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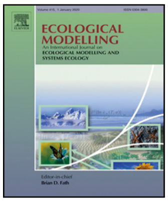

How to build Dynamic Energy Budget models: Practical guidelines for model development[☆]

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ABSTRACT

Dynamic Energy Budget (DEB) theory provides a coherent framework to describe how organisms acquire and use energy and matter throughout the life cycle in response to environmental conditions. The wide applicability suggests the generality of DEB theory and is one of its main strengths. However, this same generality introduces a substantial degree of abstraction, which can make model development challenging, particularly for newcomers. This paper aims to support more transparent, biologically grounded, and reproducible DEB modeling by proposing guidelines to make the development process more explicit and accessible. We identify three main challenges: (1) how to link biological processes to their mathematical representation, (2) which observations are needed to inform key physiological processes, and (3) how to carry out parameter estimation and model validation in a transparent and reproducible way. To help overcome these issues, we briefly introduce core concepts and discuss the six main steps in the DEB modeling workflow: model design, data collection and assessment, implementation, calibration, validation, and publication. These steps are illustrated with a case study on zebrafish (*Danio rerio*) that demonstrates how data availability influences model development and the range of predictions that can be supported. By proposing a structured workflow, we hope to encourage researchers to explore the full potential of DEB theory.

1. Introduction

Mathematical models help us translate biological phenomena into quantitative, testable predictions (Kooijman et al., 2024). A useful model requires clear assumptions, appropriate data, and robust calibration and validation (Marques et al., 2019; Lemmen and Sommer, 2024; Swannack et al., 2025). Additionally, the development process should be transparent and accessible, supported by clear protocols for data collection and model design, validation, and publication (Grimm et al., 2010; Meier et al., 2025). Although models can be powerful tools, their outcomes strongly depends on the modeler's experience, particularly when good modeling practices are not consistently applied (Holländer et al., 2009; Jakeman et al., 2024).

Bioenergetic models are frameworks that quantify how energy is used to sustain life. At the individual level, they might describe how energy is acquired and allocated to physiological processes. Among existing approaches, Dynamic Energy Budget (DEB) theory provides a general and coherent framework to describe bioenergetics, which

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is strongly based on the first principles of mass-energy-entropy balances (Kooijman, 2010; Martin et al., 2012; van der Meer, 2006; Jusup et al., 2017). Since DEB theory is founded on these first principles, it can be applied across taxa and contexts, supporting a wide range of applications, such as aquaculture (Tan et al., 2022; Cheng et al., 2025; Kiffney et al., 2026), ecotoxicology (Jager et al., 2023; Accolla et al., 2020), population dynamics (Martin et al., 2012; Marn et al., 2020; Donati et al., 2026), comparative energetics (Tan et al., 2026; Le Moan et al., 2024; Kooijman et al., 2021), ecological niche characterization (Kearney, 2012; Kearney and Porter, 2020), species interactions (Dajčman et al., 2025; Stavrakidis-Zachou et al., 2024), climate change (Pousse et al., 2022; Giacoletti et al., 2024; Lagunes et al., 2025), and conservation (Lavaud et al., 2021; Marn et al., 2022a). This versatility is perhaps best illustrated by the Add-my-Pet (AmP) collection, which currently hosts canonical DEB models for more than 7300 species (Marques et al., 2018; Add-my-Pet, 2026a).

Such a wide range of applications hints towards the generality of DEB theory. However, this same generality also brings forth abstraction, which might hinder the process of deeply understanding the theory. As a result, new users of DEB theory — whether modelers or experimental researchers — may find the framework intimidating and difficult to grasp. Building a DEB model requires a clear understanding of the theory's assumptions, equations, and terminology (Svoboda and Passmore, 2013; Swannack et al., 2025). This is why, based on our experience as both DEB theory students and instructors, we identify three major challenges for beginners: representation, data, and calibration.

The first challenge, representation, concerns linking biological processes to their mathematical counterparts in DEB theory. The modeler must distinguish between parameters, state variables, and initial conditions, while understanding the functional role or biological interpretation of each term in the model (Chiel et al., 2010; Swannack et al., 2025). This aspect is particularly important for biologists and other practitioners who are not primarily trained in mathematics, but may want to apply DEB theory to answer their research questions. Moreover, since DEB state variables cannot be measured, auxiliary theory is required to transform model outputs into real-world measurements (Lika et al., 2011a; Kearney et al., 2021). While such an abstract representation of an organism provides generality and coherence with other disciplines, it further obscures the direct link between current practices in biology and DEB theory. As such, promoting a deeper understanding of these links remains essential to make DEB theory and its applications more accessible to a broader audience.

