes and Souster 2011](#),

\* Corresponding author.

E-mail address: [charleneguillaumot21@gmail.com](mailto:charleneguillaumot21@gmail.com) (C. Guillaumot).

<https://doi.org/10.1016/j.ecolmodel.2020.109088>

Received 30 January 2020; Received in revised form 12 April 2020; Accepted 13 April 2020

0304-3800/ Crown Copyright © 2020 Published by Elsevier B.V. All rights reserved.

Waller et al. 2017, Stenni et al. 2017, Gutt et al. 2018), which are places of complex land-sea interface and ecological processes. The multiple effects of ice retreat and meltwater on nearshore marine habitats have contributed to the expansion of intertidal zones and habitat alteration due to seawater freshening and stratification, shifting near-shore sedimentation, changes in water properties and current dynamics.

However, studying Antarctic marine life is challenging. Not only do the environmental conditions make the region difficult to access and work in, but substantial financial and technical constraints make field sampling and experiments difficult to organise (e.g. cold, ice, duration of daylight; Kaiser et al. 2013, Kennicutt et al. 2014, 2015, Xavier et al. 2016, Gutt et al. 2018). However, conducting physiological studies of Antarctic marine organisms has become urgent as we aim to assess their sensitivity and potential response (resilience, distribution shift or local extinction) to environmental change, a key issue for the conservation of marine life and special protected areas (Kennicutt et al. 2014, 2015, 2019 <https://www.ccamlr.org/en/organisation/home-page>).

An alternative to completing studies in these environments is the use of modelling approaches. Data needs interpretation to test hypotheses, which involves assumptions, that need to be explicit. Using a modelling approach is therefore a good strategy. Ecological modelling is used to describe species distribution and assess their climate envelopes (Eliith et al. 2006, Peterson et al. 2011), study species tolerances to toxicants and to environmental change (Jager et al. 2014, Petter et al. 2014, Baas and Kooijman 2015) and model species energetic performance (Serpa et al. 2013, Thomas et al. 2016). Among these ecological models, the Dynamic Energy Budget (DEB) theory (Kooijman, 2010) has become increasingly popular. DEB parameters have been so far estimated for more than 2,000 animal species and collected in the 'Add-my-Pet' (AmP) collection ([http://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/](http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/)). It constitutes one of the most powerful approaches to characterize individual metabolic performances (Nisbet et al. 2012, Kearney et al. 2015, Jusup et al. 2017) and can be calibrated for data-poor animals (Mariño et al. 2019). DEB models rely on thermodynamic concepts (Jusup et al. 2017) and study how energy flows are driven within individuals during their entire life cycle (Kooijman 2010). Each individual is divided into four energetic compartments: reserve  $E$ , structure  $V$ , maturation  $E_H$  and reproduction  $E_R$  from which the energy is allocated in contrasting proportions according to the different life stages and two forcing environmental factors (i.e. food resources and temperature).

DEB models can be built with data coming from experiments and/or literature, to quantify age, length, weight of the different life stages and provide information on reproduction, growth and metabolic rates to calibrate the model (van der Meer 2006, Marques et al. 2014).

Application of DEB models to Antarctic species is increasing. They can be easily extracted from the AmP collection, using the software AmPtool. The Matlab command "select\_eco('ecozone', {'MS'})" presently gives a list of 37 species, where MS stands for "Marine, Southern Ocean". Command "select\_eco('ecozone', {'TS'})" gives another 3 species for the terrestrial Antarctic environment, among which the mite *Alaskozetes antarcticus*. Among the most common and well studied Southern Ocean benthic invertebrates are the sea star *Odontaster validus* (Agüera et al. 2015), the bivalve *Laternula elliptica* (Agüera et al. 2017), the bivalve *Adamussium colbecki* (Guillaumot 2019a) and the sea urchins *Sterechinus neumayeri* (Stainthorp and Kooijman 2017) and *Abatus cordatus* (Arnould-Pétré et al. this issue). DEB models have also been developed for some pelagic species such as the Antarctic krill *Euphausia superba*, the salp *Salpa thompsoni* (Jager and Ravagnan 2015, Henschke et al. 2018) and are under development for marine mammals such as the elephant seal *Mirounga leonina* (Goedegebuure et al. 2018). Antarctic species have a range of notable physiological traits when compared to their temperate counterparts. Among others, they are physiologically adapted to constant cold temperatures (Peck et al. 2009, Morley et al. 2009, 2014), shifting day length also

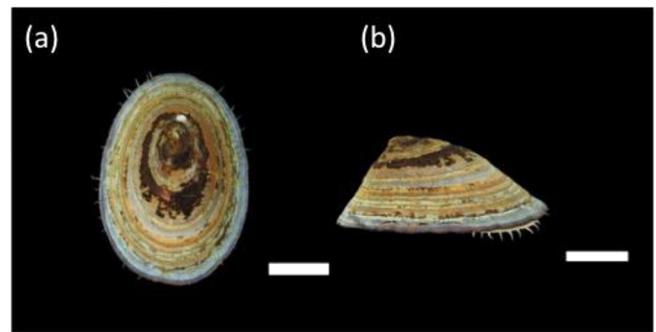


Figure 1. *Nacella concinna* in apical view (a) and lateral view (b). Scale bar: 1 cm. Source: Q. Jossart, B121 expedition.

imposes a marked seasonal feeding behaviour (McClintock 1994, Clarke et al. 2008, Halanych and Mahon 2018), and they exhibit slow metabolic and growth rates, explaining their longer lifespans and higher longevities compared to species in other regions (Peck and Brey 1996, Peck 2002).

The limpet *Nacella concinna* (Strebel, 1908) (Mollusca: Patellogastropoda) is a common and abundant gastropod of shallow marine benthic communities. Distributed all along the Western Antarctic Peninsula (González-Wevar et al. 2011, phylogeny recently reviewed in González-Wevar et al. 2018), it has widely been studied for decades (Shabica 1971, 1976, Walker 1972, Hargens and Shabica 1973, Houlihan and Allan 1982, Peck 1989, Clarke 1989, Cadée 1999, Ansaldo et al. 2007, Fraser et al. 2007, Markowska and Kidawa 2007, Morley et al. 2011, 2014, Suda et al. 2015, Souster et al. 2018). The limpet is found from intertidal rocky shores down to over 100 meters depth (Powell 1951, Walker 1972). It has a 2-5 cm long shell (Fig. 1), that grows only a few millimeters a year with a seasonal pattern. It is sexually mature after four to six years and has a life span of up to 10 years (Shabica 1976, Picken 1980, Brêthes et al. 1994). The limpet mainly feeds on microphytobenthos and microalgae (Shabica 1976, Brêthes et al. 1994). It spawns free-swimming planktonic larvae once a year, when water temperature rises in the austral summer (Shabica 1971, Picken 1980, Picken and Allan 1983). Larvae drift in the water column and metamorphose after more than two months (Stanwell-Smith and Clarke 1998).

*N. concinna* does not have a homing behaviour (Stanwell-Smith and Clarke 1998, Weihe and Abele 2008, Suda et al. 2015) and intertidal individuals can either migrate to subtidal areas in winter to escape freezing air temperatures that may drop below  $-20^{\circ}\text{C}$  (Walker 1972, Branch 1981, Brêthes et al. 1994) or shelter in rock cracks and crevices in the intertidal area. In the latter case, they do not become dormant but have a limited access to microphytobenthos, as recently observed around Adelaide Island (Obermüller et al. 2011).

Two morphotypes of *N. concinna* have been distinguished, an intertidal and a subtidal type, with the intertidal type having a taller, heavier and thicker shell compared to the subtidal one that is characterized by a lighter and flatter shell (Beaumont and Wei 1991, Hoffman et al. 2010). Initially, Strebel (1908) and Powell (1951) referred to these two morphotypes as the 'polaris' (intertidal) and 'concinna' types (below 4m depth). From that point, the potential genetic differentiation between the two morphotypes has been investigated, some of the studies concluding an absence of genetic distinction (Wei 1988, Beaumont and Wei 1991, Nolan 1991) while contrarily, de Aranzamendi et al. (2008) reported significant differences based on inter-simple sequence repeat (ISSR) markers. More recently, this last method was questioned (Hoffman et al. 2010) and several studies using different markers and populations (Chwedorzewska et al. 2010, Hoffman et al. 2010, González-Wevar et al. 2011) have concluded an absence of genetic differentiation between the two morphotypes.

Apart from the absence of genetic differences, intertidal and

subtidal populations strongly contrast in morphology and physiology, which has been explained by the prevalence of habitat heterogeneity and strong environmental gradients along rocky shore habitats, a common feature also observed in other gastropods (Johannesson 2003, Butlin et al. 2008, Hoffman et al. 2010). For instance, in *N. concinna*, the higher shell thickness observed in the shallow morphotype was hypothesised to play a role in resistance against crushing pack ice (Shabica 1971, Morley et al. 2010). Intertidal morphotypes are further resistant to air exposure thanks to higher shells, bigger inner volumes relative to their shell circumference, a combination that makes them more efficient than subtidal individuals, able to store more water and oxygen, reducing desiccation risks and delaying the metabolic switch to anaerobic fermentation (Nolan 1991, Weihe and Abele 2008). The subtidal morphotype has also proved to be less resistant to cold than the intertidal population (Waller et al. 2006), due to extra production of mucus and stress proteins in intertidal morphotypes (Clark et al. 2008, Clark and Peck 2009, Obermüller et al. 2011) and due to diverse metabolic processes that contrast between both populations (reviewed in Suda et al. 2015).

The development of ecological models enables precise models to be built, that highlight subtle differences in parameters between ecologically similar or closely related species (Freitas et al. 2010, Holsman et al. 2016, Marn et al. 2019, Lika et al. 2020). The idea of building individual-specific models for understanding of physiological processes is not new (Bevelhimer et al. 1985, DeAngelis et al. 1994) and grew from the development of computational ecology that resulted in the possibility of generating “individual-oriented” models (IOM's) (Hogeweg and Hesper 1990, DeAngelis et al. 1994). The IOM theory relies on the principle that “no two biological organisms are exactly alike, even when they have identical genes”. A group of organisms within a population can have contrasting size or physiological performances according to, for example, food conditions or competition. Modelling each individual, separately, therefore constitutes a powerful approach to enhance the understanding of the entire community (DeAngelis et al. 1994).

