

Embracing multimodal optimization to enhance Dynamic Energy Budget parameterization

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ABSTRACT

Parameterization is one of the most challenging steps in the construction of individual-based models, and it is particularly relevant for the case of Dynamic Energy Budget (DEB) theory given that DEB parameters are mapped to a multimodal fitness landscape. This multimodal fitness landscape could correspond to parameterizations that provide the right outcome for the wrong reasons. Given the lack of available data to directly parameterize some aspects of DEB models, mathematical tools are becoming the state-of-the-art approach to estimate or refine unknown parameters. The aim of this study is to explore the use of a novel mathematical algorithm that recognizes the multimodal nature of the fitness landscape as a way to provide alternative equally good parameterizations for DEB models. The Multimodal Optimization for Model CALibration (MOMCA) framework was used to calibrate a DEB model for the blue mussel *Mytilus edulis* using datasets that included environmental information, growth, and physiological rates. The inclusion of physiological rates, an uncommon approach in DEB parameterization, allowed for constraining the range of solutions, and reducing parameter uncertainty. The application of the MOMCA framework allowed for the identification of the energy acquisition sub-model as one of the top priorities for improving the mechanistic understanding of mussel bioenergetics, and consequently for enhancing model performance. The MOMCA framework could complement the standard procedures to estimate DEB parameters.

Introduction

Dynamic Energy Budget (DEB) theory (Kooijman 2010) mechanistically explains individual bioenergetics throughout the life cycle under dynamic environmental conditions. Building on thermodynamics first-principles and assuming that the mechanisms responsible for the organization of individual metabolism are not species-specific (Sousa et al. 2008), DEB theory can be applied to all species. The potential of such a mechanistic theory has led to an increase in its popularity in the scientific literature, being applied to more than 2,000 species (Add my Pet, https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/), among which bivalves are one of the most studied group (e.g. Pouvreau et al. 2006, Rosland et al. 2009). Despite the successful application of the theory, DEB has been criticized for not being 'efficient'

due to the large number of parameters, namely 14 in its standard versions, and the fact that most of them are species-specific (Marquet et al. 2014). The complex and data-demanding procedure to estimate the value of these parameters (Lika et al., 2011a) may also limit its expansion. Contrarily, it has been argued that DEB is efficient given the large number of processes that can be derived from those parameters, for instance, life cycle development, feeding, growth, maintenance, metabolic heating, reproduction, and senescence (Kearney et al. 2015). The large suite of predictions that can be derived is precisely one of the strengths of DEB implementation in ecosystem-scale models (e.g. Guyondet et al. 2010).

The need to parameterize such a relatively large number of parameters, most of them species-specific, is one of the most challenging aspects of DEB modelling. Early on, the parameterization of DEB relied

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on the empirical and independent approximation to each parameter (e.g. van der Veer et al. 2006). Mathematical calibration such as the use of the Nelder-Mead method was also implemented to estimate the values of unknown parameters or to improve model fit in populations of the same species (e.g. Bacher and Gangnery 2006). A breakthrough in DEB parameterization came with the introduction of the “covariation method” (Lika et al. 2011a), a non-linear least squares regression approach. Lika et al. (2011a) suggested that the most robust parameterization would be to simultaneously estimate all DEB parameters by minimizing the discrepancies between simulations and all available observations. These available observations range from single data-points that represent a single value (zero-variate data in DEB jargon) such as maximum reproduction rate, to arrays of values (uni-variate data) such as growth over time. This method also takes into account the inter-dependency of some parameters, avoiding potentially incoherent combinations of parameters. In addition, Lika et al. (2011a) used DEB theory principles to constraint the potential range of solutions, and introduced the concept of pseudo-data, which are well-known values for a generalized animal that could be scaled to the modelled species. The use of pseudo-data has demonstrated to be beneficial to exploit existing knowledge about parameter values that cannot be extracted from observations, and it constitutes a key component to confine potential solutions to those that make sense biologically (Marques et al. 2019). Marques et al. (2019) has replaced Lika et al. (2011a) as the standard procedure to estimate DEB parameters by adding more advanced loss functions and filters to prevent parameter sets that are not compatible with the general principles of the theory.

Despite this progress, there are still major challenges in DEB parameter estimation, which are common to most mechanistic models in biology. For example, interindividual variability is included through population-level averages, but not directly included in the parameter estimation, and similarly, the uncertainty in the estimated parameters is not usually considered (Johnson et al. 2013). Some mathematical approaches have already included this uncertainty by applying a state-space method to determine the probability distribution of the estimated parameters (Fujiwara et al. 2005). Similarly, the use of a Bayesian inference framework allows for the consideration of this uncertainty (Johnson et al. 2013), and it has already been used to estimate DEB parameters (Boersch-Supan and Johnson 2018). Another challenge for a robust estimation in DEB is related to the large number of parameters that could lead to ‘the curse of dimensionality’ type of problems (Jusup et al. 2017). The challenge of dimensionality is that an increase in the number of parameters requires an exponential increase in available empirical data to avoid sparsity and obtain parameters that are statistically significant. This problem is magnified by the fact that some DEB parameters covariate (Fujiwara et al. 2005, Chica et al. 2017), suggesting that different combinations of values can result in the same solution; which could lead to the simulation of the right solutions for the wrong reasons. For example, the same growth could be observed with high feeding and high metabolic costs or with low feeding and low costs. Therefore, the advantage of DEB regarding the potential to simulate a large variety of processes could become a weakness if the available datasets do not allow for a meaningful parameterization that addresses this multimodal optimization problem, understood as a problem without a unique global optimum solution but multiple optima, either global or local (Ehrgott 2005). The multi-dimensional space of DEB parameters together with data-gaps could be considered one of the major hurdles for DEB parameterization.

Traditionally, the uni-variate data used for DEB calibration focus on growth curves, biometric data, and datasets that can inform about the effect of temperature on the physiology of the individual. Among these datasets, long-term growth curves are usually preferred given the relative simplicity to collect them, their availability in the literature, and the straightforward calculation of growth using DEB outputs; but they lack the power to inform about short-term individual responses. Recent

optimization algorithms consider the coexistence of model parameters that are mapped to a multimodal fitness landscape (e.g. MOMCA framework, Chica et al. 2017). They aim to simultaneously locate more than one optimal solution. Subsequently, such approaches represent the nature of DEB theory and they could thus be an ideal way to move forward on DEB parameterization by providing alternative solutions rather than a single one. In this study, a combined dataset (Strohmeier et al. 2015) of growth and physiological rates (respiration and clearance rates) of the mussel *Mytilus edulis* from two locations of the Lysefjord (Norway) was used to parameterize a DEB model using a novel optimization approach that considers that DEB parameters are mapped to a multimodal fitness landscape (Chica et al. 2017). The inclusion of physiological rates in the parameterization aims to constrain the range of parameters and inform about short-term physiological responses. The ultimate goal of this study is not to provide a generalized set of parameters for *M. edulis*, but to demonstrate that this novel optimization can provide alternative solutions that could identify knowledge gaps and research priorities for further improvement of DEB parameterization. Furthermore, the provision of alternative equally good solutions becomes an ideal complement to the standard procedures to estimate DEB parameters (Marques et al. 2019).

