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

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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 the 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).

34 Despite the known morphological difference between the populations, the difference in shape coefficients was
35 small.

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

40 **Keywords:** ecological modelling; Southern Ocean; marine benthic species; model relevance; model accuracy

42 **Highlights:**

- 43 - We tested the performance of DEB models applied to an Antarctic case study
- 44 - DEB models can be easily calibrated from literature and experimental data
- 45 - Our model could not differentiate morphotypes, suggesting environmental explanations
- 46 - Temperature and food resources likely underpin the physiological differences between morphotypes
- 47 - Results encourage further research in data poor regions

49 **1.Introduction**

50 Antarctic regions have faced strong environmental change since the twentieth century (recently reviewed in
51 [Henley et al. 2019](#)), with a strong warming in some regions, such as in the Western Antarctic Peninsula ([King
52 et al. 2003](#), [Vaughan et al. 2003](#), [Meredith and King 2005](#)), leading to important shifts in sea ice regimes and
53 seasonality, including the duration and extent of sea ice cover ([Stammerjohn et al. 2012](#), [Turner et al. 2016](#),
54 [Schofield et al. 2017](#)). The increase in the rate of glacier melting has been reported as a cause of important
55 disturbance of the physical (currents, salinities) and biological environment (phytoplankton blooms,
56 communities) ([Meredith and King 2005](#), [Schloss et al. 2012](#), [Bers et al. 2013](#)). Such changes have a direct
57 impact on marine communities and particularly in coastal marine areas (both intertidal and subtidal)([Barnes
58 and Peck 2008](#), [Smale and Barnes 2008](#), [Barnes and Souster 2011](#), [Waller et al. 2017](#), [Stenni et al. 2017](#), [Gutt
59 et al. 2018](#)), which are places of complex land-sea interface and ecological processes. The multiple effects of
60 ice retreat and meltwater on nearshore marine habitats have contributed to the expansion of intertidal zones
61 and habitat alteration due to seawater freshening and stratification, shifting near-shore sedimentation, changes
62 in water properties and current dynamics.

63
64 However, studying Antarctic marine life is challenging. Not only do the environmental conditions make the
65 region difficult to access and work in, but substantial financial and technical constraints make field sampling
66 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 (Elith 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/). 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).

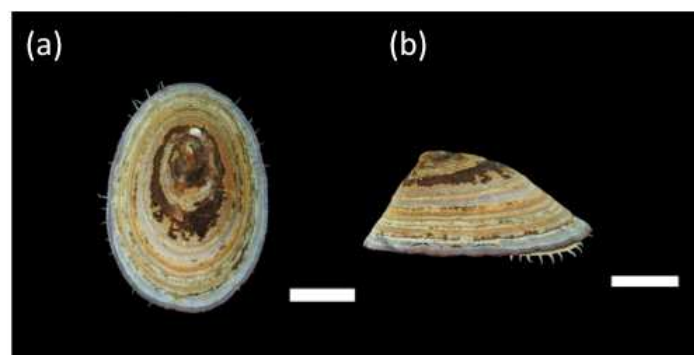
DEB models can be built with data coming from experiments and/or literature, to quantify age, length, weight of the different life stages and provide information on reproduction, growth and metabolic rates to calibrate the model (van der Meer 2006, Marques et al. 2014).

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. 2018), 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

101 seal *Mirounga leonina* (Goedegebuure et al. 2018). Antarctic species have a range of notable physiological
102 traits when compared to their temperate counterparts. Among others, they are physiologically adapted to
103 constant cold temperatures (Peck et al. 2009, Morley et al. 2009, 2014), shifting day length also imposes a
104 marked seasonal feeding behaviour (McClintock 1994, Clarke et al. 2008, Halanych and Mahon 2018), and
105 they exhibit slow metabolic and growth rates, explaining their longer lifespans and higher longevities compared
106 to species in other regions (Peck and Brey 1996, Peck 2002).

107
108 The limpet *Nacella concinna* (Strebel, 1908) (Mollusca: Patellogastropoda) is a common and abundant
109 gastropod of shallow marine benthic communities. Distributed all along the Western Antarctic Peninsula
110 (González-Wevar et al. 2011, phylogeny recently reviewed in González-Wevar et al. 2018), it has widely been
111 studied for decades (Shabica 1971, 1976, Walker 1972, Hargens and Shabica 1973, Houlihan and Allan 1982,
112 Peck 1989, Clarke 1989, Cadée 1999, Ansaldo et al. 2007, Fraser et al. 2007, Markowska and Kidawa 2007,
113 Morley et al. 2011, 2014, Suda et al. 2015, Souster et al. 2018). The limpet is found from intertidal rocky
114 shores down to over 100 meters depth (Powell 1951, Walker 1972). It has a 2-5 cm long shell (Fig. 1), that
115 grows only a few millimeters a year with a seasonal pattern. It is sexually mature after four to six years and has
116 a life span of up to 10 years (Shabica 1976, Picken 1980, Brêthes et al. 1994). The limpet mainly feeds on
117 microphytobenthos and microalgae (Shabica 1976, Brêthes et al. 1994). It spawns free-swimming planktonic
118 larvae once a year, when water temperature rises in the austral summer (Shabica 1971, Picken 1980, Picken
119 and Allan 1983). Larvae drift in the water column and metamorphose after more than two months (Stanwell-
120 Smith and Clarke 1998).