In this study, due to the known morphological and physiological differences between the morphotypes, we first separately built independent DEB models for the intertidal and subtidal morphotypes of the limpet *N. concinna*, based on field experiment and literature data, to assess the potential differences between the models. Secondly, we analyse whether the two model outputs suggest contrasting physiologies between the morphotypes, using a method recently developed in DEB theory, that tries to reduce differences in parameter values that are still consistent with the data (Lika et al. 2020). Using this method -the augmented loss function- we try to merge the information of the two species models into a single one. If DEB parameters of the two species can be merged, it means that the physiological differences between these two species are not strongly different.

These results finally help assess DEB model accuracy giving the amount of data available to build the models in the context of Antarctic case studies and help evaluate which type of information is necessary to gather in order to fill model gaps. Finally, the study evaluates if such models are valuable for studying Southern Ocean organisms in the context of altered environments.

## 2. Material and methods

### 2.1. DEB Model description

DEB models are based on an ensemble of rules that allocate energy flows to four main compartments (reserve  $E$ , structure  $V$ , maturity  $E_H$ , reproduction  $E_R$ ) according to a set of priorities and the level of complexity (i.e. maturity) gained by the organism through time (Fig. 2, Kooijman 2010). Maturity is treated as information, having mass nor energy. Food is first of all ingested and assimilated ( $\dot{p}_A$ ) and energetically stored into a reserve compartment ( $E$ ). A fraction of the

energy that is mobilised from reserve,  $\dot{p}_C$ , is divided into two branches according to the ‘kappa-rule’: a part of the energy contained in the reserve compartment ( $\kappa \cdot \dot{p}_C$ ) is allocated to somatic maintenance and structure growth, whereas the second part ( $1 - \kappa$ ).  $\dot{p}_C$  contributes to maturity (before the ‘puberty’ threshold) or reproduction (after the ‘puberty’ threshold).

The energy is allocated within and in between these branches by the establishment of some priorities, where somatic maintenance ( $\dot{p}_M$ ) has priority over growth and maturity maintenance ( $\dot{p}_J$ ) has priority over maturity and reproduction. During its lifetime, the organism allocates energy to maturity which symbolizes its complexity and reaches some life stages at some defined thresholds ( $\tau$ , birth, when the organism is capable to feed;  $E_H^J$ , metamorphosis;  $E_H^P$ , puberty, when it can reproduce). After reaching sexual maturity, the energy that was formerly allocated to maturity is attributed to the reproduction buffer and the available energy is allocated to the development of gametes.

Different types of DEB models have been developed and coded for parameter estimation, see frequently updated [https://github.com/addmy-pet/DEBtool\\_M](https://github.com/addmy-pet/DEBtool_M) page (Marques et al. 2018, 2019). Here, the *abj* model was used for *N. concinna*. This model considers that growth acceleration occurs between birth and metamorphosis (Kooijman 2010, Mariño et al. 2019).

The DEB model is forced by food availability and temperature. Temperature acts on metabolic rates following the Arrhenius principle (see Kooijman 2010, Jusup et al. 2017 for details). A temperature correction factor is applied to each rate that takes into account the lower and higher optimal boundaries of the individual tolerance range.

Food available for ingestion is represented by the functional response  $f$  comprised between [0,1], where 0 is starvation condition and 1 very abundant food.

The parameters of the DEB model can be estimated from multiple data on the eco-physiology of a species. The ones studied in this work are presented in Table 1.

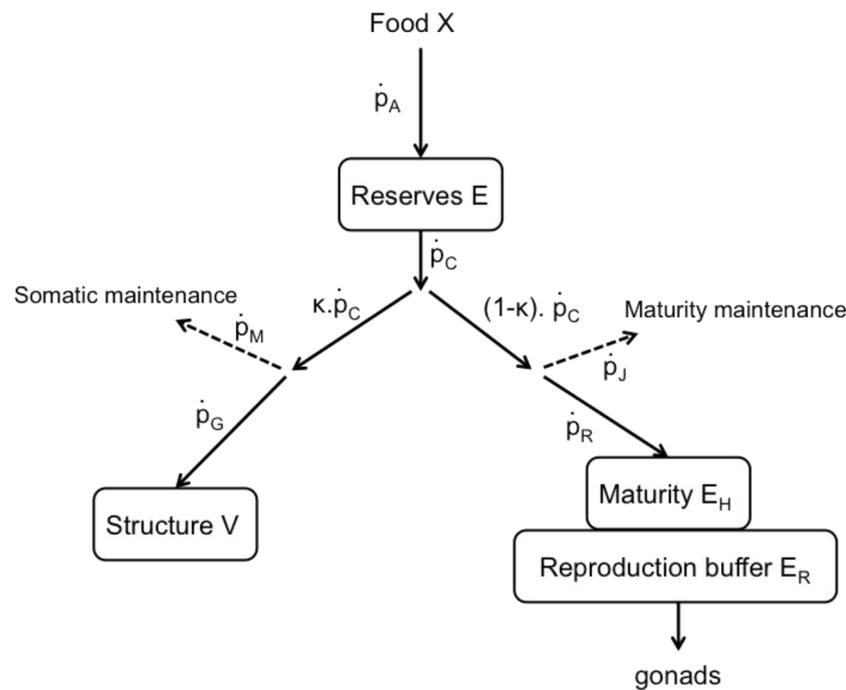
### 2.2. Data collection and DEB calibration

DEB models were calibrated using zero-variate data (single data points at defined life stages, such as length or weight at sexual maturity, number of eggs produced per female) and uni-variate data (relationships between two variables such as oxygen consumption and temperature, length~weight, weight or size~time relationships)(van der Meer 2006, Guillaumot 2019b). Data that were collected from the literature (Table 2), paying attention to the different taxonomic names adopted for the species through time (see <http://www.marinespecies.org/aphia.php?p=taxdetails&id=197296>, accessed December 2018); to the sampling area to enable the two morphotypes to be distinguished (intertidal/subtidal) and to the environmental conditions under which each dataset was recorded (available food resources and temperature).

Data from the literature were supplemented by experiments led by S. Morley at Rothera Station (Adelaide Island, Western Antarctic Peninsula) in January-February 2018 (details in Appendix A). Individual shells were brought back to Europe and processed with imagery to collect growth ring data (Appendix B).

Some data are shared between the intertidal and subtidal morphotypes due to a lack of information on the morphotypes physiology in the literature (Table 2). The characteristics of the first developmental life stage, when the larvae become able to feed (i.e. age, length and weight at birth) and the pace of development (i.e. age at puberty, maximal observed age) are assumed to be identical.

Each data set was characterised by the corresponding temperature and food resources present in the field. Food resources were represented in the model by a scaled functional response  $f$  constrained between 0 and 1, with 0 meaning no food availability and 1 maximal food abundance.  $f$  parameters were differentiated between the different stations along with temperatures. Food is very abundant in the field for the limpet and  $f$  parameters were therefore kept fixed with values  $\geq$



**Figure 2.** Schematic representation of the standard DEB model, with energy fluxes (arrows, in  $J \cdot d^{-1}$ ) that connect the four compartments (boxes). Energy enters the organism as food (X), is assimilated at a rate of  $\dot{p}_A$  into the reserve compartment (E). The mobilization rate ( $\dot{p}_C$ ), regulates the energy leaving the reserve to cover somatic maintenance ( $\dot{p}_M$ ), structural growth ( $\dot{p}_G$ ), maturity maintenance ( $\dot{p}_J$ ), maturity ( $\dot{p}_R$ ) (sexually immature individuals) and reproduction ( $\dot{p}_R$ ) (mature individuals).  $\kappa \cdot \dot{p}_C$  is the proportion of the mobilized energy diverted to  $\dot{p}_M$  and  $\dot{p}_G$ , while the remaining part  $(1-\kappa) \cdot \dot{p}_C$  is used for  $\dot{p}_J$  and  $\dot{p}_R$ .

**Table 1**  
List of the main DEB parameters, definition and units

Parameter	Description	Unit
Primary DEB parameters		
$\{\dot{p}_{Am}\}$	surface-area-specific maximum assimilation rate	$J \cdot cm^{-2} d^{-1}$
$\dot{v}$	energy conductance (velocity)	$cm \cdot d^{-1}$
$K$	fraction of mobilised reserve allocated to soma	-
$[\dot{p}_M]$	specific volume-linked somatic maintenance rate: $\dot{p}_M / V$	$J \cdot cm^{-3} d^{-1}$
$[E_G]$	volume-specific costs of structure; better replaced by $[E_V] = \kappa_G$ , where $\kappa_G$ is the fraction of growth energy fixed in structure: $[E_V] = [E_G]$	$J \cdot cm^{-3}$
$E_H^b$	maturity at birth	J
$E_H^j$	maturity at metamorphosis	J
$E_H^p$	maturity at puberty	J
$\dot{h}_a$	Weibull ageing acceleration for animals	$d^{-2}$
$s_G$	Gompertz stress coefficient	-
$\delta_M$	shape (morph) coefficient: $L = L_w$	-
$\delta_{M,larvae}$	shape (morph) coefficient of the larvae	-
Other parameters		
$Z$	zoom factor to compare body sizes inter-specifically; $z = 1$ for $L_m = 1$ cm	-
$s_M$	Acceleration factor at $f = 1$ , it is equal to the ratio of structural length at metamorphosis and birth.	-
$[E_m]$	$[E_m] = \{\dot{p}_{Am}\} / \dot{v}$ ; ratio of specific assimilation over energy conductance	$J \cdot cm^{-3}$

0.9. Food availability from the Rothera Station was described by pictures taken in the field and was estimated at  $f = 1$ . Signy and Anvers Islands  $f$  was set at 0.9 because physiological traits (growth rate, maximal size) are very close (but slightly lower) than Rothera's observations, but no precise information is available for food conditions in the different publications for these stations.

2.3. DEB parameter estimation and goodness of fit

Sets of zero and uni-variate data, supplemented by pseudo-data

were used to estimate the DEB primary parameters. Pseudo-data are extra data coming from different taxa that help calibrate the model estimation similarly to a prior element (Lika et al. 2011a). This procedure has similarities with Bayesian estimation, but are not embedded in a maximum likelihood context, since the stochastic component is not modelled. Before parameter estimation, each data set can be subjectively linked by a weight coefficient to quantify the realism of reducing variation in parameter values. Selected weight coefficients are always selected small enough in order to hardly affect parameter estimation if the information contained in the real data set is sufficient.

