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From lab to ocean: Leveraging targeted experiments for advancements in mussel aquaculture through mechanistic modelling

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ABSTRACT

The mechanistic approach and the potential predictive power of Dynamic Energy Budget (DEB) models are making this modelling framework increasingly popular in aquaculture management. The potential to mechanistically simulate life-history traits of a species in a changing environment has already been applied to many commercial species, including the New Zealand Greenshell™ mussel *Perna canaliculus*. However, the previous *P. canaliculus* model parameterisation, available in the Add-my-Pet (AmP) collection, has been carried out on a limited data set. We used data obtained through targeted laboratory experiments and combined it with literature data, to derive a new version of the model which included information on additional processes – such as feeding, respiration, and reproduction – and life stages: larvae and adults. We compared the performance of the previous version of the model, termed AmP-2018 with the revised model (AmP-2024), to predict the whole life-cycle of the mussel and life-history traits of interest in the context of aquaculture. The entry completeness score (0–10), which provides an indication of data quality and variety as well as model comprehensiveness and applicability, increased dramatically from 2.5 to 5.5, suggesting *P. canaliculus* is now the most comprehensively DEB-parameterised bivalve, while the model increased in accuracy of the predictions. The endeavour highlights several conclusions: (i) reliable temperature response data are required to establish the thermal response curve; the presence/absence of this type of data should be taken into account when assessing the completeness of a model and its applicability to predict thermal responses of a species; (ii) species-specific parameter values are preferred over general (higher taxonomic level) specific values, e.g. for tissue organics and water content, as they increase the accuracy of predictions; (iii) data pertaining to laboratory trials and to wild populations both need to be taken into account when calibrating a mechanistic model at a species level; and (iv) calculating energy requirements of any organism, including bivalves, requires data on characteristics and products often overlooked in an experimental setting. We discuss the new version of the model in the context of the knowledge and predictive power potentially gained by adding more information and data during model calibration. The obtained results and conclusions are especially relevant in aquaculture, whether for commercial rearing of mussels, or their potential application in multitrophic aquaculture systems.

1. Introduction

A well-calibrated species-specific mechanistic model can be used to reliably simulate the traits and energy allocation throughout a species' life span, under constant and varying conditions (Filgueira et al., 2011). The versatility, modular design, and mechanistic nature of the Dynamic Energy Budget (DEB) modelling approach (Jusup et al., 2017; Kearney, 2021; Kooijman, 2010) earned DEB models a place in various

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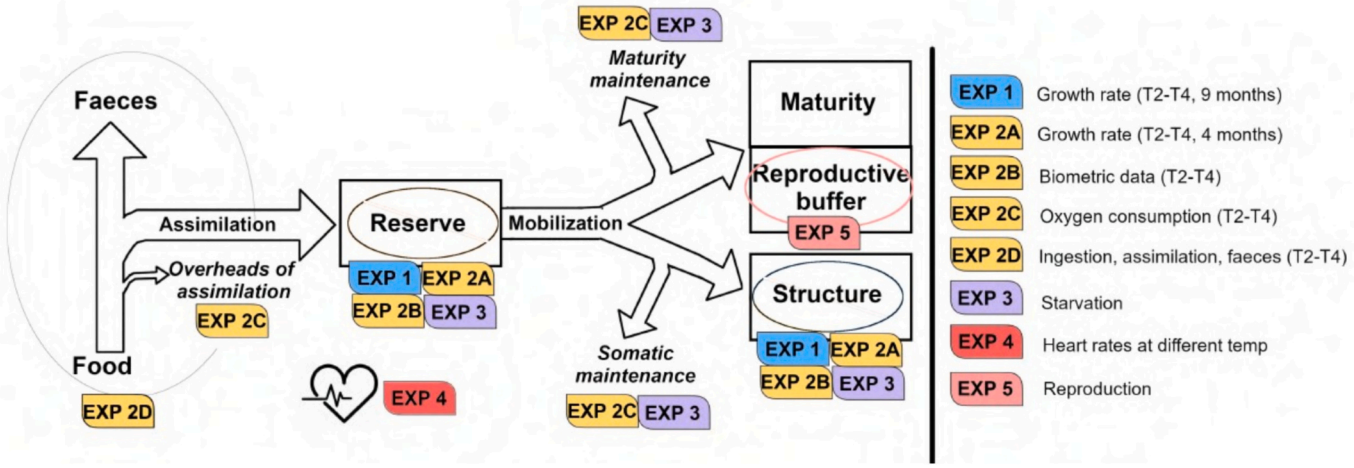


Fig. 1. Simplified conceptual diagram of DEB model after Kooijman (2010). Different targeted experiments were conducted to quantify the energy flux for different biological processes (marked on the diagram), which are temperature-dependent and defined by thermal response curve (i.e., experiment 4). Ellipses denote model compartments which have a physical volume. See Sections 2.1.2–2.1.5 for more details.

disciplines, including aquaculture (see Augustine and Kooijman, 2019). In aquaculture, DEB models of various fish, mollusc, and crustacean species have been parameterised to predict their life-history traits for aquaculture management (Alunno-Bruscia et al., 2009, 2011; Cheng et al., 2018; Filgueira et al., 2013; Haberle et al., 2024; Sarà et al., 2012, 2018; Sardi et al., 2023; Yang et al., 2020), including *P. canaliculus* (Ren and Ross, 2005; Ren et al., 2010, 2020).

The green-lipped (Greenshell™) mussel, *Perna canaliculus* (Gmelin 1791), is an important aquaculture species in New Zealand, with production exceeding 100,000 t in the past decade and export earnings exceeding 200 million USD (FAO, 2023). The DEB model for *P. canaliculus* has been used to predict growth and reproduction of these mussels in multiple locations with different environmental conditions (Ren and Ross, 2005) and to investigate the effects of environmental perturbations associated with climate change (Ren et al., 2020). To further manage the mussel resource, the model was combined with the nutrient dynamic and hydrodynamic models to estimate the carrying capacity for mussel culture in coastal waters (Ren et al., 2010). Currently the New Zealand mussel industry is transitioning towards the use of high-value hatchery produced seed stock, as well as investing in selective breeding (Camara and Symonds, 2014). The coastal aquaculture environment is also becoming increasingly challenging and volatile, experiencing unprecedented coupled ocean-atmosphere summer heatwaves (Salinger et al., 2020). These trends combine to increase the need for reliable production models, motivating the re-assessment and potential upgrade of the *P. canaliculus* model, which has previously been calibrated on a limited dataset and focused on juvenile mussels in the field.

The reliability and applicability of the model predictions depend on the quality of the model parameters, which, in turn, to a large extent depend on the data used for model calibration. To reflect the overall quality and diversity of data used in DEB model calibration, a completeness score of 1–10 is given, where a score of 10 represents the maximum possible completeness, and a relatively low completeness score implies a limited availability of (types of) data (Lika et al., 2011b). Currently, in the Add-my-Pet (AmP) database – a curated open-access collection of DEB parameters and associated data – almost all of >4500 entries have a completeness score ≤3 (AmP portal: About page[2]), suggesting that a majority of the currently available DEB models are based on somewhat limited data. This is also true for *P. canaliculus*, with a completeness score of 2.5 (Ren, 2018, AmP entry). This relatively low completeness score implies that the current *P. canaliculus* model might not be sufficiently detailed and robust to provide reliable predictions able to satisfy the increasing needs of mussel aquaculture.

