Dynamic energy budget parameterisation of *Brachidontes pharaonis*, a Lessepsian bivalve in the Mediterranean Sea

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ABSTRACT

Dynamic Energy Budget (DEB) models are used for describing the flow of energy through organisms. The most important and powerful aspect of DEB theory is that inter-specific differences can be captured in the same model by comparison of parameter values. However, estimation of these parameters is complicated and can often not be done with direct empirical measurements alone. Here, we present DEB parameter estimates obtained by combining both experimental and literature data for the filter feeder *Brachidontes pharaonis*, which is considered one among the 100 worst invasive marine species in the Mediterranean Basin. We utilize a statistical procedure based on the covariation method to obtain parameters that minimize the deviation between observed and predicted patterns of growth and reproduction.

1. Introduction

The need to provide predictions about the ecological responses of organisms as a function of environmental variability has promoted the investigation of how organisms follow first principles of energy utilization. In this context, the study of the functional traits involved in the energy budget is the key to predict the effects of environmental conditions on species' life history (LH) characteristics, such as growth and reproduction (Anthony and Connolly, 2004). The Dynamic Energy Budget (DEB) theory lends itself well to this application, as it describes how organisms allocate energy to maintenance, growth, reproduction, and maturity (Kooijman, 2010). The optimal functioning of an organism implies a positive energy budget, i.e. energy for growth and maturation or reproduction should be available. In addition, the optimization of energy resources is achieved only if the organism grows within its thermodynamic niche (Kearney et al., 2012). Hence, differences in energy allocation strategies may reflect differences in the capabilities that allow organisms to survive at varying environmental conditions. In particular, how they allocate assimilated energy under various natural or anthropogenic environmental conditions could be crucial for our understanding of how much energy organisms are able to get from the habitat. These values can be used to quantify the functioning of an organism in its habitat (Denny and Benedetti-Cecchi, 2012) and represents species' identity (Diaz and Cabido, 2001), which can be used to predict the role organisms play in communities and ecosystems (Petchey and Gaston, 2006).

Accordingly, several studies suggest the use of mechanistic models based on DEB theory to investigate functional traits and bioenergetics of organisms (e.g. Nisbet et al., 2012; Pouvreau et al., 2006; Rosland et al., 2009; van der Veer et al., 2006). The DEB theory aims to identify the processes of substrate uptake and use by organisms through on the basis of mass and energy balances. The theory assumes that metabolites from food are first converted to reserve, which is mobilized to fuel the remaining metabolic machinery, including maintenance, maturation, growth and reproduction (Bacher and Gangnery, 2006; Nisbet et al., 2000; van der Meer, 2006). A fixed fraction of mobilized reserve is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation or reproduction. This allocation strategy is known as the kappa-rule. The standard DEB model is the simplest among DEB models. Here, we extend it with the inclusion of metabolic acceleration between birth and metamorphosis, which occur in all bivalves (Kooijman, 2014–this volume; Kooijman et al., 2011) at a specific maturity level. During this acceleration both the specific maximum assimilation rate and the energy conductance increase proportionately with length. DEB model parameters have been successfully estimated for many different taxa and many of them dealing with bivalves (Barillè et al., 2011; Beadman et al., 2002; Bourles et al., 2009; Duarte et al., 2010; Emmery et al., 2011, submitted for publication; Filgueira et al., 2011; Frechette, 2012; Freitas et al., 2009; Grangerè et al., 2009; Handa et al., 2011; Hanegraaf and Kooi, 2002; Kooi and van der Meer, 2010; Ren and Schiel, 2008; Rico-Villa et al., 2009; Rosland et al., 2009; Ross and Nisbet, 1990; Sarà et al., 2011, 2012, 2013; Saraiva et al., 2011, 2012, this volume; Thomas et al., 2011; Troost et al., 2010; van der Veer et al., 2006; van Haren and Kooijman, 1990, 1993).

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Here, we consider the invasive Pharaonic mussel *Brachidontes pharaonis* (*Brachidontes variabilis*, Krauss 1848; Sarà et al., 2000) from the Indian Ocean and Red Sea, which represents a pest for Mediterranean biodiversity (Galil, 2009). Despite its currently widespread distribution throughout the Mediterranean Sea (Cilia and Deidun, 2012) detailed information on growth and reproductive potential is still limited at local scales (Sarà et al., 2013). Combining field and literature data, the main aim of the present study is to present parameter estimates for *B. pharaonis*' obtained with the recently proposed covariation method (Lika et al., 2011), which permits the simultaneous estimation of DEB parameters from experimental data on size, growth and reproduction.