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



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

129
130 Two morphotypes of *N. concinna* have been distinguished, an intertidal and a subtidal type, with the intertidal
131 type having a taller, heavier and thicker shell compared to the subtidal one that is characterized by a lighter
132 and flatter shell (Beaumont and Wei 1991, Hoffman et al. 2010). Initially, Strebel (1908) and Powell (1951)
133 referred to these two morphotypes as the ‘polaris’ (intertidal) and ‘concinna’ types (below 4m depth). From that
134 point, the potential genetic differentiation between the two morphotypes has been investigated, some of the
135 studies concluding an absence of genetic distinction (Wei 1988, Beaumont and Wei 1991, Nolan 1991) while
136 contrarily, de Aranzamendi et al. (2008) reported significant differences based on inter-simple sequence repeat
137 (ISSR) markers. More recently, this last method was questioned (Hoffman et al. 2010) and several studies
138 using different markers and populations (Chwedorzewska et al. 2010, Hoffman et al. 2010, Gonzalez-Wevar et
139 al. 2011) have concluded an absence of genetic differentiation between the two morphotypes.

140
141 Apart from the absence of genetic differences, intertidal and subtidal populations strongly contrast in
142 morphology and physiology, which has been explained by the prevalence of habitat heterogeneity and strong
143 environmental gradients along rocky shore habitats, a common feature also observed in other gastropods
144 (Johannesson 2003, Butlin et al. 2008, Hoffman et al. 2010). For instance, in *N. concinna*, the higher shell
145 thickness observed in the shallow morphotype was hypothesised to play a role in resistance against crushing
146 pack ice (Shabica 1971, Morley et al. 2010). Intertidal morphotypes are further resistant to air exposure thanks
147 to higher shells, bigger inner volumes relative to their shell circumference, a combination that makes them
148 more efficient than subtidal individuals, able to store more water and oxygen, reducing desiccation risks and
149 delaying the metabolic switch to anaerobic fermentation (Nolan 1991, Weihe and Abele 2008). The subtidal
150 morphotype has also proved to be less resistant to cold than the intertidal population (Waller et al. 2006), due
151 to extra production of mucus and stress proteins in intertidal morphotypes (Clark et al. 2008, Clark and Peck
152 2009, Obermüller et al. 2011) and due to diverse metabolic processes that contrasts between both populations
153 (reviewed in Suda et al. 2015).

154
155 The development of ecological models enables precise models to be built, that highlight subtle differences in
156 parameters between ecologically similar or closely related species (Freitas et al. 2010, Holsman et al. 2016,
157 Marn et al. 2019, Lika et al. 2020 this issue). The idea of building individual-specific models for understanding
158 of physiological processes is not new (Bevelhimer et al. 1985, DeAngelis et al. 1994) and grew from the
159 development of computational ecology that resulted in the possibility of generating “individual-oriented” models
160 (IOM’s) (Hogeweg and Hesper 1990, DeAngelis et al. 1994). The IOM theory relies on the principle that “no

161 two biological organisms are exactly alike, even when they have identical genes". A group of organisms within
162 a population can have contrasting size or physiological performances according to, for example, food
163 conditions or competition. Modelling each individual, separately, therefore constitutes a powerful approach to
164 enhance the understanding of the entire community (DeAngelis et al. 1994).

165
166 In this study, due to the known morphological and physiological differences between the morphotypes, we first
167 separately built independent DEB models for the intertidal and subtidal morphotypes of the limpet *N. concinna*,
168 based on field experiment and literature data, to assess the potential differences between the models.
169 Secondly, we analyse whether the two model outputs suggest contrasting physiologies between the
170 morphotypes, using a method recently developed in DEB theory, that tries to reduce differences in parameter
171 values that are still consistent with the data (Lika et al. 2020 this issue). Using this method, the augmented loss
172 function, tries to merge the information of the two species models into a single one. If DEB parameters of the
173 two species can be merged, it means that the physiological differences between these two species are not
174 strongly different.

175
176 These results will finally help assess DEB model accuracy giving the amount of data available to build the
177 models in the context of Antarctic case studies and help evaluate which type of information is necessary to
178 gather in order to fill model gaps. Finally, the study evaluates if such models are valuable for studying Southern
179 Ocean organisms in the context of altered environments.