Parameterisation of (the archived) *P. canaliculus* model (Ren, 2018, entry version 2018/12/11; termed here AmP-2018) was mostly based on field growth data and life-history traits reported in the literature, thus containing multiple sources of uncertainty linked to unknown environmental conditions, measurement errors etc. Moreover, observations and predictions mostly pertained to growth (in length and/or weight) during the juvenile life stage. Consequently, the AmP-2018 model available for *P. canaliculus* provided limited information on other life stages (e.g., larvae, adults), and other processes (e.g., feeding, development, reproduction). All of these traits, which are important to determine the species' performance and survival, are highly relevant in aquaculture production, particularly in the context of climate change and increasing demand for seafood. The present study was motivated by by two key aspects: How does incorporating additional information and groups of data during model calibration enhance knowledge and predictive power obtained by the model? And, conversely, does using a model with a relatively low completeness score pose an unacceptable level of commercial risk or uncertainty when predicting critical traits in aquaculture setup?

In this study, we use the AmP-2018 *P. canaliculus* model and expand it by incorporating new data obtained from targeted experiments and additional literature, to derive a new version of the model (termed 'AmP-2024'), which we uploaded to the AmP collection. The targeted experiments characterise ingestion, oxygen consumption, reproduction, and various tissue-analyses of the mussel, and were tailored to inform the model on particular parameter values or on a process of interest. We start by presenting the model structure, the analysis of the data from targeted experiments, and the model fits obtained by the reparameterised AmP-2024 model. We demonstrate how including experimental data, collected under known and controlled conditions, provides much of the fine-scale information needed for the estimation and optimisation of particular DEB parameters often involved in fine-tuning required in aquaculture optimisation protocols. Our findings also highlight the potential risks and uncertainties associated with aquaculture production and optimisation, particularly concerning biomass yield, food ingestion, and adaptation to temperature changes when utilising prediction models with lower quality parameters. We subsequently discuss the challenges associated with incorporating diverse data sources, such as literature-based data and experimentally obtained data, into DEB models, and then illustrate how variations in data from different sources and under different conditions contribute to the complexity of DEB

[2] http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/about.html.

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parameter estimation.

2. Materials and methods

2.1. Targeted experiments

The experiments were designed with a mechanistic DEB framework in mind, and were tailored to provide information on a particular process or physiological parameter. Mussels for experimentation were maintained in an indoor aquaculture facility (Cawthorn Aquaculture Park) and were fed with *ad libitum* microalgal food supply (1:1 cell ratio of cultured *Tisochrysis lutea* and *Chaetoceros calcitrans*) until sub-adult size (50–80 mm shell length). Subsequently, they were assigned to experimental tanks with the same algal cell combination at 0, 0.15, 0.5, 1.0 and 4.0 μg Chl *a* L^{-1} (hereafter named T1, T2, T3, T4, and T5 feeding regimes, respectively). All mussels were kept at comparable conditions and distributed among various experiments designed to provide information on tissue composition, growth, ingestion and defaecation, respiration, reproduction, and thermal response; see the following subsections and Fig. 1. Details on the different physiological assessment and protocols carried out can be found in Fig. S1 and Section S1 in supplementary information.

2.1.1. Growth experiment (Experiment 1 & Experiment 2A)

Approximately 320 mussels were evenly distributed among T2, T3, T4, and T5 tanks. Seawater temperature was maintained between 17 and 18 °C throughout the experiment. To examine the effects of different food conditions on mussel growth rates, biometric data (i.e., shell length and live weight) were measured over a nine months period every one to two months. After four months, a subsample of 40 mussels was collected from each food condition for further physiological measurements (see next subsection).

2.1.2. Physiological measurements (Experiment 2)

Approximately 160 mussels (40 individuals from each food condition: T2–T5; shell length: 55–80 mm) were used to obtain four types of data: (i) Growth rates: as described in the previous subsection, these mussels were monitored for four months at 17 ± 1 °C (Exp 2A); (ii) Biometric data: shell length, total (live) and flesh wet weight, dry weight, ash-free dry weight, and organic content were collected over a 1-month period, when the individuals were sacrificed at the end of the experiment 2A (Exp 2B); (iii) Oxygen consumption: respiration rates were measured over 24 h following measurements of feeding rates (Exp 2C); (iv) Ingestion and assimilation rates: feeding data, including ingestion and assimilation monitored over 16–20 h, was coupled with defaecation monitored over 12–20 h (Exp 2D). Information on ingestion rates was deduced from data on clearance rates (number and weight of algal cells removed from the water per day, and energy per day). For details on sampling procedures see Section S2.2 in the supplementary information.

2.1.3. Starvation experiment (Experiment 3)

Approximately 70 mussels (shell length: 55–79 mm) were deprived of food (T1 feeding regime) over an eight-month period. Eight of the mussels repeatedly had their respiration rate monitored by transferring them individually into flow-through respirometers, with the aim to determine the basal metabolic rate and subsequently link it to a DEB parameter governing somatic maintenance costs ($\left[\dot{p}_M\right]$). The remaining mussels were kept within the holding tank and randomly sampled (approximately 20 individuals each time) every one to two months (over six months) for measurement of biometric data (i.e., length, wet weight and organic content) to infer the flesh weight-length relationship for the calculation of shape coefficient (see Section S2.3).

2.1.4. Temperature sensitivity (Experiment 4)

Heart rates (HR) were measured from 48 mussels (shell length: 44–68 mm), experiencing a range of increasing and decreasing temperatures from 5 °C to 43 °C. The temperature-dependent heart rates were then used to derive Arrhenius temperature (T_A), lower (T_{AL}) and upper (T_{AH}) boundaries of the Arrhenius temperature and lower (T_L) and upper (T_H) tolerance temperatures by fitting the HR data with the modified Sharpe-Schoolfield model (Kooijman, 2010, 2023; Schoolfield et al., 1981). These DEB parameters describe how physiological rates of mussels change in response to temperature.

2.1.5. Reproduction (Experiment 5)

To examine the reproductive output of *P. canaliculus*, 54 adult female mussels (shell-length: 93–140 mm) were kept in aquaria for six months and fed ad libitum with food from an algal production pond. The seawater temperature was maintained at a constant temperature of 18 to 20 °C. Thermal shock was then used to induce spawning in mussels (Adams et al., 2009). This involved sequentially placing the mussels at 18 °C overnight without food, followed by a rapid temperature shift to 13 °C for 30 min and then to 23 °C for another 30 min. This thermal cycle was repeated until spawning was observed. Mussels' shell length, live weight, and the number of eggs spawned were measured and counted.

2.2. Data from literature

As a starting point, we used the AmP-2018 *P. canaliculus* entry, as the entry provided referenced data used to obtain that parameter set. Some values for life-history traits, namely age and size at birth (a_b), age at puberty (t_p), and maximum reproductive rate (R_i) needed to be adjusted to more accurately match the data reported in the literature (see Table S4). The data from the Amp-2018 entry was then supplemented with information obtained either from the targeted experiments, or from additional literature sources, e.g. data for the larval phase and energy in an egg; all the changes are documented in more detail in the revised entry submitted to the AmP collection (Ren et al., 2024, AmP - version 2024/03/08, 'AmP-2024').