2. Materials and methods

2.1. DEB model parameters

Apart from core parameters, the covariation method involves a number of "auxiliary parameters", i.e. conversion and temperature parameters (Lika et al, 2011), wet–dry weight ratios, length–weight relationships and body composition in terms of lipids, carbohydrates and proteins. These auxiliary parameters link abstract quantities, such as reserve and structure, to observable quantities, such as length, weight, reproduction, respiration, feeding rate, temperature and food density. Life history and additional temperature parameters used in the covariation method were collected from both literature sources and field observations (reported in Table 1). A total of 20 different data were used in the estimation routine: 1) 11 zero-variate values such as age/size at different life stages (extrapolated from literature; see ref in Table 1) or from empirical observations in the field, 2) 7 pseudo-data reflecting the standard parameter values for a generalized animal (Kooijman, 2010) and 3) length–age relationships estimated from mussels collected in the Stagnone di Marsala (Trapani, Italy), with the initial value for the shape coefficient δ_M set to 0.288 (Sarà et al., 2013).

The Arrhenius temperature has been included to correct rates and times for temperature, but since most rates and times were measured at the reference temperature of 20 °C (except time since birth at metamorphosis), this parameter hardly plays a role in the estimation. However, it still can play an important role in predictions. As listed in Table 1, the Arrhenius temperature (T_A) and upper and lower boundaries of the tolerance range (T_{AH} and T_{AL}) were obtained from Sarà et al. (2013), where thermal limits for *B. pharaonis* were estimated from measurements of oxygen consumptions across a range of temperatures.

2.2. DEB model simulation

Energy allocation strategies in *B. pharaonis* were estimated using DEBtool software, which has been written in MatLab® (The MathWorks™, Inc. USA) and Octave. We assumed ad libitum food conditions (energy) in the estimation procedure to avoid effects related to food availability, expressed by the functional response *f* set to 1. Indeed, a functional response is defined as the intake rate of a consumer as a function of food density (Holling, 1959) and in bivalves it describes a type II curve where processing of food and searching for food are assumed to be mutually exclusive behaviors (Kooijman, 2010; Sarà et al., 2013). Following the criteria reported in Lika et al. (2011), we assigned a completeness mark of 2.5 to the estimated parameter set, a value due to the prevalence of mostly zero-variate data used in the estimation routine.

3. Results and discussion

Parameter values for *B. pharaonis* are presented in Table 2.

The shape coefficient converts shell length to structural length, i.e. the cubic root of structural volume and both reserve and structure contribute to body volume. Thus, the shape coefficient must be determined simultaneously with energy parameters, since it has information of how to partition biomass into structure and reserve. We estimated a shape coefficient (δ_M) of 0.33, a value somewhat higher than that reported for other *Mytilus spp.* (0.225, Sarà et al., 2012; 0.297, Saraiva et al., 2011; 0.287, van der Veer et al., 2006). However it falls well within the range values reported for bivalves (0.2–0.4; Kooijman, 2010). Moreover, the shape coefficient is sensitive to the shape of the individual and there is some difference between the species shapes, apart from the contribution of structure to body volume.

Another important (compound) parameter is the zoom factor z. The product of the zoom factor and the reference length of $L_m^{ref} = 1$ cm approximates the maximum structural length (which is eventually obtained at abundant food). Under standard DEB model assumptions it is applied at all life stages, including the embryo and neonate. However, after birth (i.e. the onset of feeding), bivalves accelerate their metabolism and so increase this maximum length. To obtain the maximum structural length of a fully grown adult, we now have to multiply the zoom factor with the ratio of the lengths at metamorphosis and birth. This ratio depends on feeding conditions, however, so it cannot be treated as a primary parameter since food densities generally change in time. These lengths are obtained via the maturity thresholds at birth and metamorphosis. We arrived at the estimates of $L_b = 0.013$ cm and $L_j = 0.027$ cm, so the acceleration factor is $s_M = 0.027/0.013 = 2$ at abundant food. The zoom factor (for the neonate) is $z = 0.566$, so for the adult we arrive at a maximum structural length of 1.132 cm,

Table 1
a) Observed and predicted values from DEB parameter estimation procedure for *B. pharaonis* (1 = field observation; 2 = Monteiro-Ribas et al., 2006; 3 = Sarà et al., 2013; 4 = Morton, 1988) and b) Arrhenius temperatures and relative boundaries used to correct rates across the estimation procedure.