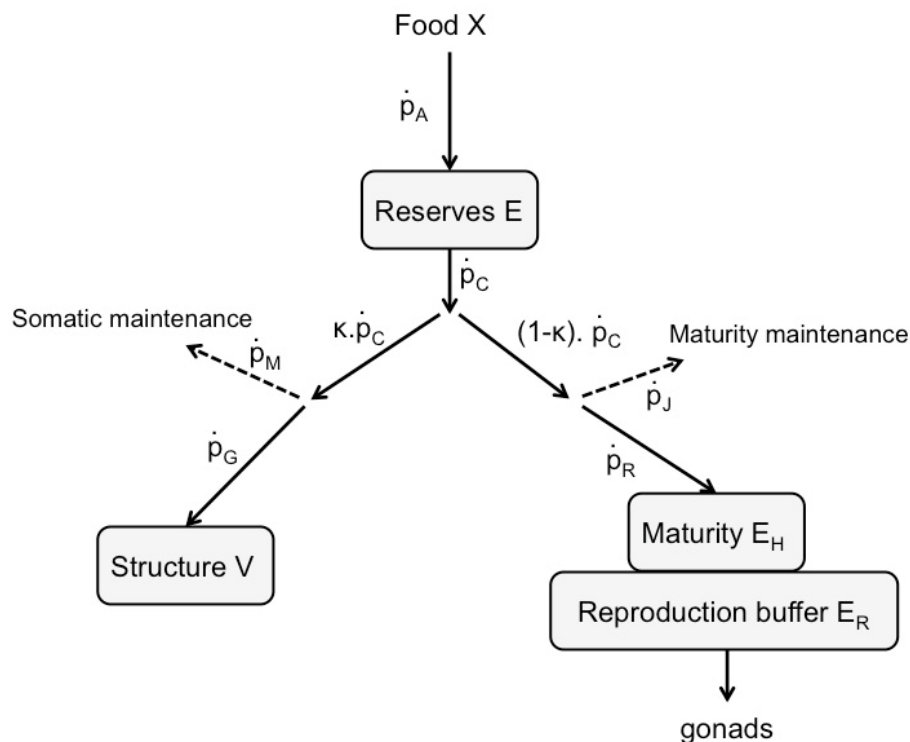
181 **2. Material and methods**

182 **2.1. DEB Model description**

183
184 DEB models are based on an ensemble of rules that allocate energy flows to four main compartments (reserve
185 E, structure V, maturity E_H , reproduction E_R) according to a set of priorities and the level of complexity (i.e.
186 maturity) gained by the organism (Fig. 2, Kooijman 2010). Maturity is treated as information, having mass nor
187 energy. Food is first of all ingested and assimilated (\dot{p}_A) and energetically stored into a reserve compartment
188 (E). A fraction of the energy that is mobilised from reserve, \dot{p}_C , is divided into two branches according to the
189 'kappa-rule': a part of the energy contained in the reserve compartment ($\kappa \cdot \dot{p}_C$) is allocated to somatic
190 maintenance and structure growth, whereas the second part $(1 - \kappa) \cdot \dot{p}_C$ contributes to maturity (before the
191 'puberty' threshold) or reproduction (after the 'puberty' threshold).

192 The energy is allocated within and in between these branches by the establishment of some priorities, where
193 somatic maintenance (\dot{p}_M) has priority over growth and maturity maintenance (\dot{p}_J) has priority over maturity and

194 reproduction. During its lifetime, the organism allocates energy to maturity which symbolizes its complexity and
 195 reaches some life stages at some defined thresholds (E_H^b , birth, when the organism is capable to feed; E_H^j ,
 196 metamorphosis; E_H^p , puberty, when it can reproduce). After reaching sexual maturity, the energy that was
 197 formerly allocated to maturity is attributed to the reproduction buffer and the available energy is allocated to the
 198 development of gametes.
 199 Different types of DEB models have been developed and coded for parameter estimation, see frequently
 200 updated https://github.com/add-my-pet/DEBtool_M page (Marques et al. 2018, 2019). Here, the *abj* model was
 201 used for *N. concinna*. This model considers that growth acceleration occurs between birth and metamorphosis
 202 (Kooijman 2010, Mariño et al. 2019).
 203 The DEB model is forced by food availability and temperature. Temperature acts on metabolic rates following
 204 the Arrhenius principle (see Kooijman 2010, Jusup et al. 2017 for details). A temperature correction factor is
 205 applied to each rate that takes into account the lower and higher optimal boundaries of the individual tolerance
 206 range.
 207 Food available for ingestion is represented by the functional response f comprised between [0,1], where 0 is
 208 starvation condition and 1 very abundant food.



209 **Figure 2:** Schematic representation of the standard DEB model, with energy fluxes (arrows, in $J \cdot d^{-1}$) that connect the four
 210 compartments (boxes). Energy enters the organism as food (X), is assimilated at a rate of \dot{p}_A into the reserve
 211 compartment (E). The mobilization rate (\dot{p}_C), regulates the energy leaving the reserve to cover somatic maintenance (\dot{p}_M),
 212

213 structural growth (\dot{p}_G), maturity maintenance (\dot{p}_J), maturity (\dot{p}_R) (sexually immature individuals) and reproduction (\dot{p}_R)
 214 (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-
 215 $\kappa) \cdot \dot{p}_C$ is used for \dot{p}_J and \dot{p}_R .