Material and methods

Dynamic Energy Budget model

DEB theory describes the energy of an individual in terms of three state variables: reserve(s), structure(s), and maturity/reproduction. In brief, the assimilated energy is stored as reserves; a fixed fraction of the mobilized energy (κ) is then directed towards maintenance and growth of the structural body and the remainder ($1-\kappa$) is directed towards maturity maintenance and maturation or gamete production, depending on the life cycle stage of the organism (Fig. 1). A description of model equations is presented in Table 1 and a detailed explanation is provided in Pouvreau et al. (2006) and Rosland et al. (2009). The mathematical formulation follows the original notation by Kooijman (2010), in which $[\]$ denotes quantities expressed as per unit structural volume, $\{ \}$ denotes quantities expressed as per unit surface-area and a dot over a symbol denotes a rate, or a dimension per time. Note that the current model aims to simulate the life cycle from the juvenile stage onwards and not the whole life cycle. The constraint $k_J = k_M$ (maturity maintenance rate coefficient = somatic maintenance rate coefficient) has also been implemented in the model to facilitate the comparison with previous DEB models. This simplification is not part of the current standard DEB model, but it was used by the three main papers in which DEB was parameterized for *M. edulis* (van der Veer et al. (2006), Rosland et al. (2009), and Saraiva et al. (2011a)). In addition, the model allowed the use of energy in reproduction buffer when energy in reserves was not enough to pay maintenance costs. The model has been forced with observed temperature and using chlorophyll concentration ($\mu\text{g L}^{-1}$) as a proxy for food density. Spawning, which implied the full release of the reproduction buffer, was triggered manually on specific dates based on field observations.

Respiration and clearance rates were modeled as follows. For simplicity, respiration rate was assumed to be proportional to the mobilization rate of reserve energy (\dot{p}_C , J d^{-1} , Table 1) following Pouvreau et al. (2006) and Guyondet et al. (2010). This simplification introduces uncertainty in the estimated value by assuming that the role of feeding in respiration is also proportional to \dot{p}_C , but it avoids the estimation of an additional parameter, κ_p , the faecation efficiency. Accordingly, the respiration rate was estimated as follows:

$$RR_{\text{DEB}} = \dot{p}_C / 13.8 \quad (1)$$

Where RR_{DEB} is the respiration rate estimated with DEB ($\text{mg O}_2 \text{ d}^{-1}$), \dot{p}_C the mobilization rate of reserve energy (J d^{-1}), and $13.8 \text{ J mg O}_2^{-1}$ a conversion factor following Guyondet et al. (2010). For the purpose of

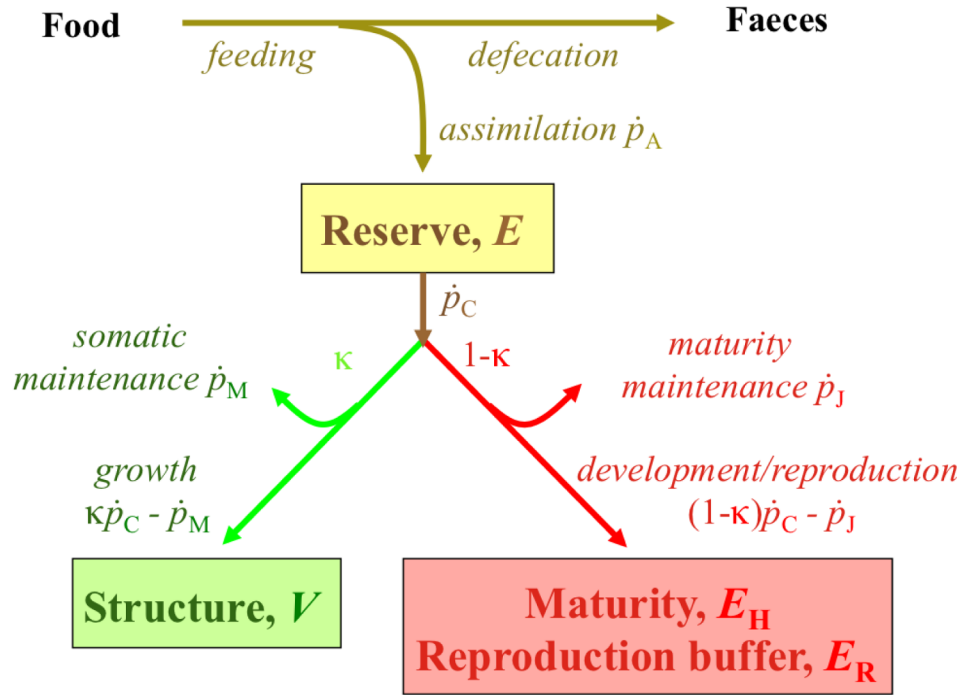


Figure 1. Dynamic Energy Budget (DEB) model scheme for juvenile (development/maturity) and adult (reproduction/reproduction buffer) life stages. See Table 1 for differential equations.

comparison with Strohmeier et al. (2015), the respiration rate was standardized to an equivalent individual of 1 g dry tissue weight as follows:

$$RR_{std} = RR_{DEB} (DW_{std}/DW_{DEB})^b \quad (2)$$

Where RR_{std} and RR_{DEB} are the respiration rates standardized to a 1 g dry tissue weight individual and estimated with DEB, respectively; DW_{std} and DW_{DEB} are 1 g and estimated dry tissue weights, respectively;

and b is the allometric exponent, 0.7 (Smaal et al. 1997). Clearance rate was derived from the assimilation rate (\dot{p}_A , $J d^{-1}$, Table 1), the assimilation efficiency (κ_X , Table 1), and the food density (X , Table 1, but expressed in $J L^{-1}$) as follows:

$$CR_{DEB} = \dot{p}_A / \kappa_X / X \quad (3)$$

Where, CR_{DEB} is the clearance rate estimated with DEB ($L d^{-1}$), \dot{p}_A the assimilation rate ($J d^{-1}$), κ_X , the assimilation efficiency

Table 1
Equations of the Dynamic Energy Budget (DEB) model.