Data	Unit	Obs	Pred	
a_b, age at birth	d	1.1	1.116	1
a_j, age at metamorphosis	d	24	1.984	2
a_p, age at puberty	d	182	215	1
a_m, life span	d	1460	1460	3
L_{wb}, physical length at birth	cm	0.009	0.013	2
L_{wj}, physical length at settlement	cm	0.0273	0.0277	2
L_{wp}, physical length at puberty	cm	0.75	1.051	4
L_i, ultimate physical length	cm	3.8	3.484	3
Ww_p, wet weight at puberty	g	0.084	0.051	1
Ww_i, ultimate wet weight	g	1.545	1.861	1
R_i, maximum reprod rate	# d^{-1}	1208	1292	3
Temperature parameters				
T_{ref}, reference temperature	K	293		3
T_A, Arrhenius temperature	K	8232		3
T_L, lower tolerance temperature	K	284		3
T_H, upper tolerance temperature	K	305		3
T_{AL}, lower boundary of the Arrhenius temp	K	6005		3
T_{AH}, upper boundary of the Arrhenius temp	K	17,957		3

Table 2
DEB core parameters resulting from the estimation procedure — covariation method (Lika et al., 2011); E = parameter estimated, F = parameter fixed.

DEB parameters	Unit	Value	
z, zoom factor	–	0.5662	E
δ_M, shape coefficient	–	0.3300	E
$\{F_m\}$, max spec searching rate	l d^{-1} cm^{-2}	6.5	F
kapX, digestion efficiency of food to reserve	–	0.75	F
v, energy conductance	cm d^{-1}	0.01868	E
kap, allocation fraction to soma	–	0.9830	E
kapR, reproduction efficiency	–	0.95	F
$[p_M]$, vol-specific somatic maintenance	J d^{-1} cm^{-3}	14.24	E
$\{p_T\}$, surface-specific som maintenance	J d^{-1} cm^{-2}	0	F
k_J, maturity maint rate coefficient	d^{-1}	0.002	F
$[E_G]$, spec cost for structure	J cm^{-3}	2478	E
E_{Hb}, energy maturity at birth	J	0.000003938	E
E_{Hj}, energy maturity at metamorphosis	J	0.0000331	E
E_{Hp}, energy maturity at puberty	J	2.163	E
h_a, Weibull aging acceleration	d^{-2}	0.00000004156	E
s_G, Gompertz stress coefficient	–	0.0001	F

and a maximum structural volume of $1.132^3 = 1.452$ cm^3, which weighs about 1.450 g (wet), so 0.145 g dry. The maximum predicted dry weight is 1.861 g (observed is 1.546 g), so a fraction of 1.450/1.861 = 0.79 g of dry weight corresponds to structure (at abundant food), while a fraction of 1–0.79 = 0.21 g of dry weight corresponds to reserve with these parameters. We report this to demonstrate that with simple measurements, we can estimate parameters that specify how to partition biomass into contributions from reserve and structure.

Within the covariation method estimation procedure, weight may be assigned to certain observations with greater confidence or accuracy than others. To overcome the uncertainty inherent when using diverse input data sources, we appended relative weights to each dataset. Specifically, due to the huge discrepancy between the observed age at metamorphosis (24 d) and the predicted value (1.9 d) we assigned to this parameter a weight coefficient equal to zero, meaning this value was not included in the estimation procedure (Kearney, 2012; Lika et al., 2011).