The second major challenge concerns data, where beginners often struggle to: identify which types of observations are needed to inform specific physiological processes, design experiments that align with fitting DEB models, and understand how data limitations constrain model structure and predictive power (Marques et al., 2019; Accolla et al., 2020; Cheng et al., 2025). Since data availability strongly influences model complexity, confidence in parameter estimation, and the reliability of model predictions, guidance for beginners on this challenge is critical (Matyja, 2023; Lika and Kooijman, 2024).

The third major challenge concerns model calibration. Experienced DEB modelers may follow well-established procedures for parameterization and validation (Lika et al., 2011b; Marques et al., 2019), but for newcomers, these steps can be unclear. The model calibration steps already require a deep understanding of the theory and existing tutorials tend to focus on its conceptual or mathematical details rather than on the practical details needed for its application (van der Meer, 2006; Kooijman et al., 2008; Nisbet et al., 2012; Jusup et al., 2017; Jusup and Kearney, 2024). Without clear consolidated guidelines in accessible language, DEB model fitting runs the risk of becoming subjective and overly dependent on personal experience.

Altogether, these aspects contribute to the common perception of DEB theory as complex and elusive, reducing accessibility and hindering its widespread application. Consequently, clear and accessible methodological guidance on how to build a DEB model is necessary to help modelers navigate the key challenges described above. We address this demand by providing clear and practical guidelines for developing DEB models.

First, we introduce the core concepts of DEB theory, limiting the mathematical details to those needed to understand the modeling workflow, and point readers to relevant resources for a deeper understanding. We then discuss each step in the development of a DEB model, from data collection and model design to model implementation, calibration and validation (Fig. 1). Throughout these steps, we discuss good modeling practices that are applicable to model development and publication.

To illustrate these concepts, we develop a DEB model for a case study species: the zebrafish (*Danio rerio*). We show how the structure of the model should be guided by the biology of the organism and when extensions of the standard DEB theory are needed to capture species-specific traits. Furthermore, we compare two DEB models of zebrafish with different levels of data availability (Box 1) to address a methodological question central to DEB model development: how does the availability of different types of data affect modeling choices, parameter estimation, and the range of predictions supported by the calibrated model?

2. Dynamic energy budget theory

2.1. DEB theory fundamentals

Several models can be derived under the umbrella assumptions of DEB theory. The simplest formulation[1] able to coherently capture the full life-cycle of an organism while retaining all the core four state variables of the DEB theory is the. This model assumes that the surface area of an organism remains proportional to its volume to the power of 2/3, a property called isomorphy. In the standard DEB model, each organism is described by four state variables: reserve E [J], structure V [cm^3], maturity E_H [J], and reproduction buffer E_R [J].

Parallel developments inspired by DEB theory have also been developed aiming for pragmatic applications rather than theoretical generality. A notable example is the reserve-less DEBkiss model (Jager et al., 2013), which shares a lot of similarities with the early developments of DEB theory (Kooijman and Metz, 1984). This model is generally used for ecotoxicological essays and environmental risk assessments. The absence of the reserve implies that the DEBkiss model cannot be derived as a simplification of the std DEB model, nor vice versa; therefore, processes and parameter values are not directly comparable between the two models. Since we aim to address challenges overarching DEB theory in a general sense, we will focus the following sections only on the standard DEB model and its derivations.

Reserve E represents stored energy and is used to fuel all metabolic processes. Structure V represents the proportion of the organism's physical biomass that determines its body size (length) and requires maintenance throughout the life cycle. Maturity E_H is the cumulative energy invested in developing complexity and determines transitions between life stages, e.g., from juvenile to adult. Lastly, the reproduction buffer E_R accumulates energy stored for gamete production in the form of reserves.