Equation	Terms and parameters	
$f = \frac{X}{X + X_K}$	f	functional response (dimensionless)
$\{\dot{p}_{Am}\} = \{\dot{p}_{Xm}\} \kappa_X$	X	food density (chlorophyll-a concentration, $\mu g L^{-1}$)
$\dot{p}_A = \{\dot{p}_{Am}\} c_T V^{2/3} f$	X_K	half-saturation constant ($\mu g L^{-1}$)
$\dot{p}_C = E \frac{[E_G] \frac{\{\dot{p}_{Am}\} c_T V^{2/3} + \dot{p}_M}{[E_m]}}{[E_G] V + \kappa E}$	$\{\dot{p}_{Am}\}$	maximum surface area-specific assimilation rate ($J cm^{-2} d^{-1}$)
$\dot{p}_M = [\dot{p}_M] c_T V$	$\{\dot{p}_{Xm}\}$	maximum surface area-specific ingestion rate ($J cm^{-2} d^{-1}$)
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	κ_X	assimilation efficiency (dimensionless)
$\frac{dV}{dt} = \frac{\kappa \dot{p}_C - \dot{p}_M}{[E_G]}$	\dot{p}_A	assimilation rate ($J d^{-1}$)
$\frac{dE_R}{dt} = (1 - \kappa) \dot{p}_C - \frac{1 - \kappa}{\kappa} [\dot{p}_M] c_T \min(V, V_p)$	c_T	Arrhenius temperature correction function
$c_T = \exp(\frac{T_A}{T_{ref}} - \frac{T_A}{T})$	V	structural volume (cm^3)
$L_w = \frac{V^{1/3}}{\delta_M}$	\dot{p}_C	reserve mobilization rate ($J d^{-1}$)
	E	Reserve energy (J)
	$[E_G]$	volume-specific costs for structure ($J cm^{-3}$)
	$[E_m]$	maximum reserve density ($J cm^{-3}$)
	\dot{p}_M	somatic maintenance rate ($J d^{-1}$)
	κ	fraction of mobilized reserve allocated to somatic maintenance and growth (dimensionless)
	$[\dot{p}_M]$	volume-specific costs for maintenance ($J cm^{-3} d^{-1}$)
	E_R	energy in reproduction buffer (J)
	V_p	Structural volume at puberty (cm^3)
	T_A	Arrhenius temperature (K)
	T_{ref}	reference temperature (K)
	T	current temperature (K)
	δ_M	shape coefficient (dimensionless)

Table 2

Characteristics of datasets, shell length, tissue dry weight, growing year, data availability (physiological and growth), and how the information from each dataset was used during the global optimization (calibration or validation of the DEB parameters).

Dataset	Shell length (cm)	Dry weight (g)	Growing year	Physiology	Growth	Global optimization
up-COH08_y2	4.8 ± 0.13	0.68 ± 0.18	2010	X	X	Calibration
up-COH09_y2	4.8 ± 0.40	0.43 ± 0.17	2011	X	X	Calibration
Noup-COH08_y2	4.7 ± 0.13	0.69 ± 0.25	2010	X	X	Calibration
Noup-COH09_y2	4.6 ± 0.37	0.43 ± 0.17	2011	X	X	Calibration
up-COH09_y1	2.4 ± 0.19	0.10 ± 0.03	2010		X	Validation
up-COH10_y1	2.5 ± 0.17	0.03 ± 0.01	2011		X	Validation
Noup-COH09_y1	2.3 ± 0.26	0.15 ± 0.05	2010		X	Validation
Noup-COH10_y1	2.5 ± 0.16	0.03 ± 0.01	2011		X	Validation

(dimensionless), and X the food density expressed in J L^{-1} assuming a carbon to chlorophyll ratio of 50:1 (Filgueira et al. 2019), and a conversion factor of 21 J mg C^{-1} (Filgueira et al. 2019). For the purpose of comparison with Strohmeier et al. (2015), the rate was standardized to an equivalent individual of 5 cm shell length as follows:

$$CR_{std} = CR_{DEB} (SL_{std}/SL_{DEB})^b \quad (4)$$

Where CR_{std} and CR_{DEB} are the clearance rates standardized to a 5 cm individual and estimated with DEB, respectively; SL_{std} and SL_{DEB} are 5 cm and estimated shell lengths, respectively; and b is the allometric exponent, 2.09 (Jones et al. 1992). Note that respiration rate has been standardized to dry tissue weight, but clearance rate has been standardized to shell length. While respiration rate is related to the weight of an individual, clearance rate is related to the surface of the gills. Therefore, the standardization of clearance rate to shell length is recommended, given that gill surface area and shell length are not affected by the fluctuation of weight over time due to the reproduction cycle (Filgueira et al. (2008). Furthermore, Strohmeier et al. (2015) standardized both rates following the same approach and using the same allometric exponents, which facilitates the comparison among both studies.

Strohmeier datasets

The *M. edulis* Strohmeier dataset (Strohmeier et al. 2015) was chosen because of the availability of growth (shell length, dry weight) and ecophysiological data (clearance and respiration rates) on a bi-weekly or monthly basis for several cohorts over long periods of time and under different environmental conditions. These experiments were carried out in Lysefjord (Norway) during 2010 and 2011. Note that Strohmeier et al. (2015) reports data only for 2010; however, the environmental conditions, bivalve growth and physiological data collected in 2011 followed the same methodology. The mussels from the same local population were deployed at 7 m depth at two sampling locations using 1 m long lantern nets at an approximate stocking density of 80 mussels per m^2 . Individually marked individuals were used to monitor shell length during the experiment, and additional individuals were sacrificed at each sampling for weight monitoring. One of the sampling locations was sited close to the head of the fjord, and the other 14 km downstream. At the station close to the head of the fjord, a pump was used to bring to the surface nutrient-rich deep waters and enhance primary productivity (see Aure et al. 2007 for technical details). This design allows to have two sampling stations with very similar salinity and temperature (27.8 and 29.7 psu, and 11.7 and 12.3 °C under upwelling and non-upwelling conditions, respectively) but statistically different food density (2.9 ± 1.8 and $1.4 \pm 0.4 \mu\text{g chla L}^{-1}$ under upwelling and non-upwelling conditions, respectively).

In summary, mussel growth from the same local population was monitored over two years (2010 and 2011) under two different environmental conditions: upwelling conditions (up- in tables and figures), and normal fjordic conditions (Noup- in tables and figures). Three different cohorts were used: 2008 (COH08), 2009 (COH09, used

twice over two consecutive years) and 2010 (COH10). A first and second year-class cohorts (y1 and y2), with approximate shell lengths of 2.4 and 4.7 cm, respectively, were monitored each year (2010 and 2011) at each site (up- and Noup-), totaling eight datasets (Table 2). Physiological data is only available for the second year-class cohorts. All methodological aspects are explained in detail in Strohmeier et al. (2015).