2.3. The dynamic energy budget (DEB) model

We use the *abj* typified DEB model (Marques et al., 2018): a one-parameter extension of the simplest DEB model, which was developed to describe the observed (slower) growth of (mussel) larvae. (Kooijman, 2010; Marques et al., 2018). The energy budget of the individual is defined by tracking four state variables: energy reserve (E), structural volume (V), maturity (E_H) and reproductive energy (E_R) (Fig. S2; Kooijman, 2010; Marques et al., 2018). The individual assimilates energy from the environment into reserves and subsequently allocates it for maintenance, development, growth and reproduction; energy fluxes are defined by a set of DEB parameters (Tables S1, S2). Parameters are generally constant (which results in isometric growth), except during the larval phase when there is an accelerated allometric growth accompanied by changes in two parameters: $\left\{\dot{p}_{Am}\right\}$ (maximum assimilation rate) and $\dot{v}$ (energy conductance), determining energy acquisition and mobilisation, respectively). This acceleration in growth is specific to the *abj* model; the change ending with metamorphosis and settlement. Food ingestion and assimilation are assumed to follow the Holling type II functional response (Holling, 1959) and are represented as a scaled functional response f; possible f values range from zero (no food) to a theoretical maximum of 1 (*ad libitum* feeding). The assimilated energy is stored in an energy reserve (E), and subsequently partitioned between somatic maintenance and growth (κ fraction of mobilised energy), and maturity maintenance and reproduction ((1-κ) fraction of mobilised energy). When the energy supply is limited, energy allocation for

Table 1
Observed and predicted zero-variate data. Source of observed data is listed under *Reference* column. Data obtained from the *P. canaliculus* AmP entry AmP-2018 (Ren, 2018) was either revised or supplemented with data from targeted experiments (this study) or from additional literature sources. Parameters of the AmP-2024, used to obtain the predictions, are listed in Table S2.

Data	Observed	Predicted	Unit	Description	Reference
a_b	4	1.93	d	Age at birth	Rusk (2012); Rusk et al. (2017)
t_j	16	17.64	d	Time since birth at metamorphosis	Rusk (2012)
t_p	150	141.6	d	Time since birth at puberty	Alfaro et al. (2001)
a_m	7300	7059	d	Life span	Guess
L_b	$1.11 \cdot 10^{-2}$	$0.738 \cdot 10^{-2}$	cm	Shell length at birth	Rusk (2012); Rusk et al. (2017)
L_j	$2.8 \cdot 10^{-2}$	$3.227 \cdot 10^{-2}$	cm	Shell length at metamorphosis	Ragg et al. (2019)
L_p	2.7	3.117	cm	Shell length at puberty	Alfaro et al. (2001)
L_i	14.5	19.48	cm	Ultimate total length	Alfaro et al. (2001)
W_d^b	$5.669 \cdot 10^{-8}$	$2.746 \cdot 10^{-8}$	g	Ash free dry weight at birth	Rusk (2012); Ragg et al. (2019)
W_d^j	$1.8 \cdot 10^{-6}$	$1.493 \cdot 10^{-6}$	g	Ash free dry weight at metamorphosis	Ragg et al. (2019)
W_d^p	0.15	0.117	g	Dry weight at puberty	NIWA*
W_d^i	35	28.52	g	Ultimate dry weight	Guess
GSI	0.14	0.211	–	Gonadosomatic index	NIWA*
R_i	$2.74 \cdot 10^5$	$3.813 \cdot 10^5$	#/d	Maximum reproductive rate	James and Jenkins (1979); This study
E_0	$4 \cdot 10^{-4}$	$6.267 \cdot 10^{-4}$	J	Energy content per egg	This study

* Unpublished data from National Institute of Water and Atmospheric Research (NIWA) originally included in AmP-2018 model.

somatic maintenance has priority over other processes to maintain essential body functions. Otherwise, basal maintenance will, to an extent, be fueled by the depletion of structural tissue to keep an organism alive. All rates (time-dependent processes) within the individual are influenced by temperature in the same way, which is accounted for by applying a temperature correction (see also Section 2.1.4 and Table S1).

To estimate parameters we used the Add-my-Pet (AmP) estimation procedure (AmPtool, 2024; Marques et al., 2019) integrated into a freely available DEBtool package (DEBtool, 2024) that run in Matlab. To evaluate the model predictions, we compared the observed growth data not included in the parameter estimation procedure (i.e., relative changes in shell length and total weight in Experiments 1 and 2A at the individual level; see Fig. S3) with predictions generated by the new AmP-2024 version of the model. Since the growth data from Exp 2A (changes in length and weight) were not used for calibration, they could also serve as a validation of the model. Metrics measuring the goodness-of-fit of the model, including the mean relative error (MRE) and symmetric mean squared error (SMSE), were calculated by the DEBtool package (DEBtool, 2024; Lika et al., 2011a; Marques et al., 2019). For more details see Section S3.

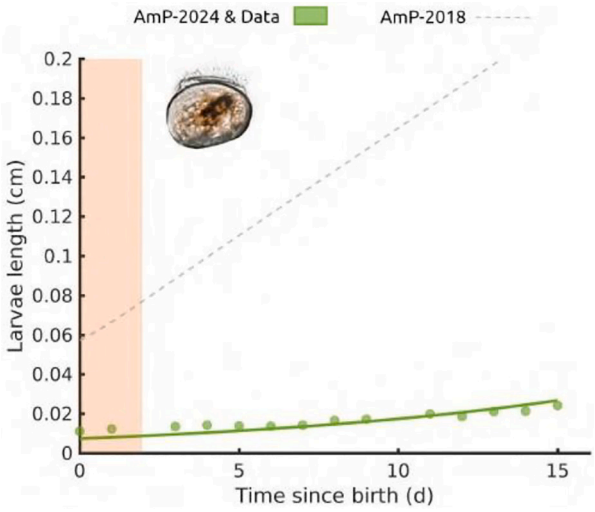


Fig. 2. Larval growth simulated by the AmP-2018 (grey dashed line) and AmP-2024 (green line and dots) versions of the model. The orange-shaded area represents the timeframe between birth and metamorphosis, as assessed by the AmP-2018. Data from Rusk (2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

Supplementing the AmP-2018 entry for *P. canaliculus* with the new experimental and literature data resulted in the completeness score of 5.5 for AmP-2024. The AmP-2024 predictions closely match the observed zero- and uni-variate data used for model parameterisation (Tables S3, S4), with satisfactory overall goodness of fit metrics (MRE: 0.135 and SMSE: 0.062). The AmP-2024 successfully predicted also the experimental growth data not used for model calibration (Fig. S3).

Here we present the main results and relevant figures, which have implications on mussel aquaculture. Additional results and comprehensive interpretation are available in Section S3 in Appendix 2, followed by the summary of descriptive statistics of experimental data (Tables S5-S10) in Appendix 3.