The DEB parameters estimation is done by simultaneously estimating each parameter using these empirical and pseudo-data by minimizing a loss function (eq. 1), using the Nelder-Mead simplex method, updated and explained in Marques et al. (2018, 2019). The loss function that is minimized is

$$\sum_{i=1}^n \sum_{j=1}^{n_i} \frac{w_{ij}}{n_j} \frac{(d_{ij} - p_{ij})^2}{\bar{d}_i^2 + \bar{p}_i^2} \tag{1}$$

where  $i$  scans datasets and  $j$  points in this dataset.  $d_{ij}$  and  $p_{ij}$  are respectively the data and the predictions and  $\bar{d}_i$  and  $\bar{p}_i$  their average values in set  $i$ .  $w_{ij}$  are the attributed coefficients,  $n$  is the number of data sets,  $n_i$  denotes the data in a dataset,  $n_j$  the data in data-points.

The value of the loss function is evaluated for each parameter trial. The goodness of fit of each prediction was quantified by the relative error (RE). The mean relative error (MRE) quantifies the overall model performance. RE corresponds to the sum of the absolute differences between observed and predicted values, divided by the predicted values. Contrarily to the loss function, the MRE does not take into consideration the weights of the different data (Marques et al. 2018). MRE values can have values from 0 to infinity, with 0 value meaning that predictions match data exactly.

2.4. Merging parameters

The augmented loss function approach developed by Lika et al.

**Table 2**  
Zero and uni-variate data used to build the intertidal and subtidal models.

INTERTIDAL GROUP			SUBTIDAL GROUP	
Zero-variate data, (unit)	Value	Reference	Value	Reference
Age at birth <i>ab</i> (days)	10	Peck et al. (2016)	Same as intertidal	
Age at puberty <i>ap</i> (years)	4	Shabica (1976)	Same as intertidal	
Maximal observed age <i>am</i> (years)	14	Shabica (1976)	Same as intertidal	
Length at birth <i>Lb</i> (cm)	0.0228	Peck et al. 2016	Same as intertidal	
Length at puberty <i>Lp</i> (cm)	1.54	S. Morley experiment (2018)	1.59	Picken (1980)
Maximal observed shell length <i>Li</i> (cm)	5.8*	Shabica (1976)	5.52**	S. Morley experiment (2018)
Wet weight of the egg <i>Ww0</i> (g)	5.8.10 <sup>-6***</sup>	Peck et al. (2016)	Same as intertidal	
AFDW at puberty <i>Wdp</i> (g)	0.0236	Shabica (1976)	0.057	S. Morley experiment (2018)
Uni-variate data, (unit)		Reference	Reference	
Length ~ AFDW <i>LWd<sub>signy</sub></i> (cm, g)		Nolan (1991), Signy Island	Nolan (1991), Signy Island	
Length ~ AFDW <i>LWd</i> (cm, g)		S. Morley experiment (2018)	S. Morley experiment (2018)	
Length ~ Gonado somatic index <i>LGSi</i> (cm, -)		S. Morley experiment (2018)	S. Morley experiment (2018)	
Length ~ Oxygen consumption <i>LJO</i> (cm, μmol/h)		S. Morley experiment (2018)	S. Morley experiment (2018)	
Temperature ~ Oxygen consumption <i>TJO</i> (K, μL/h)		Peck (1989)	Peck (1989)	
Time ~ Length <i>tL</i> (d, cm)		S. Morley experiment (2018)****	S. Morley experiment (2018)****	

\*Max sized collected individual on the field during Belgica121 expedition (Danis et al. 2019)

\*\*Shabica 1976 indicates an observed value of 5.8cm and S. Morley measurements indicate a ratio between intertidal/subtidal lengths of the morphotypes of 1.05. The unknown subtidal *Li* value was calculated as 5.8/1.05 = 5.52cm.

\*\*\*based on egg diameter of 221μm

\*\*\*\*imagery and growth ring measurements, see Appendix B

2020 is a new extension that enables to compare small variations in parameter values between (close) species. The second term (in bold) of the following equation (eq. 2) is the new extension of the ‘symmetric bounded (sb)’ loss function:

$$F_{sb} = \sum_{i=1}^n \sum_{j=1}^{n_i} \frac{w_{ij}}{n_j} \frac{(d_{ij} - p_{ij})^2}{\bar{d}_i^2 + \bar{p}_i^2} + \sum_{k=1}^N \frac{\mathbf{w}_k \mathbf{var}(\theta_k)}{\mathbf{mean}(\theta_k)^2} \quad (2)$$

where  $\mathbf{w}$ 's are weights,  $\mathbf{d}$ 's data,  $\mathbf{p}$ 's predictions,  $\theta$ 's parameters,  $\mathbf{j}$  scans data-points with a data-set of  $\mathbf{n}_i$  points ( $\mathbf{n}_i = 1$  is allowed),  $\mathbf{i}$  scans the data-sets and  $\mathbf{k}$  the parameters.

In this second term, when  $w_k = 0$ , the parameter  $\theta_k$  between species are different, but when increasing  $w_k$ , the parameter  $\theta_k$  tends to be similar between species. Therefore, the augmented loss function method uses this mathematical principle to spot potential differences between parameters of different species. First, the set of DEB parameters are separately estimated for each species and weight coefficients are set to zero. Then, for each parameter, the weight coefficient will be step-wise increased, making the loss function shift as a result. If a maximal weight value is reached without sharp changes in the loss function value along the weight increase, it means that the parameter value has a minimum variance between species. Contrarily, if the loss function value presents a sharp increase due to the change in weight coefficient, it means that the studied parameter should present contrasting values between the related species.

By applying this method to the case study of an intertidal and subtidal morphotype of the limpet *N. concinna*, we aim to evaluate whether there are any differences between both morphotypes caused by differences in parameters, or whether these differences are explained only by differences in environmental conditions (i.e. food resources and

temperature). Initially, the sets of parameters have been estimated separately for both morphotypes and all weight coefficients are set to zero. By step-wise increasing the weight coefficient for a particular shared parameter, the overall loss function may increase and a common merged DEB parameter is reached. If a common value of the DEB parameter can be found without important increase in MRE or loss function values, it means that the intertidal and subtidal morphotypes do not significantly differ for this parameter. A similar procedure is applied for each DEB parameter separately and iteratively. In order to have a quick idea of replicability in the results, the procedure was replicated five times, contrasting in different orders of DEB parameters merging (Appendix C). The order of permutation of merged parameters of these five replicates was chosen randomly among the 11! possible solutions. Changes in MRE and loss function values at each weight modification were reported and the predictions of the intertidal, subtidal and merged models were compared.

### 3. RESULTS

#### 3.1. Parameters of DEB models

DEB predictions for the separate intertidal and subtidal models are accurate, with MRE values lower than 0.2 (Table 3). Average MRE value of the AmP collection is close to 0.06. Relative Errors are quite low, with the highest values obtained for length~GSI data (RE = 0.6089 and 0.8702 for intertidal and subtidal models respectively) and time~length relationships, obtained from the sclerochronology measurements, that are highly variable between each measured shell (respectively RE = 0.3645 and 0.5924 for intertidal and subtidal models)

**Table 3**

Summary of goodness of fit, DEB model estimates at a reference temperature of  $T_{ref} = 20^{\circ}\text{C}$ . RE: Observed and predicted values for zero-variate data, relative error (RE) for the uni-variate data. See Fig. 3 for comparisons for uni-variate predictions between models. MRE = Mean Relative Error. For the merged model, the MRE values respectively correspond to the mean relative error of model prediction for data of both intertidal and subtidal populations. All DEB parameters indicated were allowed to vary during covariance estimation. The *abj* parameters that are not mentioned in that table were kept constant with the standard initial values.

	INTERTIDAL	SUBTIDAL	MERGED
<b>MRE</b>	0.166	0.192	0.196 0.227
<b>Loss function</b>	0.2441	0.2345	0.7936
<b>z (-)</b>	0.3055	0.4317	0.2579
$\{\dot{p}_{Am}\}$ (J/d. $\text{cm}^{-2}$ )	8.361	19.07	8.859
$\dot{v}$ (cm/d)	0.0501	0.0426	0.0499
<b>K (-)</b>	0.9084	0.9368	0.9256
$[\dot{p}_M]$ (J/d. $\text{cm}^{-3}$ )	19.62	31.68	24.62
$[E_G]$ (J. $\text{cm}^{-3}$ )	3956	3949	3952
$E_H^b$ (J)	0.00174	0.00115	0.0014
$E_H^j$ (J)	0.8749	0.0779	0.9206
$E_H^p$ (J)	75.23	121.4	94.66
$\dot{h}_a$ (1/d $^{-2}$ )	$5.003.10^{-8}$	$8.335.10^{-8}$	$4.24.10^{-8}$
$s_G$ (-)	$10^{-4}$	$10^{-4}$	$10^{-4}$
$\delta_M$ (-)	0.4517	0.3866	0.4247
$\delta_{M,larvae}$ (-)	0.7167	0.7125	0.7215
$s_M$ (-)	7.862	4.0491	8.5372

Zero-variate								
	Data // prediction// RE			Data // prediction// RE			prediction// RE	
<b>ab (d)</b>	10	10.62	0.0619	10	10.59	0.0586	10.61	0.0609
<b>ap (y)</b>	4	3.54	0.1141	4	3.75	0.0607	3.66	0.0845
<b>am (y)</b>	14	14	$9.4.10^{-5}$	14	13.99	$4.8.10^{-4}$	14	$1.6.10^{-4}$
<b>Lb (cm)</b>	0.0228	0.02279	$2.4.10^{-4}$	0.0228	0.0228	$6.05.10^{-4}$	0.0228	$1.424.10^{-6}$
<b>Lp (cm)</b>	1.54	1.225	0.2045	1.59	1.81	0.1384	1.49	0.0323
<b>Li (cm)</b>	6.5	5.319	0.1816	5.52	4.515	0.1827	5.184	0.2024
<b>Ww0 (g)</b>	$5.8.10^{-6}$	$5.8.10^{-6}$	0.0181	$5.8.10^{-6}$	$5.7.10^{-6}$	0.0157	$5.72.10^{-6}$	0.0138
<b>Wdp (g)</b>	0.0236	0.0263	0.1181	0.057	0.05649	0.0089	0.0396	0.6762

Uni-variate			
	RE	RE	RE
<b>LWd_signy (cm, g)</b>	0.1443	0.1698	0.1274
<b>LWd (cm, g)</b>	0.1469	0.1834	0.216
<b>LGSi (cm, -)</b>	0.6089	0.8702	0.5835
<b>LJO (cm, <math>\mu\text{mol/h}</math>)</b>	0.2567	0.2831	0.2487
<b>TJO (K, <math>\mu\text{L/h}</math>)</b>	0.1034	0.1216	0.0876
<b>tl (d, cm)</b>	0.3645	0.5924	0.4097

(Fig. 3, Table 3, Appendix B).