Optimization procedure

The Multimodal Optimization for Model Calibration (MOMCA) framework (Chica et al. 2017) was used to parameterize DEB models for the different datasets. MOMCA assumes that the parameters of the model are mapped to a multimodal fitness landscape and applies search algorithms to find the set of sub-optimal configurations that better fit the observed data. In an optimization search space, each potential solution is linked to the values for all decision variables defined by the user. These decision variables define the quality of each solution according to the fitness function (i.e., minimize the distance between prediction and observation, meeting a predefined constraint such as meeting mass conservation), which ultimately determines if the solution belongs to the set of multimodal optima. From a graphical perspective, these solutions to a multimodal landscape would be peaks in a maximization problem and valleys in a minimization problem. In such a multimodal problem, several sub-optimal solutions make it difficult to find a unique and optimal set of parameters (Goldberg and Richardson 1987). The MOMCA framework facilitates the calibration of a model by providing alternative solutions and tools to understand the relationships among parameters and the sensitivity of the model to changes in these parameters. A brief description of the MOMCA framework is given below, and a more detailed description is available in Chica et al. (2017).

In this work, the MOMCA framework applies a traditional Niching Genetic Algorithm (Back, 1997) for finding different sets of parameters for the DEB model such that the predictions obtained by the calibrated model have similar quality. In the first phase of MOMCA, the algorithm starts with a set of different possible calibrations for the model, known as the population of the algorithm, and tests the model's accuracy under each of them. A niching method, known as clearing, is then applied to the solutions of the population. This method sorts the solutions in ascending order according to their accuracy. Later, the method keeps the α -many calibration solutions (α being the niche capacity) with the best accuracy within a clearing radius and discards the rest of the population. In other words, if several calibration solutions are too close to each other in the decision space, the α best ranked solutions will be taken into account and the others will be discarded. Afterwards, the method launches an iterative process in which the best calibration solutions are selected based on their fitness by using a Stochastic Universal Sampling technique (Baker, 1987). The selected calibrations are recombined using a well-known BLX crossover operator (Herrera, 1998) and a reset mutation is also applied to increase the search diversity of the algorithm. The offspring from the latter two operators constitute the

Table. 3

Relative weight of the different observations in the optimization procedure and fitness (E_{RR}) for the optimal set of parameters described in Table 4 as Sol. 1 (Global calibration).

		Shell Length	Dry Weight	Clearance Rate	Respiration Rate	TOTAL
	Weight	0.5	0.3	0.1	0.1	
Calibration	up-COH08_y2	0.009	0.149	0.388	0.198	0.108
	up-COH09_y2	0.005	0.132	0.462	0.264	0.115
	Noup-COH08_y2	0.010	0.131	0.167	0.409	0.102
	Noup-COH09_y2	0.003	0.194	0.542	0.221	0.136
	Average	0.007	0.151	0.390	0.273	0.115
	Weight	0.6	0.4			
Validation	up-COH09_y1	0.078	0.355			0.182
	up-COH10_y1	0.064	0.198			0.114
	Noup-COH09_y1	0.085	0.218			0.135
	Noup-COH10_y1	0.113	0.275			0.174
	Average	0.085	0.262			0.151

population in the next generation and the loop continues until the set of obtained calibrations converges. For the second phase of the MOMCA framework, and after a preliminary analysis of the method behavior, a filtering mechanism is introduced to ensure the diversity of calibrations. For this work, parameter values were normalized within their given ranges, and calibration solutions were considered diverse enough if the Euclidean distance between every pair of calibrations is at least 0.1. The third phase includes a quantitative and visual analysis for understanding the set of parameters. In summary, MOMCA tackles the calibration in three automated steps: 1) search for alternative sets of parameters with equally good fitting of observed data and diverse values; 2) evaluation of the performances of the different sets of parameters and prioritization based on fitting and diversity; and 3) quantitative and visual sensitivity analysis to understand the robustness of the set of parameters.

The MOMCA framework was used to calibrate 11 DEB parameters. The range of the parameters was defined based on parameters from van der Veer et al. (2006), Rosland et al. (2009), and Saraiva et al. (2011a). The ranges were larger than reported in these studies to ensure that the confidence intervals of these parameters were included as potential solutions. The set of potential solutions was restricted by limiting the yield of structure on reserve, y_{VE} , to values below 0.8; otherwise certain combination of parameters can result in over-efficient conversion from reserves into structure that violates the principle of mass conservation (Saraiva et al. 2011a). In addition, no shrinking of structure was allowed in the model. Furthermore, the individual was assumed to be dead if maintenance costs cannot be paid. The DEB model was calibrated using only the 8 datasets described

above, i.e. no complementary zero- or uni-variate data was used. Two calibration modes were tested to explore the potential of a single parameterization for all datasets (global calibration), or the need for specific calibration for each individual dataset (local calibration):

- Global calibration: the 4 datasets with physiological and growth data were used for calibration purposes and the remaining 4 datasets were used for validation (Table 2). Different weights were assigned to the different types of measurements: 0.5 to shell length, 0.3 to dry weight, which is more affected by seasonality and reproductive cycle than shell length, and 0.1 to respiration and clearance rate, which are discrete data points in time rather than integrated measurements over time such as shell length or dry tissue weight.
- Local calibration: all 8 datasets were calibrated independently using a slightly larger range for some of the 11 parameters in order to increase the potential range of solutions to improve the fitness. In the case of the 4 datasets in which only growth data are available, weights of 0.625 and 0.375 were used for shell length and dry weight, respectively.

The goodness of fit (E_{RR}) of each set of parameters was calculated as follows:

$$E_{RR} = \sum_i^n \beta_i |Y_i - \hat{Y}_i| \quad (5)$$

Where n is the total number of observations, β_i is the relative weight

Table. 4

Ten equally good sets of parameters optimized simultaneously for all datasets (Global calibration).

	X_K	$\{p_{xm}\}$	$[p_M]$	κ	δ_M	$[E_G]$	$[E_m]$	T_A	DW%	κ_X	κ_R
Min	0.0	100.0	10.0	0.40	0.200	1500	1000	5000	0.10	0.70	0.60
Max	10.0	300.0	30.0	0.80	0.300	6500	3000	8000	0.20	0.90	1.00
Min. Value	3.0	253.5	21.4	0.49	0.282	4827	1000	5000	0.12	0.88	0.78
Max. Value	4.0	300.0	30.0	0.62	0.300	6500	1203	6074	0.16	0.90	1.00
Range	1.0	46.5	8.6	0.13	0.018	1673	203	1074	0.05	0.02	0.22
Average	3.6	294.4	27.7	0.57	0.296	5929	1021	5367	0.14	0.90	0.93
Sol.1	3.6	300.0	30.0	0.62	0.300	6428	1000	5482	0.14	0.90	0.98
Sol.2	3.9	300.0	29.3	0.62	0.294	6484	1003	5126	0.15	0.90	0.86
Sol.3	3.9	292.3	23.5	0.53	0.297	6005	1093	5000	0.13	0.90	1.00
Sol.4	3.6	300.0	29.5	0.61	0.300	6500	1016	5652	0.13	0.90	0.78
Sol.5	3.7	300.0	25.5	0.56	0.300	6484	1000	5124	0.13	0.90	0.89
Sol.6	3.7	300.0	30.0	0.62	0.300	5092	1203	5341	0.13	0.90	0.96
Sol.7	4.0	294.6	26.2	0.57	0.300	4888	1000	5000	0.14	0.88	1.00
Sol.8	3.4	300.0	29.7	0.58	0.300	5340	1000	6074	0.13	0.90	0.87
Sol.9	3.3	296.6	27.2	0.51	0.282	6481	1000	5000	0.15	0.90	0.91
Sol.10	3.1	253.5	29.0	0.62	0.299	6500	1000	5000	0.14	0.90	1.00

coefficient for each observation considering the type of data, i.e. shell length, dry weight, or respiration and clearance rate, and the number of observations within each type, and Y_i and \hat{Y}_i are the observation and the model prediction, respectively.