The biomass of an organism is composed of reserve E and structure V (and possibly the reproductive buffer E_R for mature individuals) which represent aggregated pools of compounds rather than a single

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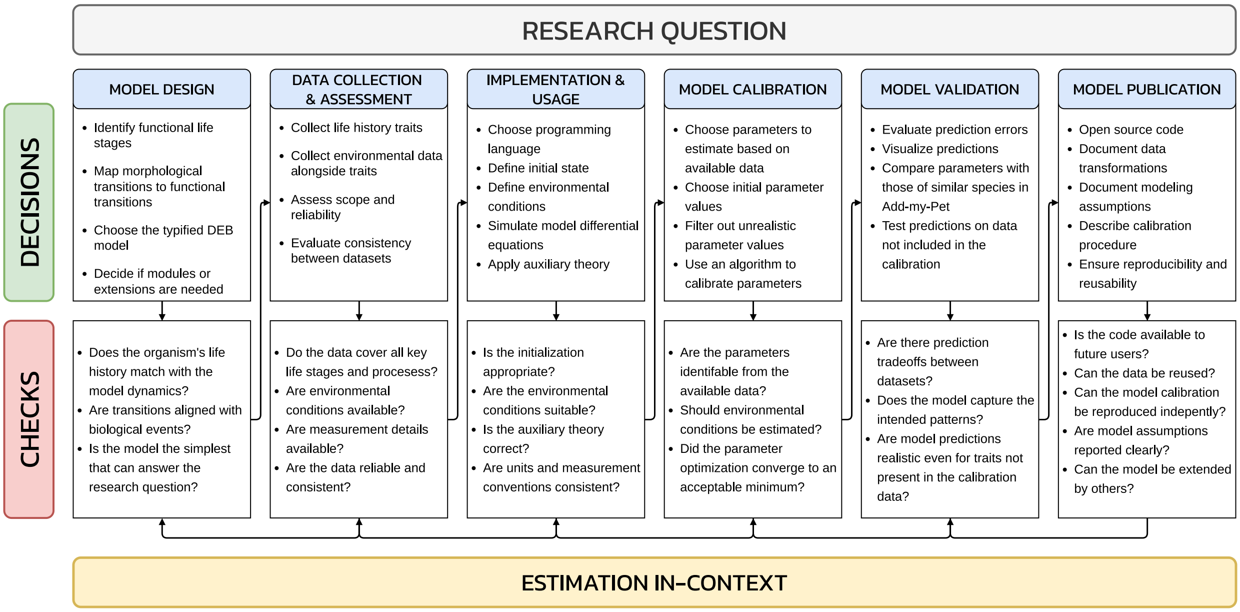
[1] An even simpler formulation is the DEBkiss model which is widely used for ecotoxicological assays and environmental risk assessments. DEBkiss models are derived from many of the standard DEB models assumptions; however they do not explicitly consider a reserve state variable. Although most of the guidelines presented are also applicable to DEBkiss models, we focus our exposition on models derived from standard DEB theory and refer to Jager et al. (2013) and Jager (2025) for further details.



MODEL DESIGN

Decisions:
- Identify functional life stages
- Map morphological transitions to functional transitions
- Choose the typified DEB model
- Decide if modules or extensions are needed

Checks:
- Does the organism's life history match with the model dynamics?
- Are transitions aligned with biological events?
- Is the model the simplest that can answer the research question?

DATA COLLECTION & ASSESSMENT

Decisions:
- Collect life history traits
- Collect environmental data alongside traits
- Assess scope and reliability
- Evaluate consistency between datasets

Checks:
- Do the data cover all key life stages and processes?
- Are environmental conditions available?
- Are measurement details available?
- Are the data reliable and consistent?

IMPLEMENTATION & USAGE

Decisions:
- Choose programming language
- Define initial state
- Define environmental conditions
- Simulate model differential equations
- Apply auxiliary theory

Checks:
- Is the initialization appropriate?
- Are the environmental conditions suitable?
- Is the auxiliary theory correct?
- Are units and measurement conventions consistent?

MODEL CALIBRATION

Decisions:
- Choose parameters to estimate based on available data
- Choose initial parameter values
- Filter out unrealistic parameter values
- Use an algorithm to calibrate parameters

Checks:
- Are the parameters identifiable from the available data?
- Should environmental conditions be estimated?
- Did the parameter optimization converge to an acceptable minimum?

MODEL VALIDATION

Decisions:
- Evaluate prediction errors
- Visualize predictions
- Compare parameters with those of similar species in Add-my-Pet
- Test predictions on data not included in the calibration

Checks:
- Are there prediction tradeoffs between datasets?
- Does the model capture the intended patterns?
- Are model predictions realistic even for traits not present in the calibration data?

MODEL PUBLICATION

Decisions:
- Open source code
- Document data transformations
- Document modeling assumptions
- Describe calibration procedure
- Ensure reproducibility and reusability

Checks:
- Is the code available to future users?
- Can the data be reused?
- Can the model calibration be reproduced indepently?
- Are model assumptions reported clearly?
- Can the model be extended by others?