In view of the substantial morphological difference between the populations, we expected to see a clear difference in the shape coefficient  $\delta_M$ . We found a slightly larger value of  $\delta_M$  for the intertidal morphotype, meaning that for the same shell length, it has slightly more structure, compared to the subtidal one.

Subtidal morphs have a lower energy conductance  $\dot{v}$  as well as double the value of maximum surface area specific assimilation rate  $\{\dot{p}_{Am}\}$  with respect to the intertidal morphs. The ratio of specific assimilation over energy conductance  $[E_m] = \{\dot{p}_{Am}\} / \dot{v}$ , determines the maximum reserve capacity of a species.

The fraction of mobilised reserve allocated to soma  $\kappa$  is also bigger (0.9368 for subtidal vs. 0.9084 for intertidal type), and the intertidal individuals also present a lower value for somatic maintenance rate  $[\dot{p}_M]$  compared to the subtidal ones. This highlights contrasts between the morphotypes in energy allocated to maturation along the first life stages ( $E_H^b$ ,  $E_H^j$ ) and more available energy for growth for the intertidal morphotype that has lower values of somatic maintenance. Intertidal morphotypes seem to accelerate metabolism with a two-fold difference in acceleration factor  $s_M$  between intertidal and subtidal types (respectively 7.862 and 4.049). The maturity threshold to reach puberty,  $E_H^p$  is also lower for the intertidal morphotype than the subtidal.

The MRE values of the merged models stay below 0.25 and the value of the loss function for the merged situation is only a little larger than the sum of both populations, reflecting that a substantial reduction

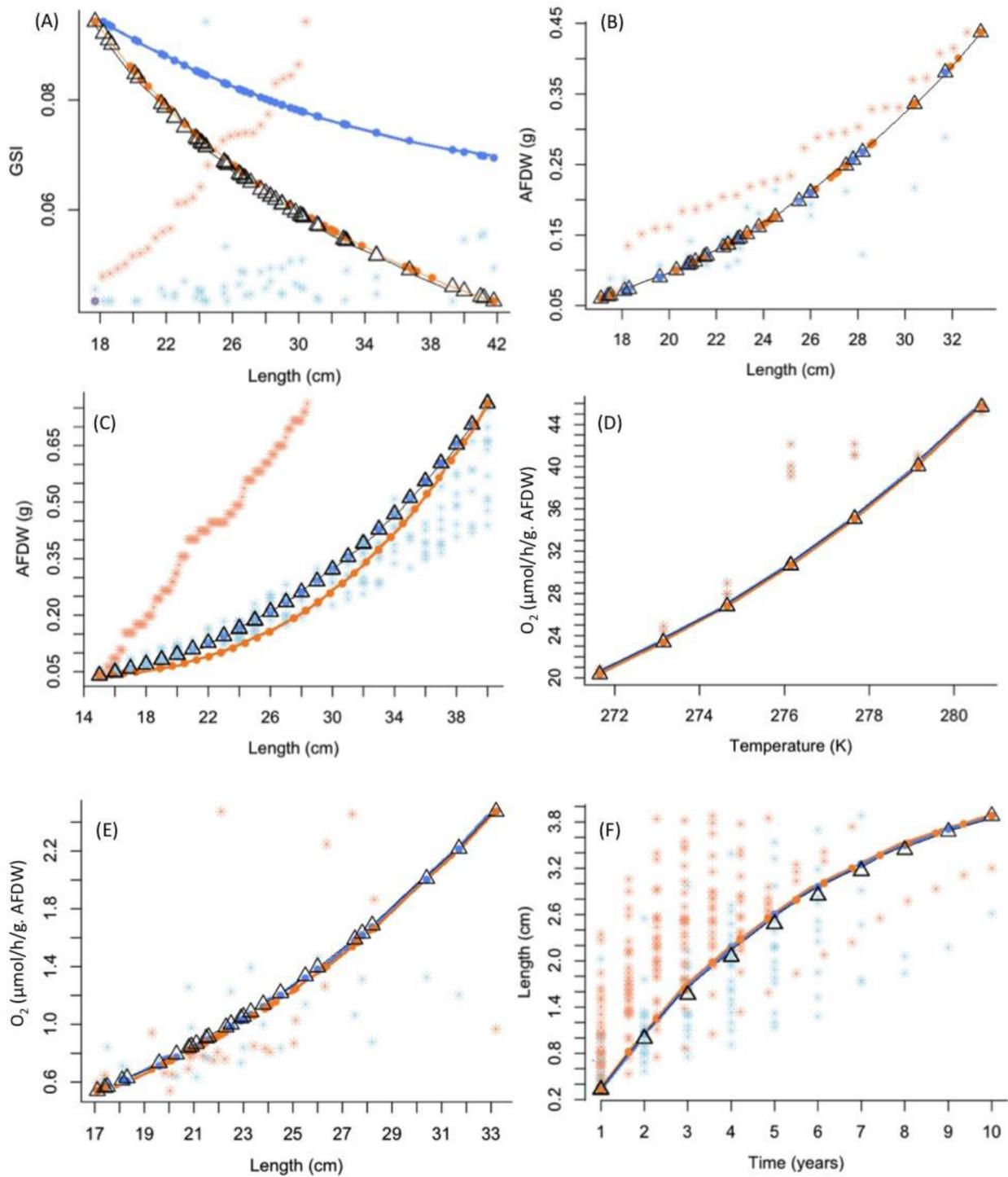
in the total number of parameters by almost a factor 2 hardly affects the goodness of fit (Table 3, Appendix C).

DEB parameters of the merged models are quite close to the values of the intertidal and subtidal models, with  $[\dot{p}_M]$ ,  $\delta_M$ ,  $E_H^b$ ,  $E_H^j$ ,  $[E_G]$  and  $\dot{v}$  merged values being almost exactly in between the values of the intertidal and the subtidal morphotypes. Parameters  $\kappa$ ,  $z$ ,  $E_H^j$ ,  $\{\dot{p}_{Am}\}$  and  $\dot{h}_a$  are closer to the intertidal predictions.

Univariate predictions are also extremely close between the two models and the merged model (Fig. 3), with only a small difference for the subtidal model for which the GSI-length predictions are higher than the intertidal and merged predictions, mainly due to errors in predictions and scatter in the data. This higher potential of energy allocation to reproduction can, however, be linked to the higher  $E_H^p$  values estimated for the subtidal type (Table 3).

### 3.2. Merging process

Along the merging procedure, the loss function and MRE values of the model at each step of the merging procedure are observed, one 'step' corresponding to the interative increase of the weight coefficient of the studied parameter (i.e. merging step, Fig. 4). Changes in loss function and MRE values are not that important between the initial step and the final step of the merging procedure (Fig. 4, Appendix D) (respectively from 0.170 to 0.196 and from 0.192 to 0.227 for the MRE intertidal and MRE subtidal values), meaning that merging parameters



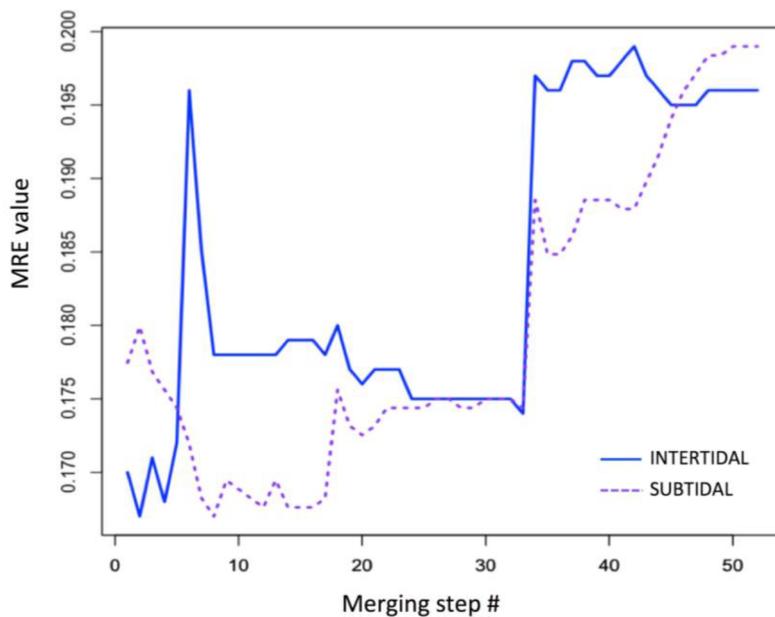
**Figure 3.** Comparison of model predictions (uni-variate data). Blue dots joined by lines: subtidal model predictions, blue stars: subtidal data (observations); orange dots joined by lines: intertidal model predictions, orange stars: intertidal data (observations); black triangle joined by lines: merged model predictions. Prediction points may overlap (D).

is possible.  $E_H^P$  and  $\delta_M$  seem to be the parameters that are the most influencing the model during the merging procedure for both the intertidal and subtidal models and  $[p_M]$  seems to further influence the intertidal model.

## 4. DISCUSSION

### 4.1. DEB models relevance

DEB models are powerful tools enabling predictions of the individuals energetic scope for survival, growth and reproduction, given the considered environmental conditions (Kooijman 2010, Jusup et al. 2017). These mechanistic approaches have been of interest for several years to the marine Antarctic community (Gutt et al. 2012,



Merged parameter	Merging step #	Merged parameter	Merging step #
$z$	2-4	$E_H^b$	26
$[\dot{p}M]$	5-12	$[E_G]$	27-29
$\delta_{M\_larvae}$	13-15	$E_H^j$	30-32
$\kappa$	16-20	$E_H^p$	33-41
$\ddot{h}_a$	21-22	$\delta_M$	42-52
$\dot{v}$	23-25		

**Figure 4.** Evolution of Mean Relative Error (MRE) values along the merging of the different parameters. MRE intertidal in solid blue line, MRE subtidal in dashed purple line. Example of Trial #5 (merging of  $z$ ,  $[\dot{p}M]$ ,  $\delta_{M\_larvae}$ ,  $\kappa$ ,  $\ddot{h}_a$ ,  $\dot{v}$ ,  $E_H^b$ ,  $[E_G]$ ,  $E_H^j$ ,  $E_H^p$ ,  $\delta_M$ ).

Constable et al. 2014, Gutt et al. 2018), and have been increasingly developed during recent years (e.g. Agüera et al. 2015, Agë 2017, Goedegebuure et al. 2018, Henschke et al. 2018).