Results

Global calibration

The best MOMCA set of parameters for the simultaneous global optimization of the four datasets used for calibration (Table 2) averaged an E_{RR} of 0.115 (Table 3), with a total of 3 and 15 solutions within a range from the best solution of 0.001 and 0.002, respectively. The fitness diverged among the different types of measurements: shell length was the best predicted observation and clearance rate the worst, with an average E_{RR} of 0.007 and 0.390, respectively (Table 3). As expected,

the fitness of each type of observation is correlated to the weight that is given to each observation in the optimization process. The fitness dropped to an average of 0.151 (Table 3) for the four datasets used for validation (Table 2). It is important to highlight that the validation datasets do not include any information on physiological rates, which reported the worst fit in the calibration datasets, and consequently the fitness of calibration and validation datasets must be compared with caution. The 10 best set of MOMCA parameters estimated with the global calibration (Table 4) revealed that three of the parameters, X_K , κ , and $DW\%$, were within the range of parameters from the literature (Fig. 2), two of them, T_A and $[E_m]$, in the lower part of the range (Fig. 2), and the remaining six parameters, $\{\dot{p}_{Xm}\}$, $[\dot{p}_M]$, δ_M , $[E_G]$, κ_X , and κ_R , in the upper part (Fig. 2). The variation of the estimated parameters within the best 10 MOMCA solutions ranged between 0.5 and 11.5% for κ_X and $[E_G]$, respectively.

The calibration dataset up-COH08_y2 was used to visualize the

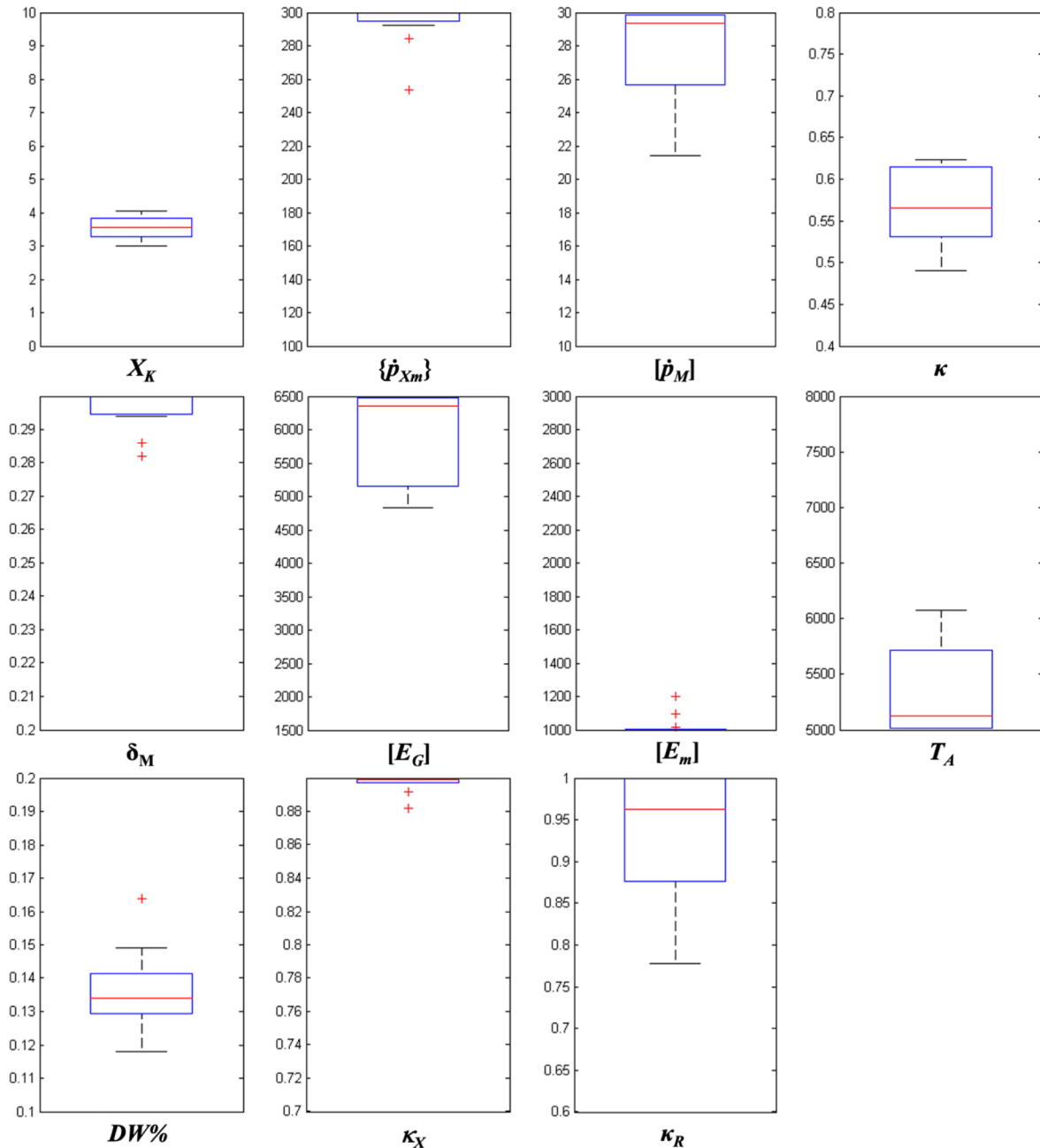


Figure 2. Summary of parameters within an E_{RR} range of 0.002 ($n = 43$) for Global calibration.