216

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

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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	$\text{J.cm}^{-2}\text{d}^{-1}$
\dot{v}	energy conductance (velocity)	cm.d^{-1}
κ	fraction of mobilised reserve allocated to soma	-
$[\dot{p}_M]$	specific volume-linked somatic maintenance rate: \dot{p}_M / V	$\text{J.cm}^{-3}\text{d}^{-1}$
$[E_G]$	volume-specific costs of structure; better replaced by $[E_V]=\kappa_G$, where κ_G is the fraction of growth energy fixed in structure: $[E_V]=[E_G]$	J.cm^{-3}
E_H^b	maturity at birth	J
E_H^j	maturity at metamorphosis	J
E_H^p	maturity at puberty	J
\ddot{h}_a	Weibull ageing acceleration for animals	d^{-2}
s_G	Gompertz stress coefficient	-
δ_M	shape (morph) coefficient: $L=Lw$	-
δ_{M_larvae}	shape (morph) coefficient of the larvae	-
Other parameters		
z	zoom factor to compare body sizes inter-specifically; $z = 1$ for $L_m = 1 \text{ cm}$	-
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.cm ⁻³

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 relationship, 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 ≥ 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.

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 ab (days)	10	Peck et al. 2016	Same as intertidal	
Age at puberty ap (years)	4	Shabica 1976	Same as intertidal	
Maximal observed age am (years)	14	Shabica 1976	Same as intertidal	
Length at birth Lb (cm)	0.0228	Peck et al. 2016	Same as intertidal	
Length at puberty Lp (cm)	1.54	S. Morley experiment 2018	1.59	Picken 1980
Maximal observed shell length Li (cm)	5.8*	Shabica 1976	5.52**	S. Morley experiment 2018
Wet weight of the egg Ww0 (g)	5.8.10 ⁻⁶ ***	Peck et al. 2016	Same as intertidal	
AFDW at puberty Wdp (g)	0.0236	Shabica 1976	0.057	S. Morley experiment 2018
Uni-variate data, (unit)	Reference		Reference	
Length ~ AFDW LWd_signy (cm, g)	Nolan 1991 , Signy Island		Nolan 1991 , Signy Island	
Length ~ AFDW LWd (cm, g)	S. Morley experiment 2018		S. Morley experiment 2018	
Length ~ Gonado somatic index LGSI(cm, -)	S. Morley experiment 2018		S. Morley experiment 2018	
Length ~ Oxygen consumption	S. Morley experiment 2018		S. Morley experiment 2018	

LJO (cm, $\mu\text{mol/h}$)		
Temperature ~ Oxygen consumption TJO (K, $\mu\text{L/h}$)	Peck 1989	Peck 1989
Time ~ Length tL (d, cm)	S. Morley experiment 2018****	S. Morley experiment 2018****

255

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

257 ** [Shabica 1976](#) indicates an observed value of 5.8cm and S. Morley measurements indicate a ratio between
258 intertidal/subtidal lengths of the morphotypes of 1.05. The unknown subtidal Li value was calculated as
259 $5.8/1.05= 5.52\text{cm}$.

260 *** based on egg diameter of $221\mu\text{m}$

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

262

263 **2.3. DEB parameter estimation and goodness of fit**

264

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

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

275
$$\sum_{i=1}^n \sum_{j=1}^{n_i} \frac{w_{ij}}{n_j} \frac{(d_{ij}-p_{ij})^2}{\bar{d}_i^2 + \bar{p}_i^2} \quad \text{eq.1}$$

276 where i scans datasets and j points in this dataset. d_{ij} and p_{ij} are respectively the data and the predictions and
277 \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
278 the data in a dataset, n_j the data in data-points.

279

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. 2020 this issue) is a new extension that enables to compare small variation 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:

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

where w 's are weights, d 's data, p 's predictions, θ 's parameters, j scans data-points with a data-set of n_i points ($n_i = 1$ is allowed), i scans the data-sets and k the parameters.

In this second term, when $w_k=0$, the parameter θ_k between species are different, but when increasing w_k , the parameter θ_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 the 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) (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 δ_M . We found a slightly larger value of δ_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 κ 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 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.