3.1. Changes in relevant model parameters

Model reparameterisation resulted in changes in several model parameters relative to those of the AmP-2018. The most relevant differences pertain to the: (i) life-stage transitions, i.e. maturity thresholds, (ii) parameters governing assimilation and mobilisation of reserve, and thus duration of the larval phase, (iii) tissue composition (specific density of structure and reserve), and (iv) thermal response.

By contrast, some primary parameters in AmP-2024 were found to have similar values as in the AmP-2018, such as the maintenance rate and the proportion of the mobilised energy allocated to soma (maintenance and growth). This similarity also extends to the shape coefficient for adults, which we experimentally confirmed (Fig. S4A) in addition to estimating it by the routines.

The introduction of a dedicated larval shape coefficient in the AmP-2024 allowed for a significantly different value of this auxiliary parameter during the larval phase. Additionally, including experiment specific parameters for relative food availability and digestibility (feeding experiments) provided good predictions not only for feeding experiments but also for respiration. A complete set of model parameters is provided in Table S2, and an in-depth analysis of parameter values is presented in Section S3.4. The implications for observed life-history traits and processes are discussed in the following section.

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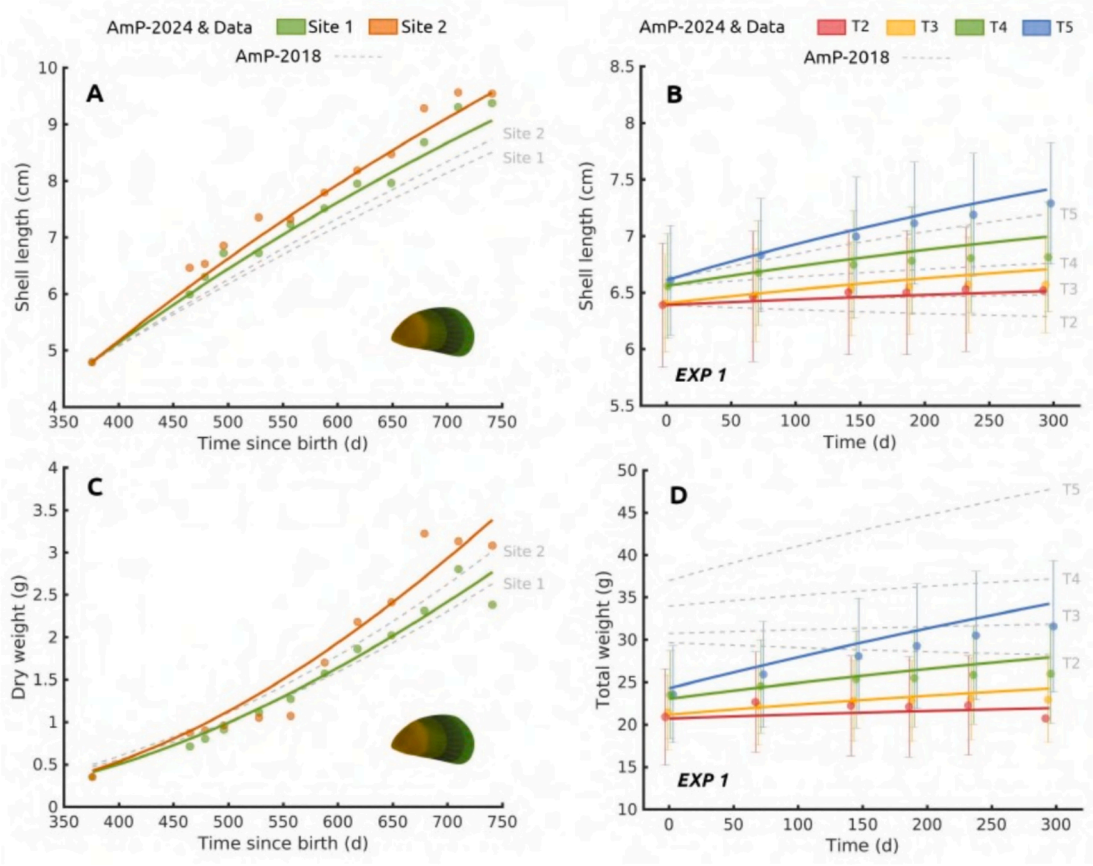


Fig. 3. Age-specific shell length (A) and dry weight (C) of mussels (data from Ren, 2018, version 2018/12/11), and mussel growth in shell length (B) and in total weight (D) obtained from experiment 1 under four food conditions, from low food (T2, red) to ad libitum food (T5, blue); see Section 2.1 for experiment description. Solid dots and lines are the data and model predictions from this study (experiments and the AmP-2024 predictions). Grey dashed lines are the predictions obtained using AmP-2018 (note: growth equations slightly differ from those originally used in the AmP-2018 entry; for details see discussion points in the revised AmP-2024 entry, Ren et al., 2024, version 2024/03/08). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Model predictions of life-history traits

Predictions for life-history traits matched well all observations when the AmP-2024 was used to obtain the prediction (Table 1). Notably, data added during reparameterisation – such as age, dry weight, and length at different life stages (birth, metamorphosis, puberty), the maximum reproduction rate, and energy content in an egg – are predicted more accurately by the AmP-2024 (Table S4).

3.3. Growth of larvae, juveniles and adults

Including new literature data in the model reparametrisation greatly improved the model's ability to predict larval growth (Fig. 2). The AmP-2018 substantially underestimates the larval phase duration (shaded area in the graph), and overpredicts the physical length of the larva. The latter is partly due to the AmP-2018's use of the same parameter to convert from the structural to physical length of the organism throughout its lifetime, thus ignoring the change in shape of the mussel.

At later life stages, growth in length and dry weight is predicted reasonably well by both versions of the model (Figs. 3 and S3A-C), but the AmP-2018 overpredicts the growth in total weight (Fig. S3D-F) measured in EXP 1 and EXP 2A. Predictions for weight are strongly influenced by the conversion factors used, and some of them differ between the model versions (see d_V and d_E, and *tw2ww* in Table S2). Biometric data on flesh ash-free dry weight and wet weight (EXP 2B, Fig. 4) provide direct measurements for the parameters $d_V(=d_E)=0.138$, defining the specific density of structure and reserve. These values deviate from the typical values of $d_V(=d_E)=0.09$ for Bivalvia in the DEBTool, which is often used as a default value with its implications mostly overlooked. Here we show that the value of d_V and d_E affect not only the predictions for (wet) weight (Fig. 4), but they have further implications for estimating the cost of growth, and can influence estimates for body composition of mussels (see Sections S3.4 and S3.8), both of which are relevant for aquaculture production.

3.4. Calculating the energy requirements of P. canaliculus: ingestion, assimilation rates, and respiration

Overall, the AmP-2024 can successfully reproduce the different ingestion rates observed under the feeding regimes (Fig. 5B). The different feeding regimes were reflected in the values of scaled functional responses, which were estimated to range from $f_2 \approx 0.3$ to $f_5 \approx 0.4$. The estimated experimental values (f_2 to f_5) are lower than those for field data stemming from the AmP-2018 entry (f_{tL1} and f_{tL2}, Table S2); field values are close to the theoretical maximum of 1 in both model versions, and thus suggest more optimal feeding conditions in the natural environment than under the experimental conditions.