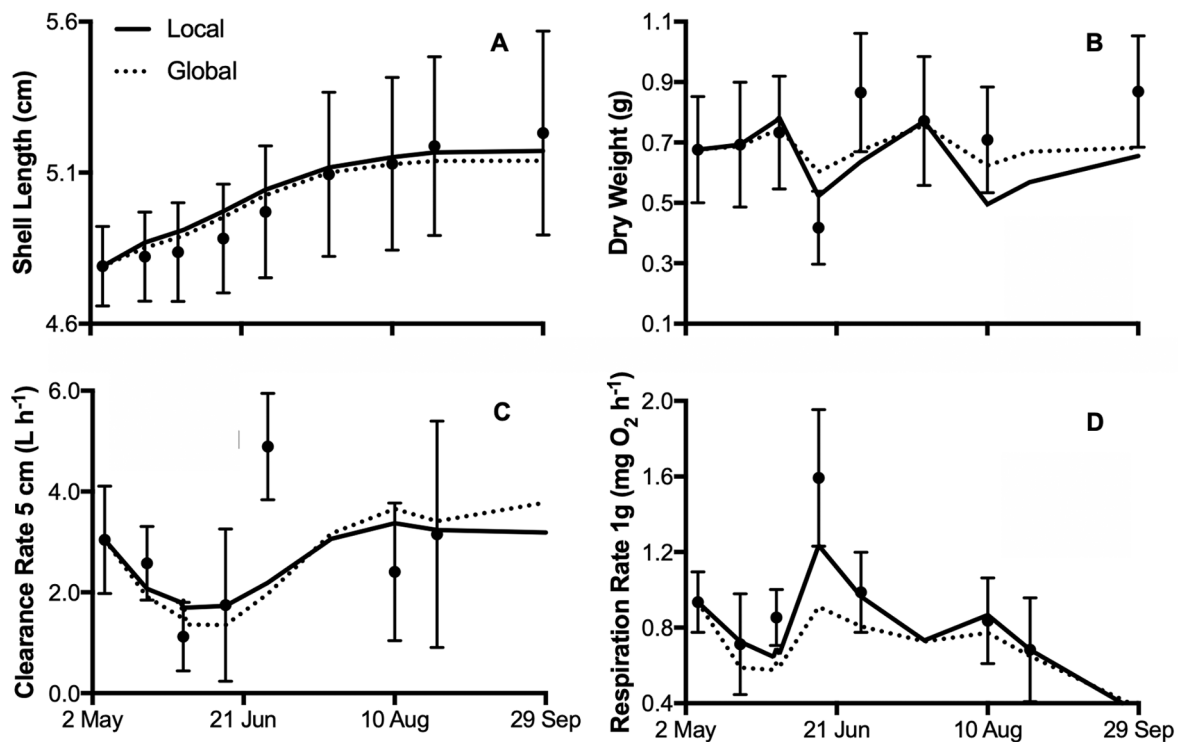


Figure 3. Shell length (A), dry weight (B), clearance rate standardized to 5 cm (C), and respiration rate standardized to 1 g dry weight (D) observations vs. model predictions over time for up-COH08_y2 in [Strohmeier et al. \(2015\)](#) dataset using the best local calibration for up-COH08_y2 and the best global calibration for all datasets in the study.

fitness over time (Fig. 3). The match between the predictions of the global calibration and observations remained similar over time for shell length (Fig. 3a); however, there was a clear mismatch in dry weight and both physiological rates during June, which coincides with a spawning event. The model overestimated dry weight at the beginning of the month, followed by an underestimation at the end (Fig. 3b). Before and after June, the predictions matched observations, suggesting that the model did not properly capture the dynamics of the spawning event. Meanwhile the observed clearance rate was correctly predicted by the model at the beginning of June and underestimated by the end (Fig. 3c). Respiration rate followed the opposite pattern, with underestimations at the beginning and good predictions at the end (Fig. 3d). It is important to note that in both situations in which the model underestimated physiological rates, the observed values were the highest ones for the whole time series. This pattern was observed to some degree in all second year-class cohorts (initial shell length > 4.5 cm, Table 2) in both growing areas, with and without upwelling (results not shown).

Local calibration

The use of MOMCA for local calibration of each dataset improved the fitness of the model (Table 5). As expected, this was more evident for the datasets that were used as validation datasets in the global calibration, in which the fitness improved from an E_{RR} of 0.155 down to 0.051. In the case of the datasets that were used for calibration, the fitness also improved when using the local calibration, but only from 0.115 to 0.103. Similar to the global calibration, shell length and clearance rate were the best and worst predicted observations, with an average E_{RR} of 0.009 and 0.367, respectively (Table 5). Regarding the specific fit of the data for dataset up-COH08_y2, the local calibration improved the fit from an E_{RR} of 0.108 up to 0.095. This improvement was most obvious in the case of respiration rate, motivated by a steeper change in respiration during the month of June (Fig. 3d). Despite this improvement in predicting the short-term changes in metabolism, the model was not able to fully capture the pattern observed during June.

The best set of parameters for the local calibrations differed among

Table 5

Relative weight of the different observations in the optimization procedure and fitness (ERR) for the optimal sets of parameters described in Table 6 (Local calibration).

	Shell Length	Dry Weight	Clearance Rate	Respiration Rate	TOTAL
Weight	0.5	0.3	0.1	0.1	
up-COH08_y2	0.010	0.162	0.335	0.083	0.095
up-COH09_y2	0.009	0.091	0.474	0.235	0.103
Noup-COH08_y2	0.013	0.121	0.160	0.325	0.092
Noup-COH09_y2	0.002	0.165	0.497	0.229	0.123
Average	0.009	0.135	0.367	0.218	0.103
Weight	0.6	0.4			
up-COH09_y1	0.005	0.134			0.053
up-COH10_y1	0.009	0.102			0.044
Noup-COH09_y1	0.009	0.115			0.049
Noup-COH10_y1	0.029	0.110			0.060
Average	0.013	0.115			0.051

Table 6
Optimal sets of parameters for each dataset (Local calibration).

	X_K	$\{p_{Xm}\}$	$[p_M]$	κ	δ_M	$[E_G]$	$[E_m]$	T_A	DW%	κ_X	κ_R
Min	0.0	100.0	10.0	0.30	0.200	1500	1000	5000	0.10	0.70	0.60
Max	10.0	600.0	45.0	0.80	0.300	6500	3000	8000	0.20	0.90	1.00
up-COH08_y2	9.3	599.3	14.3	0.36	0.293	6493	2121	5000	0.10	0.90	0.93
up-COH09_y2	7.9	600.0	43.0	0.60	0.293	6500	1000	5956	0.16	0.90	0.97
Noup-COH08_y2	5.0	530.1	39.5	0.55	0.293	6230	1335	8000	0.10	0.90	0.60
Noup-COH09_y2	6.9	434.7	34.7	0.75	0.294	5794	1080	5108	0.19	0.90	1.00
up-COH09_y1	1.5	555.3	27.5	0.36	0.261	6242	2296	5888	0.14	0.75	0.94
up-COH10_y1	6.2	558.4	41.7	0.65	0.299	5519	1812	5027	0.13	0.86	0.81
Noup-COH09_y1	0.0	113.0	15.5	0.68	0.250	5383	1892	7987	0.10	0.80	0.69
Noup-COH10_y1	7.8	600.0	19.7	0.80	0.299	6174	1000	5050	0.20	0.80	1.00

each dataset (Table 6). Both parameters controlling the ingestion of food, X_K and $\{p_{Xm}\}$, exhibited the highest variability across datasets, 59 and 33% respectively. Another parameter that displayed a large variability was $[p_M]$, with a variation of 40%. Contrarily, δ_M , $[E_G]$, and κ_X showed the lowest variation across datasets, with values $\sim 7\%$. It is important to note that the potential range of $\{p_{Xm}\}$, $[p_M]$, and κ were expanded compared to the global calibration to increase the probability of improving the fitness of the solutions. In the case of $\{p_{Xm}\}$, the average value across the different datasets, $499 \text{ J cm}^{-2} \text{ d}^{-1}$, was higher than the upper threshold used in the global calibration, $300 \text{ J cm}^{-2} \text{ d}^{-1}$, which had been defined based on literature values. Regarding $[p_M]$ and κ , although some optimized values exceeded the originally pre-defined range of values based on existing literature, the average values for all the datasets did not exceed that range.