Fig. 1. Steps, decisions, and checks in DEB model development, from model design and data collection to implementation, calibration, validation, and publication. Model development is iterative, and both the research question and the estimation-in-context principle should be considered throughout the workflow.

Box 1. The two data levels in the zebrafish case study.

Zebrafish DEB models. We developed two DEB models for zebrafish (*D. rerio*). The data-limited calibration includes basic data on development, growth, and reproduction. The data-rich calibration includes all data from the data-limited calibration, in greater quantity and with the addition of oxygen consumption and food intake data (Table 1). On the completeness scale of Lika et al. (2011a), the data-limited calibration only reaches 2.5, which is similar to the majority of entries in the AmP database. The data-rich estimation reaches a completeness of 5.0, similar to the most data-rich entries in AmP.

Table 1. Data for each zebrafish calibration.

Calibration data		Data-limited	Data-rich
	Fertilization		✓
	Birth	✓	✓
Age & length/weight	Metamorphosis		✓
	Puberty	✓	✓
	Ultimate	✓	✓
Lifespan		✓	✓
Growth trajectories (length/weight)			
	Food levels	Single	Multiple
	Temperatures	Single	Multiple
	Max. reproduction rate	✓	✓
Reproduction data	Reproduction over time		✓
	Gonado-somatic index		✓
Food intake			✓
Oxygen consumption			✓
Completeness score		2.5	5.0

Model implementation and publication. The zebrafish DEB models were derived from the zebrafish model presently in the AmP database (Augustine, 2018). Models were implemented in MATLAB with the `DEBtool` package (Add-my-Pet, 2026b) and were calibrated with the AmP estimation procedure (Kooijman, 2025). All code is open source and is archived in Zenodo (Klagkou et al., 2026b).

compound. To ensure a trackable stoichiometry, both reserve and structure are assumed to have a constant chemical composition; this simplifying assumption is known as strong homeostasis. Reserve and structure are typically composed of carbon, hydrogen, oxygen, and nitrogen atoms (e.g., $CH_aO_bN_c$) at fixed ratios. Since these ratios are invariant, their composition can be expressed in terms of C-moles (i.e., a quantity of an element scaled by one mole of carbon atoms). This is a powerful property of DEB models that ensures mass traceability, and allows the chemical composition of the whole organism to change along with the relative ratios of reserve and structure.

A pragmatic starting point to elaborate on DEB dynamics is the process of converting food into reserve E, a process referred to as assimilation. The organism ingests food at a rate $\dot{p}_X$, called the ingestion power. In DEB notation, $\dot{p}_.$ refers to power, since the quantity is measured in units of energy per time ($\mathrm{J\,d^{-1}}$), and the subscript X represents the process, in this case ingestion. The ingestion power is taken to be proportional to structural area $V^{2/3}$ in isomorphic organisms. Commonly, it is also defined to be proportional to a scaled functional response $f(X)$, which is a Michaelis–Menten function of the density of food in the environment X. Then, the organism assimilates food into reserves E at a rate $\dot{p}_A$, which is proportional to ingestion $\dot{p}_A = \kappa_X \dot{p}_X$, where $\kappa_X < 1$ is the digestion efficiency. The remaining energy in the food is dissipated with some being converted to feces at a rate $\dot{p}_P = \kappa_P \dot{p}_X$, where κ_P is the defecation efficiency.

After assimilation, reserve is mobilized at a rate $\dot{p}_C$ and used to fuel all other metabolic processes. A fraction κ is allocated to maintenance and growth. This fraction is first used to pay somatic maintenance $\dot{p}_S$. Somatic maintenance is the energy cost required to support functional somatic processes, and is associated to maintaining basal processes such as cellular integrity, protein turnover, maintenance of gradient concentrations across membranes, as well as costs associated to movement. It is typically assumed to be proportional to structural volume V. The remaining mobilized energy $\kappa \dot{p}_C - \dot{p}_S$ is used for growth, which is simply defined as the increase of structure V. The growth power is allocated at a rate $\dot{p}_G$. Under constant food availability, the reserve density $[E] = E/V$ is assumed to remain constant. This is a core property of DEB theory called the weak homeostasis assumption. Due to the constant chemical composition of reserve and structure, the chemical composition of the organism as a whole also remains the same under constant food conditions. For isomorphic organisms, this assumption results in structural length $L = V^{1/3}$ dynamics simplifying into von Bertalanffy growth whenever they are exposed to constant environmental conditions and after reserve density has equilibrated to the food level (Pütter, 1920; Kearney, 2021).