This study is based on the example of the limpet *Nacella concinna* and uses data from literature supplemented by experiments conducted in Antarctica in February 2018, to build the DEB models of the intertidal and subtidal morphotypes of the species. The separately produced models were accurate, with a reduced error between observations and model predictions, except for some scatter among data such as Length~GSI relationship. Such accuracy was mainly possible thanks to the important amount of uni-variate data that were provided by the complementary experiments conducted in Rothera, which filled knowledge gaps about reproduction, collected more precise length weight relationships to observe the morphological contrasts between intertidal and subtidal individuals and collected more precise information on the limpet's metabolic performance through its development.

Rates (and ages) depend on temperature. Here we correct for differences in temperature using an Arrhenius relationship. However, in order to meaningfully compare differences in parameters between species living in different habitats, it is useful to standardize all parameters to a common reference temperature:  $T_{ref} = 20^\circ\text{C}$ . This is the standard for presenting and comparing DEB parameters across the 2,000 different species in AmP. When comparing DEB parameters estimations of *N. concinna* to those of their temperate counterpart *Patella vulgata* (Kooijman et al. 2017) at  $T_{ref} = 20^\circ\text{C}$ , we notice clear differences between the species in term of metabolic strategies, although the limpets morphology and therefore size and volume are close between the two species (close length and predicted shape coefficient  $\delta_M$ ). For *N. concinna*, predicted  $\kappa$  is much higher and close to 1 (0.9256 vs 0.617 for *P. vulgata*), meaning that almost all the energy available in the reserve compartment is allocated to somatic maintenance and growth, and only a small amount is available for reproduction. This is clearly visible with the ultimate rate of reproduction more than 40 times lower for the Antarctic limpet compared to the temperate one. The capacity to assimilate resources  $\{\dot{p}_{Am}\}$  was estimated to be 10 times higher for *P. vulgata*, explaining the 2.5-fold lower growth rate for *N. concinna*. The two metabolisms also contrast by the fact that *P. vulgata* is predicted to store more reserves than *N. concinna* in similarly abundant food conditions. These results are consistent with published experiments, where

it was shown that rasping rates (i.e. feeding potential) were higher for temperate and tropical species than for *N. concinna* (Morley et al. 2014) and that development rates of Antarctic marine molluscs are much slower than at higher temperatures (Peck et al. 2007, 2016), which could be partially due to the increased costs of protein production in the cold (Marsh et al. 2001, Robertson et al. 2001, Pörtner et al. 2007).

Such examples of comparison of energetic performance between these two species highlight the performance of DEB models to be efficiently applied for Antarctic case studies and powerful and accurate enough to enhance physiological contrasts even between closely related species; as previously discussed in other works (van der Veer et al. 2006, Gatti et al. 2017, Marques et al. 2018, Marn et al. 2019).

#### 4.2. Comparison between morphotypes

In a second step, we evaluated if known contrasts in physiological traits between the morphotypes could be highlighted by the modelling approach. By simply comparing the two single models, we observed minimal energetic contrasts between the intertidal and subtidal morphotypes (small differences in assimilation rate and ability to store reserves, Table 3, Fig. 3). By using the augmented-loss-function method, we tried to merge the models into a single one, parameter by parameter, to evaluate the contrasts in parameters between the types (Lika et al. 2020). Results show that models were merged without generating significant changes in MRE and loss function values (Fig. 4, Appendix D). Predictions of the uni-variate data are really similar between the three models (Fig. 3), with only minor differences in temperature-corrected parameter values between both populations, meaning that the observed differences are best explained by differences in environmental conditions (temperature and food availability).

Despite the known physiological contrasts in the field, the available data did not allow the models to capture these physiological differences between the morphotypes, using only the available data. Scatter distribution of the data used to calibrate the model (Fig. 3) can hide metabolic differences, which calls for more experiments to describe the physiology of the different morphotypes. Using more complete datasets, for which all parameters are independent between intertidal and subtidal morphotypes, may also help to further constrain the differences. In our case study, several zero-variate data are shared between the intertidal and subtidal models, among which age, length and weight at

birth, that control the very beginning of the development. The observed results of a two-fold difference in metabolism acceleration of intertidal morphotypes compared to subtidal ones ( $s_M \approx 8$  and 4 for intertidal and subtidal) is in fact an artefact caused by common parameters related to birth and puberty stages (age, length, weight). Indeed, specific assimilation at birth for the subtidal is two times larger than that for the intertidal, which indicates that subtidal individuals develop faster. However, according to available data provided in the model, puberty is reached at the same time for both types.  $E_H^p$  consequently needs to be smaller for the intertidal type to reach puberty at the same age  $a_p$  and length  $L_p$ , explaining the observed contrasts between the intertidal and subtidal groups.

Improving the completeness of these models would therefore be necessary to enable further detailed conclusions.

A common approach in biology is to focus on differences between individuals, populations and species. Here we adopt a contrasting strategy in which we force models to determine in what manner the populations are similar in order to quantify in what manner they differ. This work is a first step to compare the energetics of both populations, and we discovered how (given the data) they seem more metabolically similar than what their appearance would suggest as first. We also highlight some artefacts that come from the quality of the data and the scatter therein. New data (so new knowledge) that fill current knowledge gaps will yield further insight into how the metabolisms of these populations have diverged to adapt to differences in environment. The current work is a contribution to understanding the relationship between observations (data) and metabolism for these two populations.

#### 4.3. Models drawbacks and improvements

Apart from data availability, a drawback of our model construction is the lack of information about environmental properties that makes comparisons between estimations of the two morphotypes quite difficult to perform. In the models, we just considered an average temperature for intertidal or subtidal habitats from where the limpets come from, but do not add any supplementary detail on environmental contrasts between these habitats nor in the difference of food availability between the morphotypes. However, contrasting environmental pressures (desiccation, salinity, hydrodynamism) and habitat characteristics (immersion time, substratum type, and surrounding physico-chemical factors) contribute to contrasting adaptive strategies among which morphological adaptation is really important for limpets, but have not been integrated into our DEB models (because it requires more data we do not have) (Vermeij 1973, Branch 1981, Denny & Blanchette 2000, Sa Pinto et al. 2008, Bouzaza & Mezali 2013, Grandfils 1982, Gray & Hodgson 2003, Espinosa et al. 2009). Desiccation is one of the strongest hypothesis to explain the morphological differences between the intertidal and subtidal morphotypes (Mauro et al. 2003, Bouzaza & Mezali 2018). The presence of high upstream shifted apex form for the intertidal morphotypes, more exposed to desiccation, could help to store more water and absorb more oxygen, as described for *Patella ferruginea* (Branch 1985, Paracuellos et al. 2003). Similarly, shell volumes are bigger for the intertidal type and help reduce water loss (Vermeij 1973, Wolcott 1973, Branch 1975, Branch 1981) but also infer resistance to the effects of ice damage (Morley et al. 2010). Differences in the energetic responses of the two morphotypes of *N. concinna* to the difference in mean intertidal (0.45°C) and subtidal (-0.1°C), or the much greater difference in maximum (12.3 versus 1.7°C respectively; Morley et al. 2012), could be a proximate cause of the morphological differences. Taking into consideration differences between environments is therefore important but strongly lacking in the analysis presented here.

In our study, field data show a slight difference in shell length of +5% and a small difference also in the predicted shape coefficient of 0.45 against 0.39 (Table 3) for respectively the intertidal and subtidal individuals. This indicates very small differences in inner volumes

between the studied populations as calculated by the DEB, meaning that the DEB model does not adequately reflect the difference in morphology between the intertidal and subtidal morphotypes. In the raw data, shell heights present a 33% difference between intertidal and subtidal individuals (Appendix A) but shell length was used, rather than shell height, in the model to characterize the growth structure of the species. Fine tuning the models with extra shape information could have helped to bring further contrasts between the two models, but also requires much more information on shell growth.

Moreover, the difference in food availability and quality was hypothesized between the morphotypes when calibrating the model, despite food abundance and quality knowledge being responsible for strong contrasts in DEB model outputs (Kooijman 2010, Thomas et al. 2011, Saraiva et al. 2012, Sarà et al. 2013). During winter time, the intertidal type seems to have supplementary access to ice-algae and microphytobenthos in rock crevices, whereas the subtidal type mainly grazes on diatomsfilms growing on encrusting red algae (Appendix A, Obermüller et al. 2011). But food abundance and quality were assumed for the construction of the models, as no data accurate enough were available to characterize the feeding behaviour of the limpets. Moreover, in the case of intertidal type, no clear hypothesis is available for their behaviour during winter period, as several authors hypothesize either a migration into the subtidal or a dormance period hidden into crevices during the period when ice is covering their habitat (Brêthes et al. 1994, Obermüller et al. 2011). However, this information would be essential to explain how these individuals energetically behave during this period.

#### 4.4. Potential of the approach

This study showed that it is feasible to build a DEB model for a marine Antarctic species, with few available data. Adding extra information from sampling and experiments during a single expedition in the field considerably increased the accuracy of the model and highlighted some small differences in energy allocation priorities, maintenance costs and reproductive potential between the intertidal and subtidal morphotypes. But the method is then limited by model calibration and data availability since it could not prove that these contrasts are explained by anything else but environmental conditions.

Such DEB models would already be sufficient to (1) describe the performance of the species physiological traits in spatially or temporally contrasting environmental conditions (Kearney et al. 2012, Teal et al. 2012), (2) to be upscaled to the population level to assess population structure and density dynamics (Klanjscek et al. 2006, Arnould-Pétre et al. this issue), or (3) to be integrated into a dynamic network by adding knowledge about interaction with other species (Ren et al. 2010, Ren et al. 2012). Adding some data from extra experiments would easily enable further development of these models for ecophysiological or ecotoxicological applications (Muller and Nisbet 1997, Pouvreau et al. 2006, Peeters et al. 2010, Sarà et al. 2011), or to improve knowledge about development stages, behaviour or reproduction (Pecquerie et al. 2009, Rico-Villa et al. 2010, Kooijman et al. 2011).

In this study, we wanted to explore whether the amount of data that was available to build these models were sufficient to see the known physiological and morphological differences between the two morphotypes, and results show that more data are necessary.

To conclude, we advise the use of DEB approach for ecological modelling for Antarctic case studies but modellers should be aware of the necessity to calibrate models with accurate data to fine tune results. Among these data, the description of the species habitat is complex information to be integrated into a model and most of the time only partial information is available. Working in narrow scale areas where habitat is known and described and where experiments can be run might be a good option.