346 The MRE values of the merged models stay below 0.25 and the value of the loss function for the merged
347 situation is only a little larger than the sum of both populations, reflecting the fact a substantial reduction in the
348 total number of parameters by almost a factor 2, hardly affects the goodness of fit (Table 3, Appendix C).
349 DEB parameters of the merged models are quite close to the values of the intertidal and subtidal models, with
350 $[\dot{p}_M]$, δ_M , E_H^p , E_H^b , $[E_G]$ and \dot{v} merged values being almost exactly in between the values of the intertidal and the
351 subtidal morphotypes. κ , z , E_H^j , $\{p_{Am}\}$ and \ddot{h}_a are closer to the intertidal predictions.
352 Univariate predictions are also extremely close between the two models and the merged model (Fig. 3), with
353 only a small difference for the subtidal model for which the GSI~length predictions are higher than the intertidal
354 and merged predictions, mainly due to errors in predictions and scatter in the data. This higher potential of
355 energy allocation to reproduction can, however, be linked to the higher E_H^p values estimated for the subtidal
356 type (Table 3).

357
358 **Table 3.** Summary of goodness of fit, DEB model estimates at a reference temperature of $T_{ref}= 20^\circ\text{C}$. RE:
359 Observed and predicted values for zero-variate data, relative error (RE) for the uni-variate data. See Fig. 3 for
360 comparisons for uni-variate predictions between the models. MRE= Mean Relative Error. For the merged
361 model, the MRE values respectively correspond to the mean relative error of model prediction for data of both
362 intertidal and subtidal populations. All DEB parameters indicated were allowed to vary during covariance
363 estimation. The abj parameters that are not mentioned in that table were kept constant with the standard initial
364 values.

	INTERTIDAL	SUBTIDAL	MERGED
MRE	0.166	0.192	0.196 0.227
Loss function	0.2441	0.2345	0.7936
z (-)	0.3055	0.4317	0.2579
$\{p_{Am}\}$ (J/d. cm⁻²)	8.361	19.07	8.859
\dot{v} (cm/d)	0.0501	0.0426	0.0499
K (-)	0.9084	0.9368	0.9256
$[\dot{p}_M]$ (J/d. cm⁻³)	19.62	31.68	24.62

$[E_G]$ (J. 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		
\ddot{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		
δ_M (-)	0.4517			0.3866			0.4247		
δ_{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		
ab (d)	10	10.62	0.0619	10	10.59	0.0586	10.61	0.0609	
ap (y)	4	3.54	0.1141	4	3.75	0.0607	3.66	0.0845	
am (y)	14	14	9.4.10 ⁻⁵	14	13.99	4.8.10 ⁻⁴	14	1.6.10 ⁻⁴	
Lb (cm)	0.0228	0.02279	2.4.10 ⁻⁴	0.0228	0.0228	6.05.10 ⁻⁴	0.0228	1.424.10 ⁻⁶	
Lp (cm)	1.54	1.225	0.2045	1.59	1.81	0.1384	1.49	0.0323	
Li (cm)	6.5	5.319	0.1816	5.52	4.515	0.1827	5.184	0.2024	
Ww0 (g)	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	
Wdp (g)	0.0236	0.0263	0.1181	0.057	0.05649	0.0089	0.0396	0.6762	
Uni-variate									
	RE			RE			RE		