The other $1 - \kappa$ fraction is allocated to the maturity branch. This fraction is first used to pay maturity maintenance $\dot{p}_J$ which is proportional to maturity E_H. The leftover is used to increase maturity at a rate $\dot{p}_R$. As maturity increases, the transition from one life stage to another is reached at specific thresholds with associated changes in the behavior of the model. The organism starts as an egg, developing solely from the reserve initially contained in the egg, E_0. When birth occurs ($E_H = E_H^b$), the organism will have the same reserve density as the mother (known as the maternal effect assumption) and the organism will start feeding. When the organism reaches puberty ($E_H = E_H^p$), maturity remains constant thereafter. The organism enters the adult phase where it allocates energy at a rate $\dot{p}_R$ for reproduction.

Temperature affects the rate at which all metabolic processes occur. As a result, the powers $\dot{p}_.$ are a function of both the state variables and the temperature, which will affect growth and when the organism is born or reaches adulthood. Temperature dependence is commonly modeled with an Arrhenius relationship that describes how rates changes with shifts in temperature.

The powers $\dot{p}_.$ can be organized into three fundamental transformations:

- **Assimilation.** Food is transformed into reserve, feces and mineral products.
- **Growth.** Reserve is transformed into structure and mineral products.
- **Dissipation.** Reserve is used to fuel all other metabolic processes, transforming reserve into metabolic products.

Because state variables have chemical compositions, each of these transformations can be described by an aggregated chemical reaction. In each reaction, oxygen is consumed and some energy is released as heat and mineral products in the form of carbon dioxide (CO_2), water (H_2O), and nitrogenous waste.[2] These aggregated chemical reactions are the basis for the mass-energy-entropy balances of DEB theory. Further details can be found, for example, in Nisbet et al. (2012), Jusup et al. (2017), Jusup and Kearney (2024), or Kooijman (2010), pp. 138–165.

The diagram in Fig. 2 of the standard DEB model shows how each process and transformation are connected to the model state variables. The assumptions listed in this section are sufficient to fully specify the standard DEB model mathematically. Appendix A provides the dynamics equations for each state variable, the equations for the power or rate of each process as well as details on how temperature and food are typically modeled.

2.2. Beyond the standard DEB model

The standard DEB model provides a simple, widely applicable framework for describing energy acquisition and allocation during the life cycle (Kooijman, 2020b). In many cases it is an appropriate starting point; however, some taxa exhibit specific life-history dynamics that require explicit additions to the standard structure.

For example, transitions between the three life-stages represented in the standard DEB model (embryo, juvenile, and adult) are defined by maturity thresholds (e.g., birth and puberty). However, depending on the species life-history and the modeling goal, they can also be a function of other state variables or of environmental conditions (e.g., temperature).

Moreover, some specific life-history dynamics might not be accounted in the standard DEB model. A common example relates to shape changes throughout ontogeny. Larval phases of certain organisms commonly do not express isomorphic growth. Accurately representing these phases require additional assumptions, which are captured using extensions of DEB theory (Marques et al., 2018).

Several frequently observed life-history patterns have been formalized as typified DEB models in the Add-my-Pet collection (Marques et al., 2018). These typified models share most of the assumptions of the standard DEB model, but extend it to capture specific life-history dynamics. In Section 3.1, we discuss when these and other model extensions should be applied.

2.3. From state variables to measurements

The state variables of a DEB model (structure, reserve, maturity, and reproduction buffer) offer a simple representation of an organism as abstract quantities that cannot be directly measured (Lika et al., 2011a). Nevertheless, they can be connected to measurable quantities such as length, weight, oxygen consumption or reproductive output through auxiliary theory (Lika et al., 2011a). Understanding the concept of auxiliary theory is one of the crucial bottlenecks stated in the earlier stated representation challenge. The goal of DEB auxiliary theory is to provide equations that transform abstract quantities associated to DEB theory into real-world measurements.

A simple example is that of length. Structural length L is the cubic root of structure V, and cannot be directly measured. To connect

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[2] The nitrogenous waste depends on the organism, it is typically ammonia (NH_3) for aquatic organisms and uric acid ($C_5H_4N_4O_3$) or urea ($CO(NH_2)_2$) for terrestrial organisms.