Our study also highlights the interest of DEB models to reuse data

from experiments from historical published works from Antarctic campaigns and highlights the importance of precisely documenting the associated metadata (notably the description of the environment and the conditions in which the limpets are living), data that is not always available.

### Authors' contribution

C. Guillaumot: Conceptualization, Methodology, Writing  
 T. Saucède: Supervision, Validation, review & editing  
 S.A. Morley: Data acquisition, Validation, review & editing  
 S. Augustine: Methodology, Validation, review & editing  
 B. Danis: Supervision, Validation, review & editing  
 S.A.L.M. Kooijman: Data curation, Methodology, Validation, review & editing

### Acknowledgements

We are thankful to Philippe Pernet for *N. concinna* pictures, and Jonathan Flye-Sainte-Marie, Jean-François Cudennec for sclerochronology protocol advices, Eric Dabas, Rémi Laffont for sclerochronology lab trials.

This work was supported by a "Fonds pour la formation à la Recherche dans l'Industrie et l'Agriculture" (FRIA) and "Bourse fondation de la mer" grants to C. Guillaumot. SMOR was supported by Natural Environment Research Council core funding to the British Antarctic Survey.

This is contribution no. 40 to the vERSO project ([www.versoproject.be](http://www.versoproject.be)), funded by the Belgian Science Policy Office (BELSPO, contract n°BR/132/A1/vERSO). Research was also financed by the "Refugia and Ecosystem Tolerance in the Southern Ocean" project (RECTO; BR/154/A1/RECTO) funded by the Belgian Science Policy Office (BELSPO), this study being contribution number 14.

### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109088](https://doi.org/10.1016/j.ecolmodel.2020.109088).

### References

Agüera, A., Collard, M., Jossart, Q., Moreau, C., Danis, B., 2015. Parameter estimations of dynamic energy budget (DEB) model over the life history of a key Antarctic species: the Antarctic sea star *Odontaster validus* Koehler, 1906. *PLoS one* 10 (10), e0140078.

Agüera, A., Ahn, I.Y., Guillaumot, C., Danis, B., 2017. A Dynamic Energy Budget (DEB) model to describe *Laternula elliptica* (King, 1832) seasonal feeding and metabolism. *PLoS one* 12 (8), e0183848.

Ansaldo, M., Sacristán, H., Wider, E., 2007. Does starvation influence the antioxidant status of the digestive gland of *Nacella concinna* in experimental conditions? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* 146 (1-2), 118-123.

Aranzamendi, M.C., Sahade, R., Tatián, M., Chiappero, M.B., 2008. Genetic differentiation between morphotypes in the Antarctic limpet *Nacella concinna* as revealed by inter-simple sequence repeat markers. *Marine Biology* 154 (5), 875-885.

Arnould-Pétré, M., Guillaumot, C., Danis, B., Féral, J.-P., Saucède, T. (this issue). Individual-based model of population dynamics in *Abatus cordatus*, a sea urchin of the Kerguelen (Southern Ocean), under changing environmental conditions.

Baas, J., Kooijman, S.A., 2015. Sensitivity of animals to chemical compounds links to metabolic rate. *Ecotoxicology* 24 (3), 657-663.

Barnes, D.K., Peck, L.S., 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Climate Research* 37 (2-3), 149-163.

Barnes, D.K., Souster, T., 2011. Reduced survival of Antarctic benthos linked to climate-induced icebergs scouring. *Nature Climate Change* 1 (7), 365-368.

Beaumont, A.R., Wei, J.H., 1991. Morphological and genetic variation in the Antarctic limpet *Nacella concinna* (Strebel, 1908). *Journal of Molluscan Studies* 57 (4), 443-450.

Bers, A.V., Momo, F., Schloss, I.R., Abele, D., 2013. Analysis of trends and sudden changes in long-term environmental data from King George Island (Antarctica): relationships between global climatic oscillations and local system response. *Climatic Change* 116 (3-4), 789-803.

Bevelhimer, M.S., Stein, R.A., Carline, R.F., 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 42 (1), 57-69.

Bouzaza, Z., Mezali, K., 2013. Etude systématique, phylogénétique et phylogéographique de quelques espèces de Patelles. *Rap. Comm int Mer Médit* 40, 859.

Bouzaza, Z., Mezali, K., 2018. Discriminant-based study of the shell morphometric relationships of *Patella caerulea* (Gastropoda: Prosobranchia) of the western Mediterranean Sea. *Turkish Journal of Zoology* 42 (5), 513-522.

Branch, G.M., 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. *IV. Desiccation*. *Marine Biology* 32 (2), 179-188.

Branch, G.M., 1981. The ecology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: Annual Reviews* 19, 235-380.

Branch, G.M., 1985. Limpets: evolution and adaptation. In: Clarke, M.R. (Ed.), *The mollusca*. Trueman ER. Academic Press, Orlando, pp. 187-220.

Brêthes, J.C., Ferreyra, G., De la Vega, S., 1994. Distribution, growth and reproduction of the limpet *Nacella (Patinigera) concinna* (Strebel 1908) in relation to potential food availability, in Esperanza Bay (Antarctic Peninsula). *Polar Biology* 14 (3), 161-170.

Butlin, R.K., Galindo, J., Grahame, J.W., 2008. Sympatric, parapatric or allopatric: the most important way to classify speciation? *Philosophical Transactions of the Royal Society B: Biological Sciences* 363 (1506), 2997-3007.

Cadée, G.C., 1999. Shell damage and shell repair in the Antarctic limpet *Nacella concinna* from King George Island. *Journal of Sea Research* 41 (1-2), 149-161.

Chwedorzewska, K., Korczak, M., Bednarek, P., Markowska-Potocka, M., 2010. Low genetic differentiation between two morphotypes of the gastropod *Nacella concinna* from Admiralty Bay, Antarctica. *Polish Polar Research* 31 (2), 195-200.

Clarke, A., 1989. Faecal production and an estimate of food intake in the wild of the Antarctic limpet *Nacella concinna* (Strebel). *Journal of Molluscan Studies* 55 (2), 261-262.

Clark, M.S., Fraser, K.P., Peck, L.S., 2008. Antarctic marine molluscs do have an HSP70 heat shock response. *Cell Stress and Chaperones* 13 (1), 39-49.

Clarke, A., Meredith, M.P., Wallace, M.I., Brandon, M.A., Thomas, D.N., 2008. Seasonal and interannual variability in temperature, chlorophyll and macronutrients in northern Marguerite Bay, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography* 55 (18-19), 1988-2006.

Clark, M.S., Peck, L.S., 2009. HSP70 heat shock proteins and environmental stress in Antarctic marine organisms: a mini-review. *Marine genomics* 1 (2), 11-18.

Constable, A., Costa, D., Murphy, E., Hofmann, E., Schofield, O., Press, A., Johnson, N.M., Newman, L., et al., 2014. Chapter 9.3. Assessing status and change in Southern Ocean Ecosystems. In: C., De Broyer, Koubbi, P., Griffiths, H.J., Raymond, B., d', Udekem d'Acoz C. (Eds.), *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp. 404-407.

Danis, B., Christiansen, H., Guillaumot, C., Heindler, F.M., Houston, R., Jossart, Q., Lucas, K., Moreau, C., Pasotti, F., Robert, H., Wallis, B., and Saucède, T. (2019). "Report of the Belgica121 expedition to the West Antarctic Peninsula".

DeAngelis, D.L., Rose, K.A., Huston, M.A., 1994. Individual-oriented approaches to modeling ecological populations and communities. *Frontiers in mathematical biology*. Springer, Berlin, Heidelberg, pp. 390-410.

Denny, M.W., Blanchette, C.A., 2000. Hydrodynamics, shell shape, behavior and survivorship in the owl limpet *Lottia gigantea*. *Journal of Experimental Biology* 203 (17), 2623-2639.

Elith, J., H. Graham, C., P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., ..., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29 (2), 129-151.

Espinosa, F., Rivera-Ingraham, G.A., Fa, D., García-Gómez, J.C., 2009. Effect of human pressure on population size structures of the endangered ferruginean limpet: toward future management measures. *Journal of Coastal Research* 857-863.

Fraser, K.P., Clarke, A., Peck, L.S., 2007. Growth in the slow lane: protein metabolism in the Antarctic limpet *Nacella concinna* (Strebel 1908). *Journal of Experimental Biology* 210 (15), 2691-2699.

Freitas, V., Cardoso, J.F., Lika, K., Peck, M.A., Campos, J., Kooijman, S.A., Van der Veer, H.W., 2010. Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1557), 3553-3565.

Gatti, P., Petitgas, P., Huret, M., 2017. Comparing biological traits of anchovy and sardine in the Bay of Biscay: A modelling approach with the Dynamic Energy Budget. *Ecological Modelling* 348, 93-109.

Goedegebuure, M., Melbourne-Thomas, J., Corney, S.P., McMahon, C.R., Hindell, M.A., 2018. Modelling southern elephant seals *Mirounga leonina* using an individual-based model coupled with a dynamic energy budget. *PLoS one* 13 (3), e0194950.

González-Wevar, C.A., David, B., Poulin, E., 2011. Phylogeography and demographic inference in *Nacella (Patinigera) concinna* (Strebel, 1908) in the western Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography* 58 (1-2), 220-229.

González-Wevar, C.A., Hüne, M., Rosenfeld, S., Nakano, T., Saucède, T., Spencer, H., Poulin, E., 2018. Systematic revision of *Nacella* (Patellogastropoda: Nacellidae) based on a complete phylogeny of the genus, with the description of a new species from the southern tip of South America. *Zoological Journal of the Linnean Society* 186 (2), 303-336.

Grandfils, R., 1982. Contribución al conocimiento de *Patella ferruginea* (Gmelin, 1789). *Iberus* 2, 57-69.

Gray, D.R., Hodgson, A.N., 2003. Growth and reproduction in the high-shore South African limpet *Helcion pectunculus* (Mollusca: Patellogastropoda). *African Zoology* 38 (2), 371-386.

Guillaumot, C. (2019a). AmP *Adamussium colbecki*, version 2019/05/20, [http://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/entries\\_web/Adamussium\\_colbecki/Adamussium\\_colbecki\\_res.html](http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Adamussium_colbecki/Adamussium_colbecki_res.html).

Guillaumot, C. (2019b). AmP *Nacella concinna* [https://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/entries\\_web/Nacella\\_concinna/Nacella\\_concinna\\_res.html](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Nacella_concinna/Nacella_concinna_res.html).