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

365

366

367

368

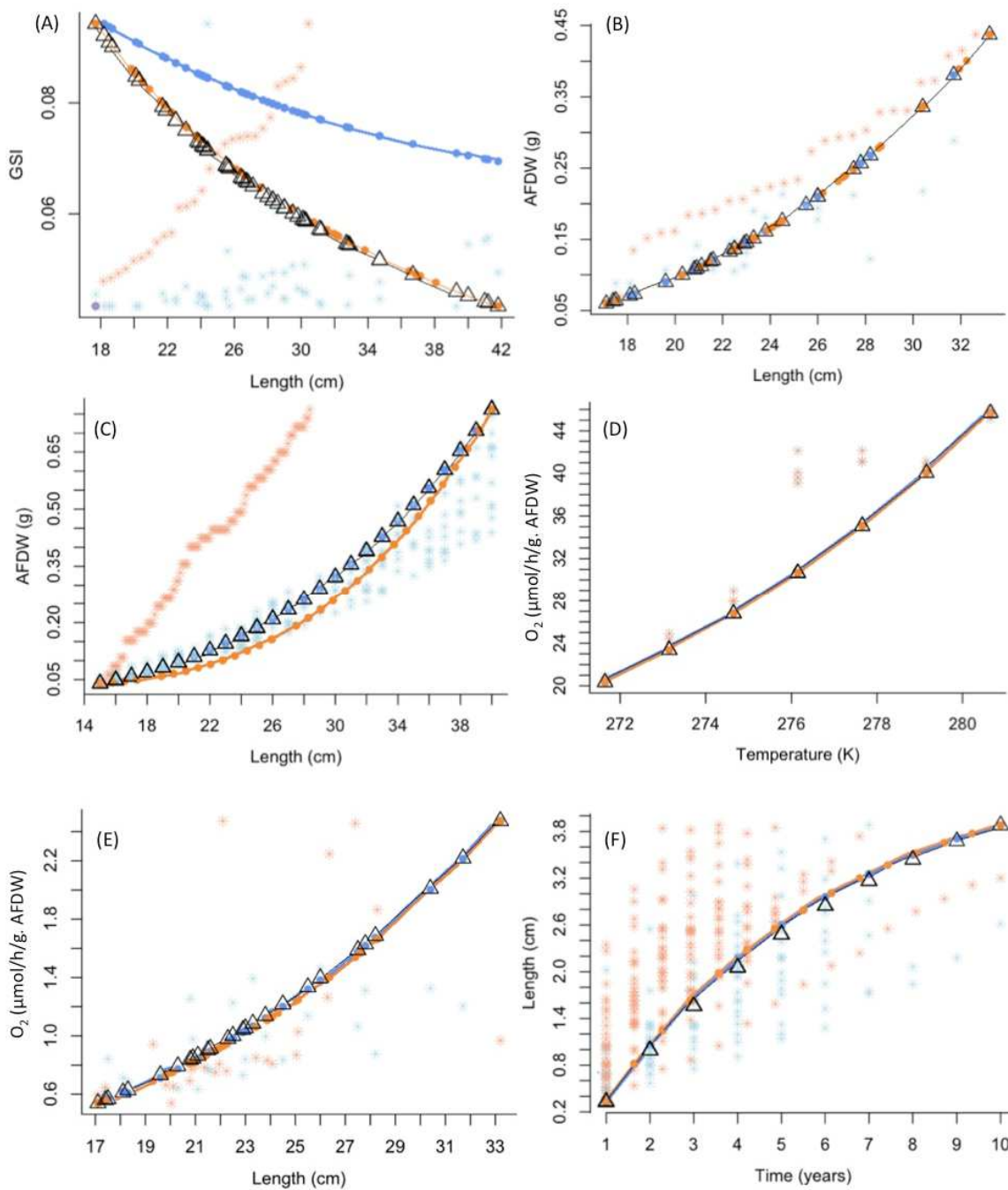
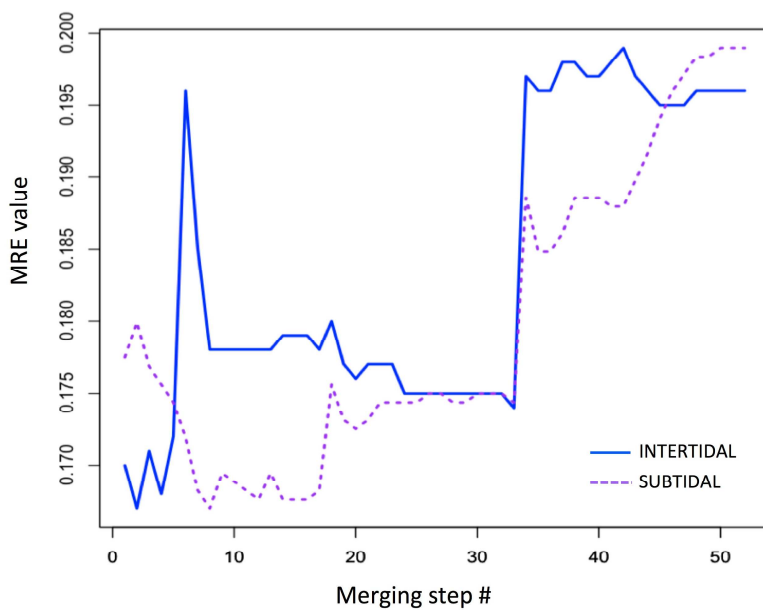


Figure 3. Comparison of model predictions (uni-variate data). Blue dots joined by lines: subtidal model predictions, blue stars: subtidal data (observations); orange dots joined by lines: intertidal model predictions, orange stars: intertidal data (observations); black triangle joined by lines: merged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

3.2. Merging process

376 Along the merging procedure, the loss function and MRE values of the model at each step of the merging
 377 procedure are observed, one 'step' corresponding to the iterative increase of the weight coefficient of the
 378 studied parameter (i.e. merging step, Fig. 4) . Changes in loss function and MRE values are not that important
 379 between the initial step and the final step of the merging procedure (Fig. 4, Appendix D) (respectively from
 380 0.170 to 0.196 and from 0.192 to 0.227 for the MRE intertidal and MRE subtidal values), meaning that merging
 381 parameters is possible. E_H^p and δ_M seem to be the parameters that are the most influencing the model during
 382 the merging procedure for both the intertidal and subtidal models and $[\dot{p}_M]$ seems to further influence the
 383 intertidal model.



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

384 **Figure 4.** Evolution of Mean Relative Error (MRE) values along the merging of the different parameters. MRE
 385 intertidal in solid blue line, MRE subtidal in dashed purple line. Example of Trial #5 (merging of z , $[\dot{p}_M]$, δ_{M_larvae} ,
 386 κ , \ddot{h}_a , \dot{v} , E_H^b , $[E_G]$, E_H^j , E_H^p , δ_M).