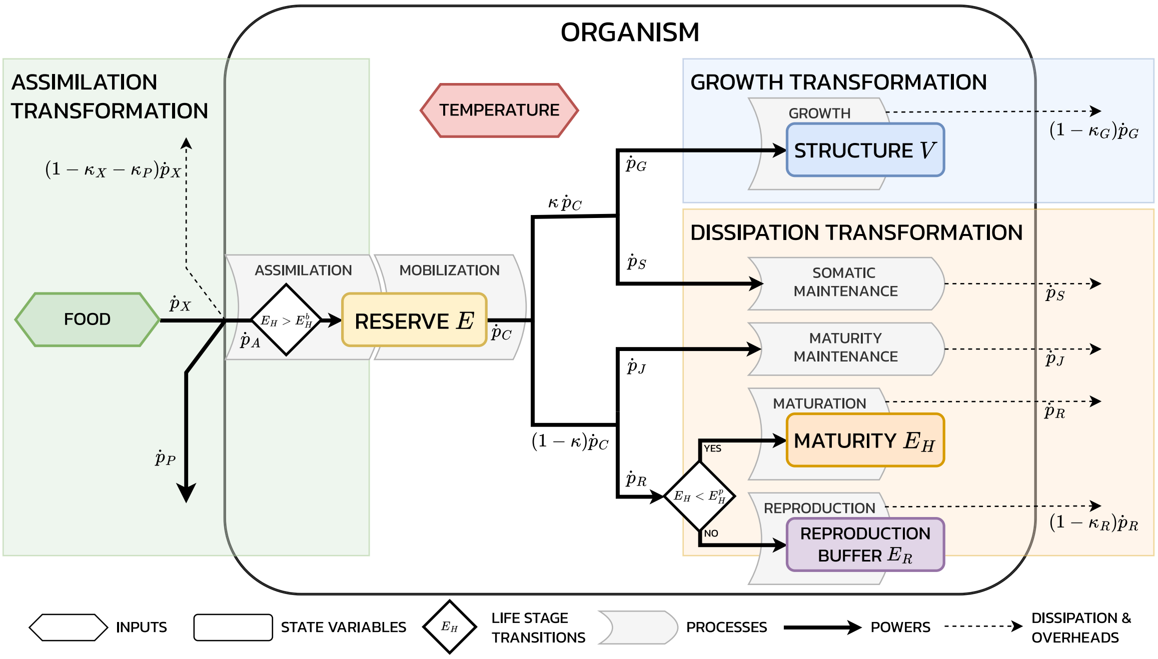

Fig. 2. A diagram of the standard dynamic energy budget model.

structure V to a measured length L_w, a shape coefficient δ_M to is used:

$$L_w = L/\delta_M = V^{1/3}/\delta_M, \tag{1}$$

where δ_M is associated with type of length measurement, e.g., shell width and shell length will have different shape coefficients. Another common example is that of wet weight W_w, a model prediction that requires the values of three state variables:

$$W_w = d_V V + (E + E_R)\frac{w_E}{\bar{\mu}_E}, \tag{2}$$

where d_V is the wet density of structure, commonly taken to be equal to $1\,\mathrm{g\,cm^{-3}}$, w_E is the molecular mass of reserve, and $\bar{\mu}_E$ is the chemical potential of reserve. These three parameters are examples of chemical parameters as they represent chemical properties of organic compounds (reserve, structure, food, and feces) (Jusup et al., 2017; Jusup and Kearney, 2024).

Since DEB theory respects mass and energy conservation, and describes organisms throughout ontogeny, several measurable quantities can be modeled with DEB theory. These measurable quantities are often referred to as “implied traits” (Kearney et al., 2021). Over 200 different traits ranging from the aforementioned observed length, to age at birth, survival time when starved, and ultimate reproduction rate can be calculated. As the name suggests, these traits are implied by converting state variables and parameters to measurable quantities often through the application of auxiliary theory. Species-specific implied traits are also showcased in the Add-my-Pet collection website (Add-my-Pet, 2026a).

3. Steps in DEB model development

DEB models are representations of how organisms acquire and allocate energy and matter to growth, development and reproduction in response to environmental conditions throughout their life-cycle. As such, the primary objective when building a DEB model is not to achieve a perfect fit between calibration data and predictions, but instead, coherence: DEB models must remain consistent with known species physiology throughout ontogeny and across the ecologically relevant environmental conditions experienced by the species. This idea is a pillar of DEB model calibration and is known as the estimation-in-context principle (Lika et al., 2011a; Kooijman et al., 2024).

Building a DEB model starts with linking an organism’s biology to an appropriate model structure (Section 3.1). The structure will then inform what data can be used for calibration and how it should be collected (Section 3.2). After implementation (Section 3.3), the model can be simulated (Section 3.3.1) and compared with real-world data via auxiliary theory (Section 3.3.2). Predictions of calibration data allow the estimation of parameters (Section 3.4). The parametrized model must then be validated while considering the estimation-in-context principle (Section 3.5). Finally, the modeling process should follow best practices to be reproducible and transparent (Section 3.6).