Gutt, J., Zurell, D., Bracegridle, T., Cheung, W., Clark, M., Convey, P., ..., Griffiths, H.,

2012. Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept. *Polar Research* 31 (1), 11091.
- Gutt, J., Isla, E., Bertler, A.N., Bodeker, G.E., Bracegirdle, T.J., Cavanagh, R.D., ..., De Master, D., 2018. Cross-disciplinary in the advance of Antarctic ecosystem research. *Marine genomics* 37, 1–17.
- Halanych, K.M., Mahon, A.R., 2018. Challenging Dogma Concerning Biogeographic Patterns of Antarctica and the Southern Ocean. *Annual Review of Ecology, Evolution, and Systematics* 49, 355–378.
- Hargens, A.R., Shabica, S.V., 1973. Protection against lethal freezing temperatures by mucus in an Antarctic limpet. *Cryobiology* 10 (4), 331–337.
- Henley, S.F., Schofield, O.M., Hendry, K.R., Schloss, I.R., Steinberg, D.K., Moffat, C., ..., Rozema, P.D., 2019. Variability and change in the west Antarctic Peninsula marine system: Research priorities and opportunities. *Progress in Oceanography* 173, 208–237.
- Henschke, N., Pakhomov, E.A., Groeneveld, J., Meyer, B., 2018. Modelling the life cycle of *Salpa thompsoni*. *Ecological modelling* 387, 17–26.
- Hoffman, J.L., Peck, L.S., Hillyard, G., Zieritz, A., Clark, M.S., 2010. No evidence for genetic differentiation between Antarctic limpet *Nacella concinna* morphotypes. *Marine Biology* 157 (4), 765–778.
- Holsman, K.K., Ianelli, J., Aydin, K., Punt, A.E., Moffitt, E.A., 2016. A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species climate-enhanced stock assessment models. *Deep Sea Research Part II: Topical Studies in Oceanography* 134, 360–378.
- Houlihan, D.F., Allan, D., 1982. Oxygen consumption of some Antarctic and British gastropods: an evaluation of cold adaptation. *Comparative Biochemistry and Physiology Part A: Physiology* 73 (3), 383–387.
- Hogeweg, P., Hesper, B., 1990. Individual-oriented modelling in ecology. *Mathematical and Computer Modelling* 13 (6), 83–90.
- Jager, T., Barsi, A., Hamda, N.T., Martin, B.T., Zimmer, E.I., Ducrot, V., 2014. Dynamic energy budgets in population ecotoxicology: Applications and outlook. *Ecological Modelling* 280, 140–147.
- Jager, T., Ravagnan, E., 2015. Parameterising a generic model for the dynamic energy budget of Antarctic krill *Euphausia superba*. *Marine Ecology Progress Series*, 519, 115–128.
- Johannesson, K., 2003. Evolution in Littorina: ecology matters. *Journal of Sea Research* 49 (2), 107–117.
- Jusup, M., Sousa, T., Domingos, T., Labina, V., Marn, N., Wang, Z., Klanjšček, T., 2017. Physics of metabolic organization. *Physics of life reviews* 20, 1–39.
- Kaiser, S., Brandão, S.N., Brix, S., Barnes, D.K., Bowden, D.A., Ingels, J., ..., Bax, N., 2013. Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in knowledge and understanding. *Marine biology* 160 (9), 2295–2317.
- Kearney, M.R., Matzelle, A., Helmut, B., 2012. Biomechanics meets the ecological niche: the importance of temporal data resolution. *Journal of Experimental Biology* 215 (6), 922–933.
- Kearney, M.R., Domingos, T., Nisbet, R., 2015. Dynamic energy budget theory: an efficient and general theory for ecology. *Bioscience* 65 (4) 341–341.
- Kennicutt, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Massom, R., Peck, L.S., ..., Sutherland, W.J., 2014. Polar research: six priorities for Antarctic science. *Nature News* 512 (7512), 23.
- Kennicutt, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Peck, L.S., Massom, R., ..., Allison, I., 2015. A roadmap for Antarctic and Southern Ocean science for the next two decades and beyond. *Antarctic Science* 27 (1), 3–18.
- Kennicutt II, M.C., Bromwich, D., Liggett, D., Njåstad, B., Peck, L., Rintoul, S.R., ..., Cassano, J., 2019. Sustained Antarctic Research: A 21st century imperative. *One Earth* 1 (1), 95–113.
- King, J.C., Turner, J., Marshall, G.J., Connolley, W.M., Lachlan-Cope, T.A., 2003. Antarctic Peninsula climate variability and its causes as revealed by analysis of instrumental records. *Antarctic Peninsula climate variability: historical and paleoenvironmental perspectives* 79, 17–30.
- Klanjšček, T., Caswell, H., Neubert, M.G., Nisbet, R.M., 2006. Integrating dynamic energy budgets into matrix population models. *Ecological modelling* 196 (3–4), 407–420.
- Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organisation. Cambridge university press.
- Kooijman, S.A.L.M., Pecquerie, L., Augustine, S., Jusup, M., 2011. Scenarios for acceleration in fish development and the role of metamorphosis. *Journal of sea research* 66 (4), 419–423.
- Kooijman, B., Jean, F., Augustine, S. (2017). AmP *Patella vulgata*, version 2017/01/30, [https://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/entries\\_web/Patella\\_vulgata/Patella\\_vulgata\\_res.html](https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Patella_vulgata/Patella_vulgata_res.html).
- Lika, K., Kearney, M.R., Freitas, V., van der Veer, H.W., van der Meer, J., Wijsman, J.W., ..., Kooijman, S.A., 2011a. The “covariation method” for estimating the parameters of the standard Dynamic Energy Budget model I: Philosophy and approach. *Journal of Sea Research* 66 (4), 270–277.
- Lika, K., Augustine, S. & Kooijman S.A.L.M. (2020). The use of augmented loss functions for estimating Dynamic Energy Budget parameters.
- Mariño, J., Augustine, S., Dufour, S.C., Hurford, A., 2019. Dynamic Energy Budget theory predicts smaller energy reserves in thysirid bivalves that harbour symbionts. *Journal of Sea Research* 143, 119–127.
- Markowska, M., Kidawa, A., 2007. Encounters between Antarctic limpets, *Nacella concinna*, and predatory sea stars, *Lysasterias* sp., in laboratory and field experiments. *Marine biology* 151 (5), 1959–1966.
- Marques, G.M., Mateus, M., Domingos, T., 2014. Can we reach consensus between marine ecological models and DEB theory? A look at primary producers. *Journal of sea research* 94, 92–104.
- Marques, G.M., Augustine, S., Lika, K., Pecquerie, L., Domingos, T., Kooijman, S.A., 2018. The AmP project: comparing species on the basis of dynamic energy budget parameters. *PLoS computational biology* 14 (5), e1006100.
- Marques, G.M., Lika, K., Augustine, S., Pecquerie, L., Kooijman, S.A.L.M., 2019. Fitting Multiple Models to Multiple Data Sets. *J. Sea Res.* 143, 48–56.
- Marn, N., Jusup, M., Catteau, S., Kooijman, S.A.L.M., Klanjšček, T., 2019. Comparative physiological energetics of Mediterranean and North Atlantic loggerhead turtles. *Journal of sea research* 143, 100–118.
- Marsh, A.G., Maxson, R.E., Manahan, D.T., 2001. High macromolecular synthesis with low metabolic cost in Antarctic sea urchin embryos. *Science* 291 (5510), 1950–1952.
- Mauro, A., Arculeo, M., Parrinello, N., 2003. Morphological and molecular tools in identifying the Mediterranean limpets *Patella caerulea*, *Patella aspera* and *Patella rustica*. *Journal of Experimental Marine Biology and Ecology* 295 (2), 131–143.
- McClintock, J.B., 1994. Trophic biology of Antarctic shallow-water echinoderms. *Marine ecology progress series*. Oldendorf 111 (1), 191–202.
- Meredith, M.P., King, J.C., 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32 (19).
- Morley, S.A., Lurman, G.J., Skepper, J.N., Pörtner, H.O., Peck, L.S., 2009. Thermal plasticity of mitochondria: a latitudinal comparison between Southern Ocean molluscs. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 152 (3), 423–430.
- Morley, S.A., Clark, M.S., Peck, L.S., 2010. Depth gradients in shell morphology correlate with thermal limits for activity and ice disturbance in Antarctic limpets. *Journal of Experimental Marine Biology and Ecology* 390 (1), 1–5.
- Morley, S.A., Lemmon, V., Obermüller, B.E., Spicer, J.I., Clark, M.S., Peck, L.S., 2011. Duration tenacity: a method for assessing acclimatory capacity of the Antarctic limpet. *Nacella concinna*. *Journal of experimental marine biology and ecology* 399 (1), 39–42.
- Morley, S.A., Martin, S.M., Day, R.W., Ericson, J., Lai, C.H., Lamare, M., ..., Peck, L.S., 2012. Thermal reaction norms and the scale of temperature variation: latitudinal vulnerability of intertidal nautilus limpets to climate change. *PLoS one* 7 (12).
- Morley, S.A., Lai, C.H., Clarke, A., Tan, K.S., Thorne, M.A., Peck, L.S., 2014. Limpet feeding rate and the consistency of physiological response to temperature. *Journal of Comparative Physiology B* 184 (5), 563–570.
- Muller, E.B., Nisbet, R.M., 1997. Modeling the effect of toxicants on the parameters of dynamic energy budget models. *Environmental Toxicology and Risk Assessment: Modeling and Risk Assessment Sixth Volume*. ASTM International.
- Nisbet, R.M., Jusup, M., Klanjšček, T., Pecquerie, L., 2012. Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *Journal of Experimental Biology* 215 (6), 892–902.
- Nolan, C.P., 1991. Size, shape and shell morphology in the Antarctic limpet *Nacella concinna* at Signy Island. *South Orkney Islands. Journal of Molluscan Studies* 57 (2), 225–238.
- Obermüller, B.E., Morley, S.A., Clark, M.S., Barnes, D.K., Peck, L.S., 2011. Antarctic intertidal ecophysiology: A winter–summer comparison. *Journal of experimental marine biology and ecology* 403 (1–2), 39–45.
- Paracuellos, M., Nevado, J.C., Moreno, D., Giménez, A., Alesina, J.J., 2003. Conservation status and demographic characteristics of *Patella ferruginea* Gmelin, 1791 (Mollusca, gastropoda) on the Alboran Island (Western Mediterranean). *Animal Biodiversity and Conservation* 26 (2), 29–37.
- Peck, L.S., 1989. Temperature and basal metabolism in two Antarctic marine herbivores. *Journal of Experimental Marine Biology and Ecology* 127 (1), 1–12.
- Peck, L.S., Brey, T., 1996. Radiocarbon bomb signals verify biennial growth bands in the shells of 50 year old brachiopods from Antarctica. *Nature* 380, 206–207.
- Peck, L.S., 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. In: *Ecological Studies in the Antarctic Sea Ice Zone*. Springer, Berlin, Heidelberg, pp. 221–230.
- Peck, L.S., Powell, D.K., Tyler, P.A., 2007. Very slow development in two Antarctic bivalve molluscs, the infaunal clam *Laternula elliptica* and the scallop *Adamussium colbecki*. *Marine Biology* 150 (6), 1191–1197.
- Peck, L.S., Clark, M.S., Morley, S.A., Massey, A., Rossetti, H., 2009. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology* 23 (2), 248–256.
- Peck, L.S., Heiser, S., Clark, M.S., 2016. Very slow embryonic and larval development in the Antarctic limpet *Nacella polaris*. *Polar Biology* 39 (12), 2273–2280.
- Peeters, F., Li, J., Straille, D., Rothhaupt, K.O., Vijverberg, J., 2010. Influence of low and decreasing food levels on Daphnia-algal interactions: Numerical experiments with a new dynamic energy budget model. *Ecological Modelling* 221 (22), 2642–2655.
- Pecquerie, L., Petitgas, P., Kooijman, S.A., 2009. Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. *Journal of Sea Research* 62 (2–3), 93–105.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. Ecological niches and geographic distributions (MPB-49) 56 Princeton University Press.
- Petter, G., Weitere, M., Richter, O., Moenicks, S., 2014. Consequences of altered temperature and food conditions for individuals and populations: a dynamic energy budget analysis for *Corbicula fluminea* in the Rhine. *Freshwater biology* 59 (4), 832–846.
- Picken, G.B., 1980. The distribution, growth, and reproduction of the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *Journal of experimental marine biology and ecology* 42 (1), 71–85.
- Picken, G.B., Allan, D., 1983. Unique spawning behaviour by the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *Journal of Experimental Marine Biology and Ecology* 71 (3), 283–287.
- Pörtner, H.O., Peck, L., Somero, G., 2007. Thermal limits and adaptation in marine Antarctic ectotherms: an integrative view. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362 (1488), 2233–2258.