The difference between ingestion and assimilation (the energy from food being assimilated into the reserve of the mussel) is reflected as the assimilation efficiency (κ_X): higher feeding regimes have a lower assimilation efficiency (Tables S2, S11). By contrast, defecation efficiency, which indicates the energy losses involved in faeces formation, was found to be relatively high under high feeding levels (κ_P in Table S2), which is in agreement with the measurements (Table S11; see

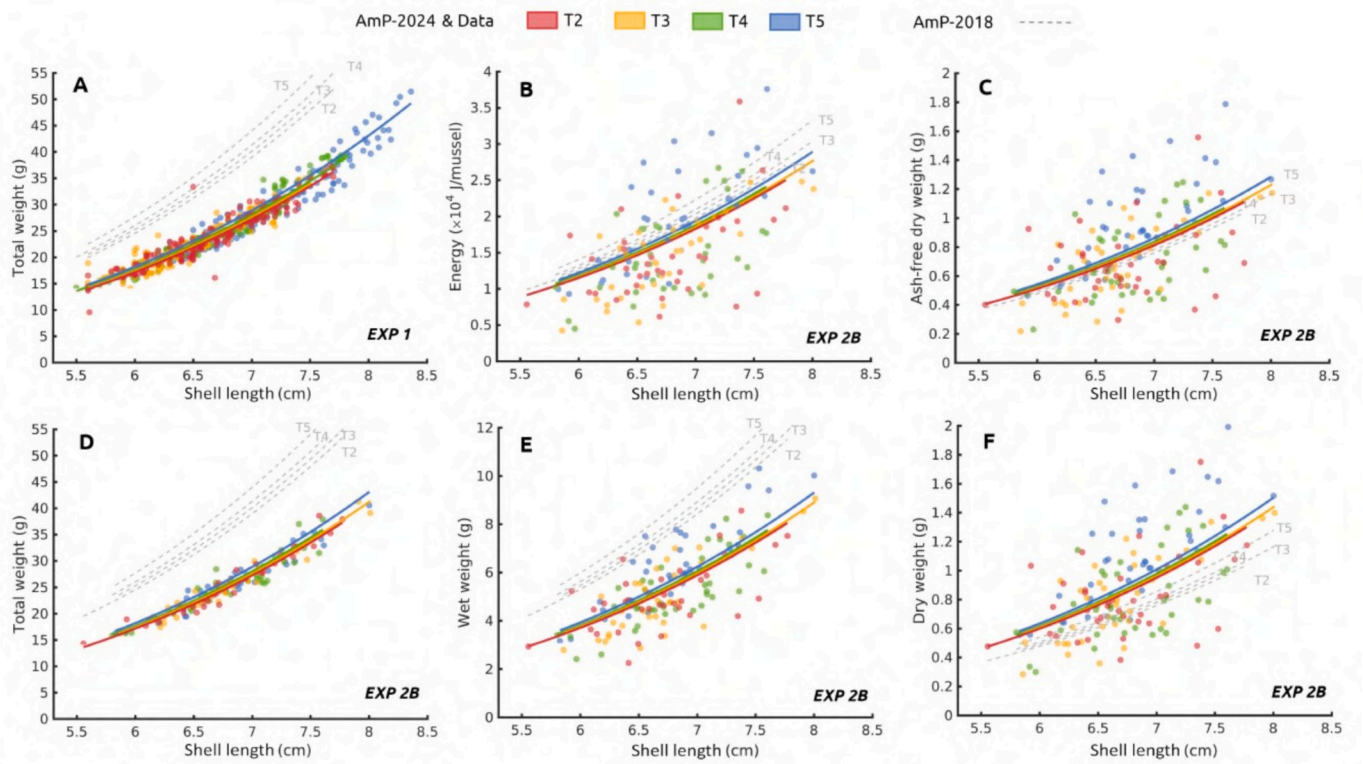


Fig. 4. Shell length and total weight relationship (A, D) obtained from experiment 1 and 2, and relationship between shell length and (B) energy content, (C) ash-free dry weight, (E) flesh wet weight and (F) flesh dry weight of mussels obtained from experiment 2 at low food (T2, red) to ad libitum food (T5, blue) conditions; see Section 2.1 for experiment description. Solid lines are predictions using AmP-2024 based on the data with the same colours. The grey dashed lines are the predictions by using AmP-2018. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also the final paragraph of this subsection). Both the assimilation and the defecation efficiency, together with maintenance and overheads of growth, will contribute to the respiration flux in the form of dissipated energy (Fig. 5A, Section S3.10). This becomes relevant when traits such as food-conversion-ratio are tracked or predicted, as our results imply that the ratio would be lower (more food required per mussel tissue gain) at higher food abundance.

Oxygen consumption differed between feeding regimes (Fig. 5A, see Table S8 for descriptive statistics), which was successfully reproduced by AmP-2024 but less so by AmP-2018. These differences arise because respiration (oxygen consumption) in feeding animals includes contributions from feeding-related overheads. As a result, predictions for dissipated energy (i.e., respiration) are influenced by the coefficients for assimilation and defaecation efficiency. With detailed data from targeted experiments, we were able to estimate realistic values for these coefficients in AmP-2024, and allowed them to differ between feeding regimes (κ_X and κ_P in Table S2). By contrast, AmP-2018 relied on standard placeholder values ($\kappa_X = 0.7$and $\kappa_P = 0.1$), which are typically used when there is insufficient data to determine κ_X and κ_P, and for AmP-2018 model predictions we assumed them equal between feeding regimes. Contribution of feeding to the energy consumption is evident in the data as an increase in O_2 uptake (μg O_2/g/min) with increased food availability, translated as an increase in standard metabolic energy consumption (J/mussel/g/d) (Table S7).

The underlying metabolic costs are determined by the metabolic rate parameter $\left[\dot{p}_M\right]$, which is similar between the models. The estimated value for $\left[\dot{p}_M\right]$ is close to that calculated from respiration data during starvation (while there is no contribution to oxygen consumption from feeding), where it's scaled to the structural volume (Fig. S4B).

Knowing the rates for ingestion, assimilation, defaecation, metabolic energy consumption, and growth, one can in theory calculate an energy budget, and thus energy requirements, of a mussel. We attempted this by combining data on all of these processes measured as part of Exp 2. However, there seems to be a substantial part of the energy 'missing' between the amount of energy ingested, and the sum of energy fixed in the tissue, dissipated, and excreted in the form of faeces, especially at the highest feeding regime T5: 75% of ingested energy is not accounted for (Table S11). By contrast, at the two lowest feeding regimes T2 and T3, all or most of the ingested energy is accounted for through the tracked processes (Table S11). We come back to this in the discussion.

3.5. Thermal response curve

The measurements from the temperature experiment (EXP 4), where heart rate was observed across a wide range of temperature, led to notable alterations in almost all parameters (T_A, T_{AL}, T_L, and T_H) that characterise the relationship between the rate of metabolic processes and temperature. The newly derived parameter values introduce a significant shift in the shape of the metabolic rate-temperature relationship curve, expanding the temperature range for an optimal growth of *P. canaliculus* (as predicted by the model) (Fig. 6).