The specific maximum assimilation rate follows from the relationship $z \times L_m^{ref} = \kappa \times \{p_{Am}\} / [p_M]$ and amounts to $0.5662 * 14.24 / 0.983 = 8.2$ J d^{-1} cm^{-2} for a neonate and s_M times as much, so 16.4 J d^{-1} cm^{-2}, post-metamorphosis at 20 °C. The reserve capacity $[E_m] = \{p_{Am}\}/v = 8.2/0.018 = 439$ J d^{-1} cm^{-3} after birth and does not change by acceleration, since both $\{p_{Am}\}$ and v increase with length. The ratio of the reserve capacity and the specific somatic maintenance, $[E_m]/[p_M] = 439/14.24 = 31$ d, gives a rough indication of how long an individual can survive without food at 20 °C (i.e. using exclusively metabolites stored in the reserve), before the shrinking of structure.

The standard DEB model treats reserve as a generalized chemical compound, i.e. a mixture of a large number of chemical compounds that do not change composition. The maximum average residence time of metabolites in the reserve is given by the ratio of the maximum structural length and the energy conductance, $L_m / v = \kappa \times [E_m] / [p_M]$, which amounts to $0.566/0.018 = 30$ d at 20 °C. This can be seen as a quantifier for metabolic memory. It is not affected by metabolic acceleration, but for small individuals at low food densities, this memory is shorter. Since kappa is close to one, the maximum starvation time and residence times are almost equal.

3.1. Volume-specific maintenance costs $[p_M]$ and specific cost for structure $[E_G]$

Maintenance costs depend on the processes needed by the organism to survive, including all the biochemical processes necessary for basal metabolism, e.g. turnover of proteins (Sarà et al., 2013; Widdows and Hawkins, 1989) and production of specific structures such as scales in fish or leaves in trees (Kooijman, 2010). The volume-specific maintenance cost $[p_M]$ was estimated to be 14 J d^{-1} cm^{-3}, which is similar to the values found for *Crassostrea gigas*, *Cerastoderma edule* and *Mya arenaria* being respectively 12.69, 16.13 and 15.37 J d^{-1} cm^{-3}. Conversely, $[p_M]$ for *Ruditapes philippinarum* (28.24 J d^{-1} cm^{-3}), *Pecten maximus* (29.05 J d^{-1} cm^{-3}), *Mytilaster minimus* (39.61 J d^{-1} cm^{-3}) and the Asian green mussel *Perna viridis* (39.61 J d^{-1} cm^{-3}) were found to be two times as high (see www.bio.vu.nl/thb/deb/deblab/add_my_pet/). The specific somatic maintenance for *Macoma balthica* and *Ensis directus* was found to be around 60 J d^{-1} cm^{-3} at 20 °C, so 4 times as high. While these are the most current $[p_M]$ values reported, it is important to note that more data is needed to confirm these patterns. Such differences among species probably reflect their respective differences in life history strategies (Stearns, 1992) and might reflect the positive connection that exists between somatic maintenance and production (growth and maintenance): the waste-to-hurry hypothesis (Kooijman, 2013). Indeed, it states that the typical specific somatic maintenance costs is some 20 J d^{-1} cm^{-3} (for the structural part of the body) at 20 °C, but small-bodied species that live of blooming resources can have higher costs to boost their production, in combination with a torpor state under non-blooming conditions. Thus, a greater

accuracy of somatic maintenance estimation could be crucial for our understanding of the ability of species to successfully colonize new geographical areas. Somatic maintenance cost may play a key ecological role in enhancing the capability of organisms to cope with environmental variability typical of intertidal habitats (Helmuth, 1999) making them able to persist throughout a wide range of physical, chemical (Sarà and De Pirro, 2011) and trophic conditions (Sarà, 2007). Consequently, increasing the accuracy of measuring $[p_M]$ could benefit studies exploring the ecological responses of intertidal populations to global change. Indeed as for other LH-traits (sensu Chave, 2013), maintenance costs reflect the genetic makeup of a species and being the major factor in affecting allocation to growth and reproduction, could provide important insights on the specific tolerance limits of species to environmental factors (e.g. temperature and food availability). This in turn could represent an implicit measure of the ability of species to spread throughout its geographical range (Petchey and Gaston, 2006).