- Pouvreau, S., Bourles, Y., Lefebvre, S., Gangnery, A., Alunno-Bruscia, M., 2006. Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. *Journal of Sea Research* 56 (2), 156–167.
- Powell, A.W.B., 1951. Antarctic and subantarctic mollusca: Pelecypoda and Gastropoda. *Discov Rep (USA)* 26, 49–196.
- Ren, J.S., Ross, A.H., Hadfield, M.G., Hayden, B.J., 2010. An ecosystem model for estimating potential shellfish culture production in sheltered coastal waters. *Ecological Modelling* 221 (3), 527–539.
- Ren, J.S., Stenton-Dozey, J., Plew, D.R., Fang, J., Gall, M., 2012. An ecosystem model for optimising production in integrated multitrophic aquaculture systems. *Ecological Modelling* 246, 34–46.
- Rico-Villa, B., Bernard, I., Robert, R., Pouvreau, S., 2010. A Dynamic Energy Budget (DEB) growth model for Pacific oyster larvae, *Crassostrea gigas*. *Aquaculture* 305 (1–4), 84–94.
- Robertson, R., El-Haj, A., Clarke, A., Peck, L., Taylor, E., 2001. The effects of temperature on metabolic rate and protein synthesis following a meal in the isopod *Glyptonotus antarcticus* Eights (1852). *Polar Biology* 24 (9), 677–686.
- Sa Pinto, A., Branco, M., Sayanda, D., Alexandrino, P., 2008. Patterns of colonization, evolution and gene flow in species of the genus *Patella* in the Macaronesian Islands. *Molecular ecology* 17 (2), 519–532.
- Sarà, G., Kearney, M., Helmuth, B., 2011. Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels. *Chemistry and Ecology* 27 (2), 135–145.
- Sarà, G., Palmeri, V., Rinaldi, A., Montalto, V., Helmuth, B., 2013. Predicting biological invasions in marine habitats through eco-physiological mechanistic models: a case study with the bivalve *Brachidontes pharaonis*. *Diversity and Distributions* 19 (10), 1235–1247.
- Saraiva, S., Van der Meer, J., Kooijman, S.A.L.M., Witbaard, R., Philippart, C.J.M., Hippler, D., Parker, R., 2012. Validation of a Dynamic Energy Budget (DEB) model for the blue mussel *Mytilus edulis*. *Marine ecology progress series* 463, 141–158.
- Schloss, I.R., Abele, D., Moreau, S., Demers, S., Bers, A.V., González, O., Ferreyra, G.A., 2012. Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Potter Cove (Antarctica). *Journal of marine Systems* 92 (1), 53–66.
- Schofield, O., Saba, G., Coleman, K., Carvalho, F., Couto, N., Ducklow, H., ..., Montes-Hugo, M., 2017. Decadal variability in coastal phytoplankton community composition in a changing West Antarctic Peninsula. *Deep Sea Research Part I: Oceanographic Research Papers* 124, 42–54.
- Serpa, D., Ferreira, P.P., Ferreira, H., da Fonseca, L.C., Dinis, M.T., Duarte, P., 2013. Modelling the growth of white seabream (*Diplodus sargus*) and gilthead seabream (*Sparus aurata*) in semi-intensive earth production ponds using the Dynamic Energy Budget approach. *Journal of sea research* 76, 135–145.
- Shabica, S.V., 1971. General ecology of Antarctic limpet *Patinigera-Polaris*. *Antarctic Journal of the United States* 6 (5), 160.
- Shabica, S.V., 1976. The natural history of the Antarctic limpet *Patinigera polaris* (Hombron and Jacquinot). Ph. D. Thesis. Oregon State University, Corvallis, Oregon, USA, pp. 294.
- Smale, D.A., Barnes, D.K., 2008. Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century, based primarily on evidence from the West Antarctic Peninsula region. *Ecography* 31 (3), 289–305.
- Souster, T.A., Morley, S.A., Peck, L.S., 2018. Seasonality of oxygen consumption in five common Antarctic benthic marine invertebrates. *Polar Biology* 41 (5), 897–908.
- Stainthorpe, R., Kooijman, B. (2017). AmP *Sterechinus neumayeri*, version 2017/07/06. [http://www.bio.vu.nl/thb/deb/deblab/add\\_my\\_pet/entries\\_web/Sterechinus\\_neumayeri/Sterechinus\\_neumayeri\\_res.html](http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Sterechinus_neumayeri/Sterechinus_neumayeri_res.html).
- Stammerjohn, S., Massom, R., Rind, D., Martinson, D., 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. *Geophysical Research Letters* 39 (6), L06501.
- Stanwell-Smith, D., Clarke, A., 1998. The Timing of reproduction in the Antarctic limpet *Nacella concinna* (srebel, 1908)(Patellidae) at Signy Island, in relation to environmental variables. *Journal of Molluscan Studies* 64 (1), 123–127.
- Stenni, B., Curran, M.A., Abram, N., Orsi, A., Goursaud, S., Masson-Delmotte, V., ..., Steig, E.J., 2017. Antarctic climate variability on regional and continental scales over the last 2000 years. *Climate Past* 13, 1609–1634.
- Strebel, H. (1908). *Dei Gastropoden. Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition, 1901-1903.* 6:1-112.
- Suda, C.N., Vani, G.S., de Oliveira, M.F., Rodrigues, E., Lavrado, H.P., 2015. The biology and ecology of the Antarctic limpet *Nacella concinna*. *Polar Biology* 38 (12), 1949–1969.
- Teal, L.R., van Hal, R., van Kooten, T., Ruardij, P., Rijnsdorp, A.D., 2012. Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa L.*) and sole (*Solea solea L.*) to climate change. *Global Change Biology* 18 (11), 3291–3305.
- Thomas, Y., Mazurié, J., Alunno-Bruscia, M., Bacher, C., Bouget, J.F., Gohin, F., ..., Struski, C., 2011. Modelling spatio-temporal variability of *Mytilus edulis* (L.) growth by forcing a dynamic energy budget model with satellite-derived environmental data. *Journal of Sea Research* 66 (4), 308–317.
- Thomas, Y., Dumas, F., Andréfouët, S., 2016. Larval connectivity of pearl oyster through biophysical modelling; evidence of food limitation and broodstock effect. *Estuarine, Coastal and Shelf Science* 182, 283–293.
- Turner, J., Lu, H., White, I., King, J.C., Phillips, T., Hosking, J.S., ..., Deb, P., 2016. Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. *Nature* 535 (7612), 411.
- van der Meer, J., 2006. An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation. *Journal of Sea Research* 56 (2), 85–102.
- van der Veer, H.W., Cardoso, J.F., van der Meer, J., 2006. The estimation of DEB parameters for various Northeast Atlantic bivalve species. *Journal of Sea Research* 56 (2), 107–124.
- Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., ..., Turner, J., 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic change* 60 (3), 243–274.
- Vermeij, G.J., 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* 20 (4), 319–346.
- Walker, A.J.M., 1972. Introduction to the ecology of the antarctic limpet *Patinigera polaris* (Hombron and Jacquinot) at Signy Island, South Orkney Islands. *Br Antarctic Surv Bull* 28, 49–71.
- Waller, C.L., Worland, M.R., Convey, P., Barnes, D.K.A., 2006. Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. *Polar Biology* 29 (12), 1077–1083.
- Waller, C.L., Overall, A., Fitzcharles, E.M., Griffiths, H., 2017. First report of *Laternula elliptica* in the Antarctic intertidal zone. *Polar Biology* 40 (1), 227–230.
- Wei, J. H. (1988). *Morphological and genetic variation in natural populations of Antarctic limpet Nacella concinna* (Doctoral dissertation, University of Wales (UCNW, Bangor: Ocean Sciences)).
- Weihe, E., Abele, D., 2008. Differences in the physiological response of inter- and subtidal Antarctic limpets *Nacella concinna* to aerial exposure. *Aquatic Biology* 4 (2), 155–166.
- Wolcott, T.G., 1973. Physiological ecology and intertidal zonation in limpets (Acmaea): a critical look at "limiting factors" *The Biological Bulletin* 145 (2), 389–422.
- Xavier, J.C., Brandt, A., Ropert-Coudert, Y., Badhe, R., Gutt, J., Havermans, C., ..., Kennicutt, M.C., 2016. Future challenges in Southern Ocean ecology research. *Frontiers in Marine Science* 3, 94.