3.6. Reproduction

The new reproductive data obtained from EXP 5 (fecundity vs. size, distribution of egg diameter; see Table S9 for descriptive statistics) provided information on the fraction of mobilised reserves allocated to reproduction (1-κ), and on the energy of an egg. While the value of κ did not substantially change in the reparameterisation process, the predictions for egg energy content differ over two orders of magnitude between the model versions (E_0, Table S4). This, in turn, results in a higher fecundity estimate (number of eggs) in AmP-2024 (Fig. 7), along

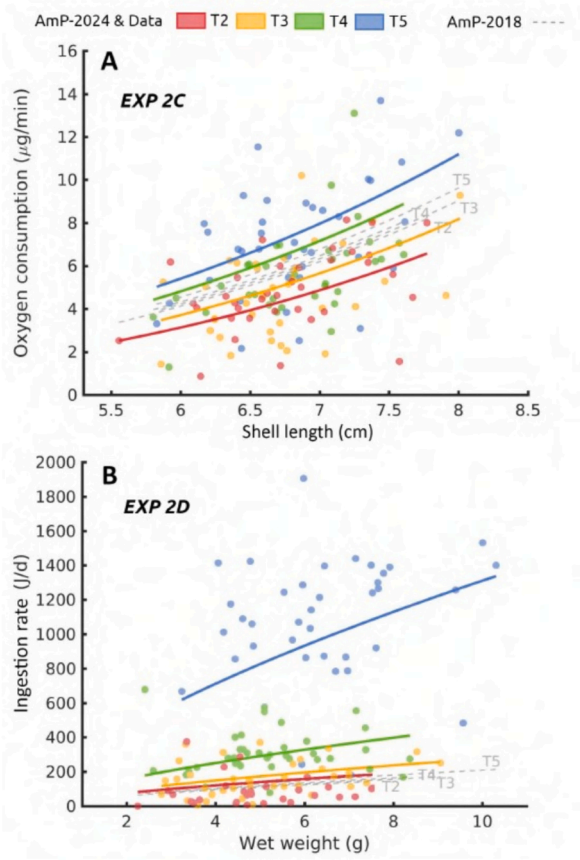


Fig. 5. Oxygen consumption rate in relation to shell length (A) and ingestion rate in relation to live wet weight (B) of mussels at low food (T2, red) to ad libitum food (T5, blue) conditions (A; see Section 2.1 for experiment description, and Table S8 for descriptive statistics). Solid lines are predictions by AmP-2024 based on the data with the same colours; the grey dashed lines are the predictions by AmP-2018. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

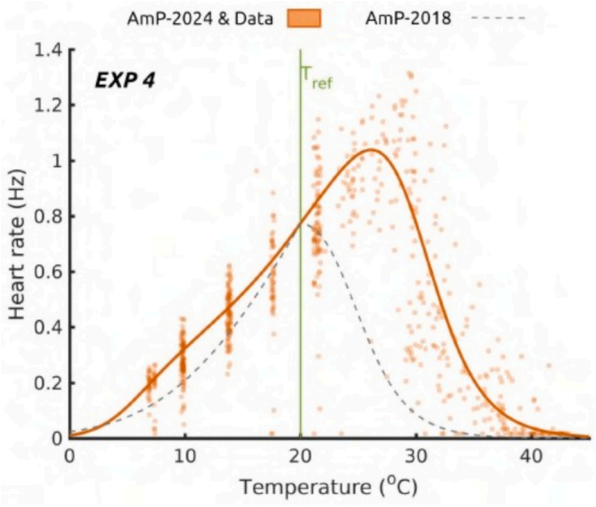


Fig. 6. Thermal response curve fitted by the mussel heart rate data. The orange points and solid line respectively represent the data and thermal response curve created in this study (AmP-2024) and the grey solid line represent the thermal response curve created using AmP-2018.

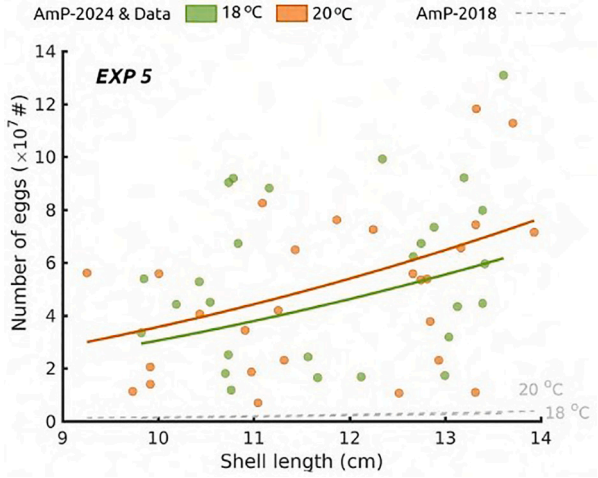


Fig. 7. Number of eggs in relation to mussel shell length at 18 °C (green) and 20 °C (red), as predicted by AmP-2024 (solid lines), and AmP-2018 (grey dashed lines, mostly overlapped). See Table S9 for descriptive statistics. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with smaller energy per egg compared to AmP-2018 predictions. The gonadosomatic index, GSI, calculated as: (mass of gonads)/(total body mass-mass of gonads), is over-predicted by AmP-2024. The value of 0.14 (AmP-2018) is, however, debatable as the AmP-2024 predictions and data obtained by EXP 5 suggest a GSI closer to a value of 0.25, or even higher. For shell length-body weight relationship, we introduced an additional shape coefficient, assuming that reproducing adults could have a slightly different body composition to non-reproducing adults, which would affect the conversions from model predictions to observable length and weight. The AmP-2024 fits the data well (Fig. S5), while AmP-2018 overpredicts the total weight, similarly to predictions in Fig. 4A,D,E.

4. Discussion

The mechanistic approach and the potential predictive power of DEB models make this modelling framework increasingly popular in aquaculture management: DEB models can, using mass and energy as tokens, mechanistically simulate life-history traits of a species in changing environmental conditions (Cheng et al., 2018; Giacoletti et al., 2021; Jusup et al., 2017; Kooijman, 2010; Steeves et al., 2018; Yang et al., 2020). In the case of *P. canaliculus*, DEB models have already been used to predict the mussel's growth and reproduction in multiple locations (Ren and Ross, 2005), determine a location's carrying capacity for the mussel (Ren et al., 2010), and to investigate the effects of environmental changes associated with climate change (Ren et al., 2020). AmP-2024 expands the array of possible applications further.

By using DEB models, we can also explore how a species performs in presence of another (aquaculture) species, providing valuable information for setting up or analysing the viability of integrated multi-trophic aquaculture (IMTA) (Chary et al., 2020; Giacoletti et al., 2024; Granada et al., 2018; Guyondet et al., 2010; Krupandan et al., 2022; Mangano et al., 2023; Montalto et al., 2017; Palmer et al., 2021; Sara et al., 2012; Saraiva et al., 2019). Here, filtration and growth rates are of particular interest, as the basic idea is to use food excess of one level (e.g., fish) as food for other levels (e.g., mussels or sea cucumbers) (Chary et al., 2020; Granada et al., 2018; Montalto et al., 2017; Saraiva et al., 2011).