Discussion

Selecting the correct parameters of a model is key for its successful application. The multidimensional space in which DEB parameters co-exist increases the complexity of parameterization. Furthermore, different parametrizations are typically mapped to equally optimal solutions (i.e., a multimodal landscape). In this study, the application of a novel mathematical tool together with the combination of growth and physiological data was used to estimate new sets of parameters for the *Mytilus edulis* DEB model in a Norwegian fjord. This novel mathematical tool provides a range of equally good solutions, which captures the fact that different physiological strategies can result in similar growth patterns.

Existing sets of parameters

DEB models for *M. edulis* have been parameterized multiple times in the scientific literature, with van der Veer et al. (2006), Rosland et al. (2009), and Saraiva et al. (2011a) being the most relevant contributions. Although Saraiva et al. (2011a) had correctly pointed out that the parameters from van der Veer et al. (2006) and Rosland et al. (2009) violate the principle of mass conservation, they have been used in this study to define potential ranges of parameters and for comparative purposes. The estimated parameters using the MOMCA framework to Strohmeier et al. (2015) were farther from Saraiva et al. (2011a) than from van der Veer et al. (2006) and Rosland et al. (2009). A plausible explanation for this finding could be related to the fact that Saraiva et al. (2011a) focused on wild populations of *M. edulis* growing on the benthic zone, but Rosland et al. (2009) focused on farmed populations cultivated suspended in the water column, while van der Veer et al. (2006) used a mixed source of data. It is well-known that wild populations grow at a lower rate than farmed populations. Wild mussels are exposed to additional stressors such as currents, waves, and predators, as well as a higher fluctuation in seston quantity and quality (Lachance et al. 2008). These stressors require additional energy expenditures in wild mussels, namely more byssus production

(Babarro and Carrington 2013) and investment in thicker shells (Beadman et al. 2003) to cope with a high energy environment and predators, respectively. In addition, despite the physiological plasticity of mussels, when individuals from different origins are transferred to the same environment, there is an acclimation period before reaching similar physiological rates (Labarta et al. 1997).

The mechanistic nature of DEB should be able to cope with environmental changes over time, but due to the simplicity that is required to construct a model, not all environmental drivers are included in it. In the current DEB model only temperature and food are used as forcing functions, and for example, hydrodynamics and the presence of predators are not included, despite being relevant for individual bioenergetics, especially in the case of wild populations. Choosing different parameterization could be a simple solution for the use of the same modelling structure to simulate both wild and farmed populations. This new parameterization would need to focus on the parameters affecting the physiology of the individual under different conditions, e.g. byssus production, shell thickness, or inter- and intra-specific competition affecting food searching rate.

Predicting growth and physiology in Lysefjord

The inclusion of physiological data in the parameterization process aims to constraint the range of valid solutions. Without constraining the parameters using physiological rates, the model could correctly predict growth based on the combination of erroneous rates. For example, an individual with high ingestion and maintenance could result in similar growth to an individual with low ingestion and maintenance. To a certain degree, the pre-defined range of parameters account for this, e.g. the value of the maximum surface-area-specific ingestion rate ultimately determines the maximum clearance rate. However, the addition of physiological rates to the parameterization process provides information regarding the short-term variability and plasticity of individuals. In fact, the mismatch between observations and predictions in clearance rate shortly after spawning suggest that the current version of the DEB model cannot fully capture this short-term physiological response. This is expected given that clearance rate in DEB is a function of food availability and temperature, but Strohmeier et al. (2015) had already suggested that clearance rate is not correlated with seston characteristics in this specific dataset. Similar conclusions could be extracted for respiration rates, although it is important to acknowledge the simplification in the mathematical formulation to estimate respiration rates from DEB. In general, the overall fitness of the model in terms of growth and physiology for the validation datasets is within 15% error, which is within the acceptable range expected for these types of exercises.

The punctual mismatches on physiological rates suggests that additional exogenous or endogenous drivers should be added to the DEB model to properly simulate short-term plasticity. For example, several studies have aimed to improve the characterization of food proxies that could result in a fully mechanistic ingestion model (e.g.

Bourlès et al. 2009, Picoche et al. 2014). Similarly, the use of ‘synthesizing units’ is intended to improve this aspect of DEB by accounting for the capacity of mussels to select food types based on their quality (Saraiva et al. 2011b), which inherently tackles an aspect often overlooked in DEB modelling, the digestive processes, including differential assimilation efficiency of seston and gut passage time (e.g. Bayne et al. 1987).

Most of the efforts for improvement are directed towards the understanding of exogenous drivers; however, the endogenous status could play a relevant role in short-term physiological responses. For example, it has been suggested that an immediate decrease in filtration activity is observed after spawning as a mechanism to avoid the ingestion of gametes (Newell and Thompson 1984). Although the temporal frequency of Strohmeier's dataset does not allow for testing such an immediate response, the highest clearance observed in the study occurs a couple of weeks after spawning and coincides with a rapid rebuilding of mussel's tissue (Strohmeier et al. 2015). Based on these results, it could be hypothesized that spawning might trigger additional physiological responses and not only the release of gametes. For example, Brigolin et al. (2009) stopped the allocation of energy towards reproduction in *M. galloprovincialis* after the second spawning, diverting all energy towards somatic growth. Diverting energy towards somatic growth after spawning would not explain the observations in Strohmeier's dataset using the current version of DEB given that the observed increase in tissue is not concomitant with an increase in shell length, which is mostly the case in DEB theory, with the exception of the role that reserves play on tissue mass. Shell is not directly modelled in the present DEB model but is indirectly estimated based on the amount of energy allocated in the structure and the shape coefficient. Shell is considered in DEB theory as a product of the growth flux (proportional to growth overheads). Therefore, some adjustments of the model would be required to account for the well-known decoupling of shell and tissue growth observed in the literature (e.g. Hilbish 1986), which has already been incorporated in other modelling frameworks by adding additional energy allocation rules (Fuentes-Santos et al. 2019). A dynamic allocation of energy between structure and reproduction, and/or additional allocation rules, together with a change in energy acquisition triggered by an endogenous driver such as spawning could result in a better short-term agreement between observations and simulations. Another option would be to model explicitly shell accretion (Pecquerie et al., 2012). In any case, empirical data at a higher temporal resolution would be needed to validate these structural changes in DEB, and to generate further hypotheses on other potential effects of spawning on the physiological of mussels.