Models are often developed with specific goals and research questions in mind, e.g., “How will fish populations change with increasing temperatures driven by climate change?” or “How will polar bear food access and reproduction be impacted by reduced sea ice cover?”. These goals guide the model development and will help determine the appropriate level of detail. However, research questions can only be answered appropriately with a coherent and realistic DEB model. For this reason, DEB modeling is an iterative process that often requires revisiting assumptions and re-estimating parameters until the model is consistent with the species biology, the available data, and the intended use (see Fig. 1).

3.1. Model design

Model design is the first step in DEB model development and focuses on translating the biology of the species into a DEB representation suitable for the research question. In this section, we discuss how to identify the relevant life stages (Section 3.1.1), choose an appropriate typified model (Section 3.1.2), and decide whether additional modules or extensions are needed (Section 3.1.3). These choices determine which processes are represented explicitly and provide the basis for subsequent data collection, implementation, calibration, and validation. Although model design is presented here as a sequence of decisions, later steps may require revisiting the model structure and its underlying assumptions.

3.1.1. Identifying life stages

The life cycle of an organism can be described as a series of life stages, where each transition between stages is associated with major changes in form or function. In DEB theory, ontogeny can be described as a series of building blocks, called functional life stages, together with the logical conditions that govern the transitions between them.

Functional life stages are defined by stage-specific dynamics (e.g., feeding vs. non-feeding, reproductively immature vs. allocating to reproduction) and by the assumptions that apply during that period. The most common functional life stages are egg, juvenile, and adult. Some organisms may need other functional life stages, such as fetus, baby, pupa, or imago, or additional variants to account for processes such as metabolic acceleration or the absence of growth. For example, many fish exhibit a period with increased growth rate after birth (Pecquerie et al., 2009; Lika et al., 2014b), and holometabolous insects pass through a pupal stage before emerging as an imago (Klagkou et al., 2024a,b).

In DEB theory, transitions are events or conditions dependent on the values of the state variables that define when the model switches from one set of stage-specific dynamics to the next. The most common type is maturity thresholds, defined as conditions on the value of the maturity state variable E_H.

To fully represent the energetics of an organism over its life cycle, the qualitative behavior of each real-world life stage must be matched to its equivalent DEB functional stage. Here, the distinction between morphological and functional life stages is important. Morphological life stages are defined by recognizable changes in form or developmental milestones such as birth, hatching, weaning, or molts. As such, most collected data refer to morphological rather than functional life stages (Kearney et al., 2021). Morphological and functional life stages might not always align, and care must be taken when mapping one to the other.

Similarly, life-stage transitions may not correspond to changes in morphology. Instead, they are best identified by changes in behavior, as these are more directly linked to the underlying processes. Nevertheless, morphology and function are connected, and changes in morphology often hint at shifts in energetic dynamics.[3] An illustrative example is given in Box 2: for zebrafish, hatching marks a morphological transition, whereas the functional transition (birth) occurs later, once feeding starts after the loss of the yolk sac.

3.1.2. Choosing a typified DEB model

A simple and robust starting point for choosing a model structure is to use a typified DEB model. Typified models are prebuilt model structures that specify a sequence of functional life stages and transitions between them. As mentioned earlier, these structures summarize key patterns in life histories and have been applied extensively across species in the Add-my-Pet (AmP) collection (Marques et al., 2018). They provide a practical default structure that allows comparability of parameter estimates across taxa (Kooijman et al., 2021; Augustine et al., 2019; Kooijman et al., 2020; Tan et al., 2026).[4]

Typified DEB models can be grouped into three classes, identified by the first letter of their three-letter acronym. The `s`–models are the closest to the standard DEB model and can have modifications such as fetal development or non-feeding and non-growing stages. The `a`–models apply to most species with a larval species and are characterized by a period of metabolic acceleration starting at, or soon after, birth and ending around morphological metamorphosis. The `h`–models are mainly used for holometabolous insects and include additional functional life stages, such as pupa and imago. Appendix B lists each existing typified model, their functional life stages, and transitions between them.

In practice, choosing a typified model often starts by checking taxonomically similar species in AmP. Taxonomically similar species are likely to have similar ontogenies and consequently can be represented by the same typified models. For instance, most fish species are modeled using the `abj` typified model, which captures metabolic acceleration after birth. Appendix B lists common taxa alongside the typified models most frequently used to represent them; the cited sources provide further details on each typified model.