389 4. DISCUSSION

390 4.1. DEB models relevance

391 DEB models are powerful tools enabling predictions of the individuals energetic scope for survival, growth and
 392 reproduction, given the considered environmental conditions (Kooijman 2010, Jusup et al. 2017). These
 393 mechanistic approaches have been of interest for several years to the marine Antarctic community (Gutt et al.
 394 2012, Constable et al. 2014, Gutt et al. 2018), and have been increasingly developed during recent years (e.g.
 395 Agüera et al. 2015, 2018, Goedegebuure et al. 2018, Henschke et al. 2018).

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

405
406 Rates (and ages) depend on temperature. Here we correct for differences in temperature using an Arrhenius
407 relationship. However, in order to meaningfully compare differences in parameters between species living in
408 different habitats, it is useful to standardize all parameters to a common reference temperature: $T_{ref}= 20^{\circ}\text{C}$.
409 This is the standard for presenting and comparing DEB parameters across the 2,000 different species in AmP.
410 When comparing DEB parameters estimations of *N. concinna* to those of their temperate counterpart *Patella*
411 *vulgata* (Kooijman et al. 2017) at $T_{ref}= 20^{\circ}\text{C}$, we notice clear differences between the species in term of
412 metabolic strategies, although the limpets morphology and therefore size and volume are close between these
413 species (close length and predicted shape coefficient δ_M). For *N. concinna*, predicted κ is much higher and
414 close to 1 (0.9256 vs 0.617 for *P. vulgata*), meaning that almost all the energy available in the reserve
415 compartment is allocated to somatic maintenance and growth, and only a small amount is available for
416 reproduction. This is clearly visible with the ultimate rate of reproduction more than 40 times lower for the
417 Antarctic limpet compared to the temperate one. The capacity to assimilate resources $\{p_{Am}\}$ was estimated to
418 be 10 times higher for *P. vulgata*, explaining the 2.5-fold lower growth rate for *N. concinna*. The two
419 metabolisms also contrast by the fact that *P. vulgata* is predicted to store more reserves than *N. concinna* in
420 similarly abundant food conditions. These results are consistent with published experiments, where it was
421 shown that rasping rates (i.e. feeding potential) were higher for temperate and tropical species than for *N.*
422 *concinna* (Morley et al. 2014) and that development rates of Antarctic marine molluscs are much slower than at
423 higher temperatures (Peck et al. 2007, 2016), which could be partially due to the increased costs of protein
424 production in the cold (Marsh et al. 2001, Robertson et al. 2001, Pörtner et al. 2007).

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

429 **4.2. Comparison between morphotypes**

430

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

441 Despite the known physiological contrasts in the field, the available data did not allow the models to capture
442 these physiological differences between the morphotypes, using only the available data. Scatter distribution of
443 the data used to calibrate the model (Fig. 3) can hide metabolic differences, which calls for more experiments
444 to describe the physiology of the different morphotypes. Using more complete datasets, for which all
445 parameters are independent between intertidal and subtidal morphotypes, may also help to further constrain
446 the differences. In our case study, several zero-variate data are shared between the intertidal and subtidal
447 models, among which age, length and weight at birth, that control the very beginning of the development. The
448 observed results of a twofold difference in metabolism acceleration of intertidal morphotypes compared to
449 subtidal ones ($s_M \approx 8$ and 4 for intertidal and subtidal) is in fact an artefact caused by common parameters
450 related to birth and puberty stages (age, length, weight). Indeed, specific assimilation at birth for the subtidal is
451 two times larger than that for the intertidal, which indicates that subtidal individuals develop faster. However,
452 according to available data provided in the model, puberty is reached at the same time for both types. E_H^p
453 consequently needs to be smaller for the intertidal type to reach puberty at the same age a_p and length L_p ,
454 explaining the observed contrasts between the intertidal and subtidal groups.

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

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

464 work is a contribution to understanding the relationship between observations (data) and metabolism for these
465 two populations.