The specific cost for structure $[E_G]$, i.e. the amount of energy invested by an organism to convert reserve into body structure, is largely determined by the dry/wet-weight ratio. Measurements of wet weight should include body fluids but exclude environmental water (Kooijman, 2010). Although this is not easy to measure for bivalves, allowing the valves to drain of excess water for a standardized time prior to weighing can provide close approximations. We applied a dry–wet weight ratio of 0.1 for *B. pharaonis*, a value similar to those of related species. Seeing as $[E_G]$ values should be similar to the dry–wet weight ratios in related species (van der Veer et al., 2006), not surprisingly, similar $[E_G]$ values across bivalves were reported ($[E_G] \sim 2800$ J cm^{-3} for a dry–wet weight ratio of 10). In *B. pharaonis*, the $[E_G]$ value was 2478 J cm^{-3} again falling in the range reported for the other bivalves currently present in the add my pet collection (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet; lower $[E_G] = 2279$ J cm^{-3} in *M. balthica*, higher $[E_G] = 3123$ J cm^{-3} in *P. viridis*). To date, the only exception is *Mytilus edulis* for which Saraiva et al. (2011) proposed a $[E_G]$ value of 5993 J cm^{-3} (although it is reported as 4783 J cm^{-3} in the "add my pet" collection).

3.2. Allocation fraction to soma (κ) and reproduction efficiency (κ_R)

Parameter κ represents the fraction of mobilized reserve that is allocated to maintenance and growth and κ_R the fraction of energy allocated to reproduction that is actually fixed into offspring. While the value for κ_R is set by default to 0.95, the fraction of energy allocated to soma in *B. pharaonis* was estimated to be 0.983, similar to that of *P. viridis* (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet). Reproduction (of a fully grown adult at abundant food) has an optimum relationship with κ so that (depending on other parameter values) maximum reproduction occurs somewhere around $\kappa = 0.45$. When κ is larger, organisms exhibit rapid growth and low reproduction but for much lower values little is invested in growth, and since food uptake fuels reproduction, low κ values can result in low reproduction rates as well. This could be another feature of energy budgets of invasive species that should be taken into account when predicting the colonization success and the degree of invasiveness. To corroborate this idea, the fraction of energy allocated to maintenance and growth by non-invasive *M. edulis* and *P. maximus* is 0.81, a value much higher than that of the invasive species *C. gigas* at 0.3. Conversely, other invasive bivalves such as *R. philippinarum*, *E. directus*, *P. viridis* and *Crepidula fornicata* and non-invasive species (i.e. *C. edule*) could also have very high kappa values suggesting perhaps that non-invasive species can afford to invest less in their soma, but it is too early for firm conclusions. Hence, further research is required to conclude whether κ may be a useful indicator of potential ecological strategies.

4. Conclusion

DEB theory provides a conceptual framework, based on the utilization of energy at the individual level, to explain possible mechanisms

on how emergent and classical anthropogenic factors may drive biodiversity loss (Sarà, submitted). Indeed, due to the huge impact anthropogenic stressors have on wild ecological dynamics and *equilibria*, there is a pressing need to identify approaches to rapidly assess the degree of stress experienced by populations. Importantly, this should be done by integrating the effects of multiple stressors to predict for population persistence (Sokolova et al., 2012) and to provide information on the invasiveness degree of out-competitors of local native biota (sensu Simberloff, 2009; Sarà et al., 2013). In a similar vein, while we are aware that ecology is the study of emergent properties (Odum, 1953) and systems are highly variable and complex, we point out that possible bottlenecks in energy flow, at both habitat and individual levels, have important consequences at population and community levels. This is a point of view that is often neglected in studying anthropogenic effects on ecological responses of organisms and to explore effects at higher hierarchal ecological levels (viz. population, community and, then, biodiversity). Functional trait-based models as those based on energy budgets may help in disentangling many aspects of ecological responses. The estimation procedure to get primary DEB parameters for a theoretical individual of species represents the core of that approach. Indeed, increasing the knowledge of the functioning of metabolic machinery provides a general snapshot of the energy budget strategies adopted for species under conditions of environmental variability. In particular, in this study, as expected for an invasive species, our estimation procedure suggested that *B. pharaonis* should have large capability in controlling the energy intake from the environment and wide ability in mobilizing energy toward somatic growth. Similarly, in the case of this pest species the energetic costs needed to survive seem to be consistent with those reported in the literature for other bivalve species, allowing also to infer on the invasiveness related to this species. Thus, increasing our understanding of how ecological features of individuals (e.g. the invasiveness degree of pest species) can be derived by the mechanistic functional trait-based approach based on Dynamic Energy Budget theory (Kooijman, 2010) is crucial.

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