DEB as a multimodal problem

The mathematical estimation of a set of parameters of a non-linear dynamic model is a complex task. Automated calibration packages and search algorithms facilitate this process, but the solution, or solutions, should be carefully analyzed or there is a risk of treating the model as a black box (Saleh et al. 2010). This problem is amplified when the model operates in a multimodal environment, which could result in multiple sub-optimal solutions (Muñoz et al. 2015). The challenge is magnified with the increase in the number of parameters (Jusup et al. 2017) and the potential dependence among these parameters (Muñoz et al. 2015, Moya et al. 2019). This is the case for DEB, in which the relatively large number of parameters (Kearney et al. 2015) and the inter-dependence of some of them (Fujiwara et al. 2005, Chica et al. 2017) are mapped to a multimodal continuous landscape. The existence of multiple sub-optimal solutions is a challenge from the mathematical perspective, but it could be an advantage from the biological perspective. The analysis of sub-optimal solutions that are close to the best solution can be used to inform about the impact of the parameters on model performance and the relationships among themselves. In addition, these sub-optimal solutions could reflect the inter-individual variability within a

population, which could reflect different physiological strategies that could result in similar outcomes in terms of growth. Usually, the scaling up from individual to population in DEB is carried out by simulating several individuals with different initial conditions, namely length and dry weight (e.g. Gourault et al. 2019), but keeping the same set of parameters. It has been suggested in the past that future improvement in DEB modelling could come from focusing on genetic and phenotypic traits to integrate inter- and intra-specific variability (Lika et al. 2011b, Marques et al. 2018). Therefore, the set of equally good solutions provided by the MOMCA framework would not only provide valuable information regarding the parameters, but also become a tool to improve the scaling up from individual based models to population model, allowing a direct analysis on the set of returned solutions (i.e., set of values to the calibrated variables of the model).

The challenge of the mathematical estimation of parameters is amplified by the methodological and logistic challenges to collect the appropriate datasets for calibration and validation. Despite the numerous scientific studies and monitoring programs tackling the growth of mussels and bivalves in general, the number of available datasets with growth and environmental data collected at the right temporal resolution is still limited. Despite the numerous scientific studies and monitoring programs tackling the growth of mussels and bivalves in general, the number of available datasets with growth and environmental data collected at the right temporal resolution is still limited. For example, one limitation in this study is the high dependence of three parameters, X_K , $\{\dot{p}_{X_m}\}$, and κ_X , on the information provided by clearance rate. In this case, the number of potential solutions can only be constrained by restricting the theoretical range of the parameters, but additional information would be needed to fully disentangle their inter-dependency. In any case, the information from multiple equally good solutions from the MOMCA framework can also be used to define future priorities for data collection. In this regard, the high variability in the half-saturation constant X_K and the maximum surface-area-specific ingestion rate $\{\dot{p}_{X_m}\}$, which average value is higher than the upper threshold reported in the literature, suggests that further research should focus on food ingestion. Despite the long history of studies on mussel feeding behaviour (e.g. Bayne et al. 1987, Riisgard et al. 2011), it seems that these types of studies together with an improved characterization of seston are still critical to improve our understanding of the trophic interactions of bivalves. Similar to the need of data at a higher temporal resolution for physiological responses, the characterization of seston for the identification of food proxies should also be carried out at a more detailed temporal resolution.

From a practical perspective of modelling parameterization, it is essential to emphasize that MOMCA solutions, similarly to all automatic optimization tools, need to be considered carefully by the user. As it was stated above, the upper limit for the maximum surface area-specific ingestion rate, $\{\dot{p}_{X_m}\}$, was reached in five out of ten solutions in the global calibration and was reached twice in the local calibration of Strohmeier datasets. While physiological plasticity is well known in bivalves, especially regarding feeding activity, values of $600 \text{ J cm}^{-2} \text{ d}^{-1}$ seem unlikely. The user must make a decision to prioritize more physiologically relevant solutions compared to others. This highlights the necessity of a critical evaluation of the optimized parameter set. This can be done as in Marques et al. (2019), where the combination of pseudo-data and a series of filters ensures that the solutions are compatible with DEB theory, e.g. ensuring mass conservation. Additional functionalities could also be included in MOMCA to inform the user. For example, when a parameter is reaching the boundary of the pre-defined range and is having too much impact on the solutions, an alert could be displayed. Subsequently, the optimization could automatically explore the implications of increasing the range of the parameter in terms of fitness; something that has been manually done in this study. The implementation of these filters and functionalities in MOMCA is beyond the scope of this study. While these upgrades could be included in MOMCA, a better solution would be incorporating MOMCA into the

current standard procedure to estimate DEB parameters developed by Marques et al. (2019). This approach would complement the state-of-the-art DEB theory with the power of multimodal optimization, e.g. equally good solutions and confidence intervals for parameters. Including MOMCA in the standard procedures to estimate DEB parameters, i.e. Marques et al. (2019), could provide an additional tool to scope the potential parameter range. This would bring together multimodal optimization with the benefits from the use of pseudo-data, relevant filters to ensure the compatibility with DEB theory, user-friendly tools and extensive learning materials, and still allowing control on the tuning of the DEB parameters.

Conclusions

Individual based models such as DEB are critical tools to explore the current understanding of bivalve bioenergetics. These models are also cornerstone in ecosystem modelling, for example, in models that explore the effects of aquaculture on the environment or the suitability of an area for aquaculture development. However, the parameterization of these models is challenging. In this study, the MOMCA framework, a novel multimodal optimization approach, has been used to parameterize DEB for *Mytilus edulis* in a Norwegian fjord. The inclusion of physiological rates to constraint the range of the parameters, together with the analysis of multiple equally good solutions rather than a single optimal one, suggest that: 1) DEB can effectively simulate mussel growth and physiology in the long-term, but punctual physiological changes such as the response to spawning can compromise the performance of the model in the short-term; and 2) DEB's energy acquisition sub-model, namely feeding and characterization of seston, should be a priority for improving model performance. These data gaps are bottlenecks for the ultimate goal of constructing a truly mechanistic model. Furthermore, the successful use of MOMCA has demonstrated the potential for complementing the current state-of-the-art procedures to estimate DEB parameters (i.e. Marques et al. 2019) with multimodal optimization.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109139](https://doi.org/10.1016/j.ecolmodel.2020.109139).

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