Simulations such as these are, however, meaningful only if the model used to obtain the predictions has been calibrated on sufficient data (see e.g., (Bernard et al., 2011; Bourles et al., 2009; Hawkins et al., 2002; Troost et al., 2010). Our results show that data obtained from various sources could be incomplete, and might include variation and

uncertainty. In our particular case, the most prominent examples were the thermal response curve, constitution of mussel tissue, and the predictions for the larval phase and reproduction, where adding specific data greatly improved the accuracy of model predictions for those particular aspects of the *P. canaliculus* life cycle. Somewhat intuitively, many (life-stage or environment) specific predictions are generally limited by the data available during model parameterisation; should new (types of) data become available, any model would benefit from parameter refinement.

4.1. Improving model predictions and applicability

Previous *P. canaliculus* model parameterisation (AmP-2018) was mostly based on field growth data and life-history traits reported in the literature (Ren, 2018, archived AmP entry). AmP-2018 performs poorly in predicting larval growth and (adult) reproduction. Including data on these two life stages greatly increased the predictive power and accuracy of the model for larvae and adults (Figs. 2 and 7), which may be pivotal to aquaculture (Alver et al., 2007): for example, to help determine the optimum conditions and development time for larvae, or fecundity of adults. In many - if not most - cases, a complete life cycle of a species needs to be considered when deciding on an appropriate species or strategy in aquaculture. Our results imply that models built with limited data for specific life stages or processes (e.g., growth only) have limited applicability and fine-tuning is required.

Inclusion of specific biometry data enabled accurately determining allometric weight-length relationships, which provide valuable information for mussel aquaculture management. For example, the predictions for adult live weight and shell length provide information on the body condition of bivalves, which is a useful indicator to determine the time for harvest and indicative value of the aquaculture product (Hemachandra and Thippeswamy, 2008; Noor et al., 2021; Orban et al., 2002). Lastly, we showed that including more detailed data (from a single experiment) could change the shape of the thermal response curve (Fig. 6), especially at temperatures approaching or even exceeding thermal thresholds. Being ectotherms, bivalves' physiological processes are highly dependent on the environmental temperature. The shape of the thermal response curve is governed by Arrhenius temperature parameters (T_A, T_{AH}, T_H, T_{AL}, T_L, Table S2), which are ideally estimated from thermal response data. The AmP-2018 *P. canaliculus* entry did not provide referenced sources for the Arrhenius temperature parameters used in the entry (Ren, 2018), suggesting that the parameters used in the AmP-2018 lack a foundation in actual measurements conducted on the species. The resolution and quality of the thermal response data becomes particularly important if the model needs to predict thermal responses for *P. canaliculus* (or any other species) under varying thermal conditions, in the context of climate change (e.g., Ren et al., 2020).

4.2. Designing and performing targeted experiments

Experimental data such as oxygen consumption, reproduction, and weight-length relationship data, collected under known and controlled conditions, provide the much finer scale information needed for the estimation and optimisation of the DEB parameters – such as tissue energy and water content, somatic maintenance rate, maximum assimilation rate – especially for fine-tuning often required in aquaculture optimisation protocols.

Biometry experiments provided direct information on energy, water, and organic content of tissue. Values for these parameters are often assumed to be the default value of the taxon (AmPtool, 2024, estimation routines), but determining the species-specific value can improve estimates for weight predictions and body composition of the mussel.

Feeding experiments, during which filtration and defaecation rates were measured at four feeding regimes, provided important information for determining metabolic parameters of *P. canaliculus*. In addition – and perhaps more importantly – they highlighted some valuable take-home messages for designing such experiments. Namely, the combination of the measured filtration rates and energy content of the faeces does *not* provide all of the necessary information to calculate the energy budget of the mussel, even when combined with information on tissue energy content, respiration, and growth rates: e.g., the material in the pseudofaeces (not routinely measured) has actually never been ingested, but is removed from the water column.

Reasons for difficulties in closing the mass-energy balance may be many-fold: for example, a sub-optimal flow rate in experimental tanks (Petersen et al., 2004) may cause either water re-circulation and food dilution within the chamber, resulting in an over-estimate of food ingestion (Filgueira et al., 2006), or it can flush away produced faeces, resulting in an under-estimate of excreted matter (Iglesias et al., 1998). In addition, the process of energy acquisition (from food) might require further experiment-specific calibration, where factors such as particle content and composition in the water column might affect the body composition (and thus energy content of the whole mussel) (Grant and Cranford, 1991; Smaal and Vonck, 1997), as well as filtration efficiency (and thus pseudofaeces production) (Gardner, 2000; Kooijman, 2010; Riisgård, 2001; Hawkins et al., 1999). In our particular case, the ingested energy was estimated to be far greater than that accounted for by the tracked processes of respiration, weight gain, and defaecation, especially for high food regimes (Table S11). We hypothesise this is due to: (i) the clearance rate calculations overestimating the actual ingestion; (ii) defaecation rate data under-representing the excretion, or (iii) a combination of both. All of these processes are relevant in estimating the filtration potential of a species, inlcuding its potential to remove excess organic matter from a water column in a multitrophic aquaculture setting (Chary et al., 2020; Granada et al., 2018; Krupandan et al., 2022; Montalto et al., 2017; Palmer et al., 2021; Sarà et al., 2012; Saraiva et al., 2019). Generally, in targeted experiments like these, we strongly recommend tracking both pseudofaeces production and food particle deposition on experimental containers: as both processes remove food from the water column, neglecting them might lead to over-estimating energy ingestion.

4.3. Combining literature data and targeted experiments

Species-specific data for model calibration can be acquired from two main sources: published literature, and targeted (often DEB-inspired) experiments. Data from literature provide a broad representation of the species, as they often refer to individuals from different locations in different studies, potentially belonging to various populations. Thus, literature data can provide a solid first approximation of all the species metabolic processes, if data on all major traits of a species are available. The literature data, however, may be highly variable and lack coordinated measurements of DEB-informative variables, or may be focusing only on a specific life stage or environment, hampering the model's ability to predict more biological processes with relatively high certainty.

Targeted experiments to measure variables of (DEB) interest in controlled conditions, on the other hand, enable the estimation of specific DEB parameters (van der Veer et al., 2006; Sarà et al., 2013). Such experiments can be designed to take into account inter-individual variability in life-history traits and/or metabolic responses, allowing for higher precision in parameter estimation. Targeted experiments, however, can be costly and labour-intensive, they often pertain also only to a specific (relatively short) part of a species' life cycle, and finally, the model's outputs may often deviate from the data due to more complex and challenging fitting and parameter estimation procedure as we include more data. Both data sources, therefore, can result in a relatively poor representation of a complete life cycle and of the variety of species' possible metabolic responses. Therefore, to develop a DEB (mechanistic) model with strong predictive power across different life stages and conditions, it is recommended to combine data from both literature and targeted experiments.