467 **4.3. Models drawbacks and improvements**

468
469 Apart from data availability, a drawback of our model construction is the lack of information about
470 environmental properties that makes comparisons between estimations of the two morphotypes quite difficult
471 to perform. In the models, we just considered an average temperature for intertidal or subtidal habitats from
472 where the limpets come from, but do not add any supplementary detail on environmental contrasts between
473 these habitats not in the difference of food availability between the morphotypes. However, contrasting
474 environmental pressures (desiccation, salinity, hydrodynamism) and habitat characteristics (immersion time,
475 substratum type, and surrounding physico-chemical factors) contribute to contrasting adaptative strategies
476 among which morphological adaptation is really important for limpets, but have not been integrated into our
477 DEB models (because it requires more data we don't have) (Vermeij 1973, Branch 1981, Denny & Blanchette
478 2000, Sa Pinto et al. 2008, Bouzaza & Mezali 2013, Grandfils 1982, Gray & Hodgson 2003, Espinosa et al.
479 2009). Desiccation is one of the strongest hypothesis to explain the morphological differences between the
480 intertidal and subtidal morphotypes (Mauro et al. 2003, Bouzaza & Mezali 2018). The presence of high
481 upstream shifted apex form for the intertidal morphotypes, more exposed to desiccation, could help to store
482 more water and absorb more oxygen, as described for *Patella ferruginea* (Branch 1985, Paracuellos et al.
483 2003). Similarly, shell volumes are bigger for the intertidal type and help reduce water loss (Vermeij 1973,
484 Wolcott 1973, Branch 1975, Branch 1981) but also infer resistance to the effects of ice damage (Morley et al.
485 2010). Differences in the energetic responses of the two morphotypes of *N. concinna* to the difference in mean
486 intertidal (0.45°C) and subtidal (-0.1°C), or the much greater difference in maximum (12.3 versus 1.7°C
487 respectively; Morley et al., 2012), could be a proximate cause of the morphological differences. Taking into
488 consideration differences between the environments is therefore important but strongly lacking in the analysis
489 presented here.

490
491 In our study, field data show a slight difference in shell length of +5% and a small difference also in the
492 predicted shape coefficient of 0.45 against 0.39 (Table 3) for respectively the intertidal and subtidal individuals.
493 This indicates very small differences in inner volumes between the studied populations as calculated by the
494 DEB, meaning that the DEB model does not adequately reflect the difference in morphology between the
495 intertidal and subtidal morphotypes. In the raw data, shell heights present a 33% difference between intertidal
496 and subtidal individuals (Appendix A) but shell length was used, rather than shell height, in the model to
497 characterize the growth structure of the species. Fine tuning the models with extra shape information could

498 have helped to bring further contrasts between the two models, but also requires much more information on
499 shell growth.

500
501 Moreover, the difference in food availability and quality was hypothesized between the orphotypes when
502 calibrating the model, despite food abundance and quality knowledge being responsible for strong contrasts in
503 DEB model outputs (Kooijman 2010, Thomas et al. 2011, Saraiva et al. 2012, Sarà et al. 2013). During winter
504 time, the intertidal type seems to have supplementary access to ice-algae and microphytobenthos in rock
505 crevices, whereas the subtidal type mainly grazes on the diatoms films growing on encrusting red algae
506 (Appendix A, Obermüller et al. 2011). But food abundance and quality were assumed for the construction of
507 the models, as no data accurate enough were available to characterize the feeding behaviour of the limpets.
508 Moreover, in the case of intertidal type, no clear hypothesis is available for their behaviour during winter period,
509 as several authors hypothesize either a migration into the subtidal or a dormance period hidden into crevices
510 during the period where ice is covering their habitat (Brêthes et al. 1994, Obermüller et al. 2011). However, this
511 information would be essential to explain how these individuals energetically behave during this period.

512 513 **4.4. Potential of the approach**

514
515 This study showed that it is feasible to build a DEB model for a marine Antarctic species, with the few available
516 data. Adding extra information from sampling and experiments during a single expedition in the field
517 considerably increased the accuracy of the model and highlighted some small differences in energy allocation
518 priorities, maintenance costs and reproductive potential between the intertidal and subtidal morphotypes. But
519 the method is then limited by model calibration and data availability since it could not prove that these
520 contrasts are explained by anything else but environmental conditions.

521
522 Such DEB models would already be sufficient to (1) describe the performance of the species physiological
523 traits in spatially or temporally contrasting environmental conditions (Kearney et al. 2012, Teal et al. 2012), (2)
524 to be upscaled to the population level to assess population structure and density dynamics (Klanjscek et al.
525 2006, Arnould-Pétré et al. 2020 this issue), or (3) to be integrated into a dynamic network by adding knowledge
526 about interaction with other species (Ren et al. 2010, 2012). Adding some data from extra experiments would
527 easily enable further development of these models for ecophysiological or ecotoxicological applications (Muller
528 and Nisbet 1997, Pouvreau et al. 2006, Peeters et al. 2010, Sarà et al. 2011), or to improve knowledge about
529 development stages, behaviour or reproduction (Pecquerie et al. 2009, Rico-Villa et al. 2010, Kooijman et al.
530 2011).

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

535
536 To conclude, we advise the use of DEB approach for ecological modelling for Antarctic case studies but
537 modellers should be aware of the necessity to calibrate models with accurate data to fine tune results. Among
538 these data, the description of the species habitat is complex information to be integrated into a model and most
539 of the time only partial information is available. Working in narrow scale areas where habitat is known and
540 described and where experiments can be run might be a good option.

541 Our study also highlights the interest of DEB models to reuse data from published experiments from historical
542 published works from Antarctic campaigns and highlights the importance of precisely documenting the
543 associated metadata (notably the description of the environment and the conditions in which the limpets are
544 living), data that is not always available.

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557 **Authors’ contribution**

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