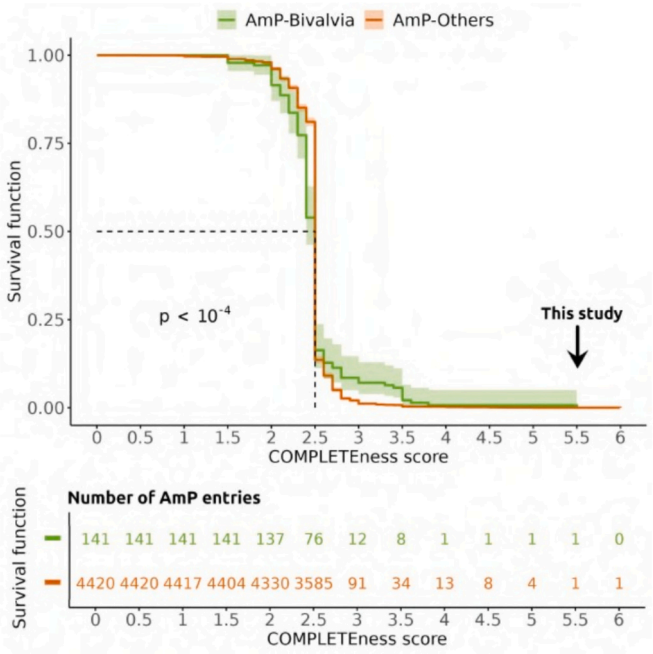


Fig. 8. The probability that the completeness score of the AmP entry exceeds a certain value (survival function). Gehan-Breslow (generalised Wilcoxon) test was used for comparing survival curves between two groups ($p < 10^{-4}$). Data were retrieved on 07/05/2024 from the Add-my-Pet collection (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/species_list.html) using the corresponding routines in AmPtool (2024).

4.4. Completeness score considerations

We assessed the completeness score of AmP-2024 *P. canaliculus* entry to be 5.5, based on the fact that we still needed to guess maximum weight (a trait rarely achieved in this aquaculture species, generally scored as completeness 0; Lika et al., 2011a), but we did provide data on respiration and energy content of tissue at several food levels (scored as completeness 6 and 7, respectively; Lika et al., 2011b). This sets *P. canaliculus* as the most comprehensively parameterised bivalve, and one of the two most 'complete' animal entries in general (Fig. 8), the other being *Daphnia magna*.

Overall, bivalves have a rather different distribution of completeness scores than other entries in the AmP collection (Fig. 8). The higher proportion of entries with a relatively high completeness score in Bivalvia is likely a result of many bivalves having a commercial value, combined with their relatively short life cycle and small size, which enables targeted experiments. Invested interest and ease-of-access to data are a fruitful combination for data-intensive models (such as DEB), and, with increased model use and applications, we might observe a rise in completeness score of other AmP entries as well.

Currently, the majority of AmP entries have a completeness score of $\leq$2.5 (Fig. 8). Even though this is a relatively low score on the scale of 0 to 10 (Lika et al., 2011b), an appropriate data combination should provide enough information to determine most parameter values (Accolla et al., 2020). Generally, an AmP entry can be made species (the majority of the entries) or sub-species (breed or population) specific (see for example entries for chickens, geckos, and sea turtles in the collection), and occasionally capturing the variability of the species/population is prioritised over maximising the goodness-of-fit. Adding data could lead to a reduced model goodness-of-fit, and can be a challenge in parameter estimation procedures, as different parameters have different sensitivities to the data perturbation (Filgueira et al., 2020; Matyja, 2023). The current AmPtool and DEBtool routines, however, are well equipped to simultaneously handle multiple types of data (Marques et al., 2018). In addition, parameter estimation is often assisted by so-called 'estimation in context', where the parameter sets of closely related species are compared for consistency, and parameter values of a generalised animal or of closely related species are used as initial values for parameters of species of interest (Lika et al., 2011a; Marques et al., 2018; AmPtool, 2024). We have used this functionality to compare the obtained parameter set of *P. canaliculus* (Table S2) with that of closely related species (*Perna viridis* and *P. perna*), and have confirmed that our parameter set is consistent with other members of the same genus present in the collection (results not shown; automated output of estim_options('results_output',5); in AmPtool routines).

To summarise, the completeness score is a good indicator of data quality and variety, and can serve as a good approximation for model comprehensiveness and applicability: the lower the completeness score, the smaller the number of reliable extrapolations and predicted processes, and vice versa. Additionally, well defined (and ground-truthed) parameters can provide meaningful predictions even at a lower completeness of an entry. However, the completeness score currently does not explicitly incorporate the thermal response measurements (Lika et al., 2011b), which should perhaps be revisited and revised. With DEB models increasingly used to explore climate change impacts (e.g., Agüera et al., 2015, 2017; Giacoletti et al., 2024; Lavaud et al., 2021, 2024; Mangano et al., 2019, 2023; Moreira et al., 2022), a reliable method to assess the suitability of parameter sets for thermal predictions would be highly beneficial and should be established.

5. Conclusions

We have demonstrated that performing targeted experiments, and including such experimental data in the process of model (re)calibration, improves the model's predictive power and its applicability for exploring life-stages and processes of interest. This enables a wider use of models for predicting responses of aquaculture species to environmental perturbations, including climate change.

A comprehensive dataset for parameter estimation would ideally include both experimental (laboratory) data and in-situ measurements, since there are different physiological and behavioural responses between laboratory-acclimated and field-acclimatised mussels. Alternatively, a breed- or population-specific parameter set can be established if a particular sub-specific level is of interest. Furthermore, inclusion of accurate temperature response data can change the thermal response curve of a species, which may have repercussion on mussel's life-history traits. This is an important consideration if we use the DEB model to predict the effect of climate change on aquaculture species performance including growth and reproduction, which are the crucial factors influencing the profit of mussel aquaculture industry.

The completeness score can serve as a good model assessment metrics and crude approximation of model applicability, when types and variety of data are of interest. However, the completeness score does not take species' thermal responses into account. Given the importance of the temperature response data on shaping the thermal response curve, the presence/absence of quality temperature response data should also be considered for model assessment in oderd to increase the applicability of DEB models in the aquaculture sector.

Overall, the present study has significantly improved the utility of the *P. canaliculus* DEB model to project performance and support aquaculture management decision-making. Effort could now be directed towards understanding the value of DEB modelling to characterise phenotypes and performance differences between selectively-bred families, supporting further current mussel aquaculture needs (Camara and Symonds, 2014).

CRediT authorship contribution statement

Martin C.F. Cheng: Conceptualization, Data curation, Methodology, Visualization, Writing – original draft. **Sunčana Geček:**

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Conceptualization, Data curation, Formal analysis, Visualization, Software, Writing – original draft. **Nina Marn:** Conceptualization, Data curation, Formal analysis, Visualization, Software, Funding acquisition, Writing – original draft. **Antonio Giacoletti:** Writing – review & editing. **Gianluca Sarà:** Writing – review & editing. **Nick King:** Investigation, Resources, Data curation, Project administration, Funding acquisition. **Norman L.C. Ragg:** Investigation, Methodology, Resources, Data curation, Project administration, Funding acquisition, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known conflicts of interest that could have appeared to influence the work in this paper.

Data availability

Data and underlying code used for model calibration are available in the AmP repository: https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Perna_canaliculus/Perna_canaliculus_res.html, version 2024/03/08.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2024.741434.

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