Finally, the functional life stages of the chosen typified DEB model should be checked against the ontogeny of the organism to verify that they match, whilst taking into account the considerations discussed previously. Although taxonomy is often sufficient to determine an appropriate DEB model structure, it may not lead always to the best choice, particularly for underrepresented taxa in the AmP collection. Additionally, existing choices of typified models in AmP should be critically evaluated as to whether the choice was driven by biology or by limited data availability. Since building a model is an iterative cycle, assumptions about life stage should be re-evaluated throughout the modeling process.

3.1.3. Adding modules and extensions

Although most DEB applications can be addressed with a typified model, some research questions may require additional levels of detail. DEB theory is explicitly modular, and several extensions have been developed that seamlessly integrate with the core framework. In general, these additions either introduce new metabolic pathways or refine mechanisms already present in typified DEB models.

Common extensions included in DEB models introduce mortality processes, namely aging and starvation (Kooijman, 2010, pp. 214–221, 114–124, respectively). While starvation mortality emerges as an endogenous process from DEB dynamics, the aging module introduces an additional hazard rate to simulate senescence allowing, for example, to predict species intrinsic lifespan.

In ecotoxicology, DEB models are often coupled with toxicokinetic–toxicodynamic (TKTD) modules that link exposure to physiological effects (Jager et al., 2006; Augustine et al., 2012; Jager et al., 2023; Klagkou et al., 2026a). Other modules target specific structures or byproducts, such as methane production (Marques et al., 2020), otolith formation (Fablet et al., 2011), or shell growth (Klok et al., 2014; Stechele and Lavaud, 2024). Advanced DEB models with multiple reserves and structures have also been proposed for higher plants (Schouten et al., 2020), phytoplankton (Lorena et al., 2010; Livanou et al., 2019), macroalgae (Lavaud et al., 2020; Venolia et al., 2020; Lagunes et al., 2026), and corals (Muller et al., 2009).

Extensions have been developed to add more detail to feeding (Stavrakidis-Zachou et al., 2025), starvation (Augustine et al., 2011b; Klagkou et al., 2024b), and reproduction (Llandres et al., 2015; Marn et al., 2022b; Firkus et al., 2023). DEB models have also been integrated into individual-based modeling (IBM) approaches (Martin et al., 2012; Desforges et al., 2019; Donati et al., 2026) and coupled with other biophysical models (Kearney and Porter, 2020; Lagunes et al., 2025).

Modules and extensions increase the detail with which biological processes can be described. However, the increased detail often comes with the requirement to estimate additional parameters which can lead to increased uncertainty. For this reason, we recommend simplicity: modules and extensions should only be added when they are specifically required to answer the research question.

3.2. Data collection and assessment

When building a DEB model for a given species, it is strongly recommended to establish a data collection plan beforehand. The chosen DEB model structure and research question determine which observations are needed, while data availability constrains what parameters can be calibrated. Here, we first discuss how to plan data collection (Section 3.2.1) and then how to assess whether the available data are sufficiently informative, reliable, and consistent for model calibration (Section 3.2.2). Later, Section 3.4.2 will discuss how available data impact the calibration process.

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[3] Morphological transitions can nevertheless be tracked as developmental milestones, for example as maturity thresholds, if they are of interest to the research question. See Augustine et al. (2011a) for an example for zebrafish larval development.

[4] A comprehensive list of comparative energetics works is available at https://debportal.debtheory.org/docs/DEBpapers.html.

Box 2. DEB model structure for zebrafish.

Life stages. The life-history of zebrafish is shown in Fig. 3. After fertilization, zebrafish embryos develop externally and progress rapidly through early stages, reaching hatching within 2–3 days (Best et al., 2010). Larvae begin swimming and feeding 1–2 days after hatching, while continuing to develop. From a DEB perspective, birth is defined as the moment the organism starts feeding, and therefore happens 1–2 days after hatching (Augustine et al., 2011a). After birth, zebrafish experience accelerated growth (Schilling, 2002; Eaton and Farley, 1974a). Only after growth slows down do zebrafish mature and start to reproduce (Eaton and Farley, 1974b).

Typified model. Most fish are modeled with an `abj` typified DEB model, including all species of the Danionidae family and the Cypriniformes order present in the AmP collection. This typified DEB model is characterized by accelerated growth after birth, which is consistent with growth data (see Box 3).

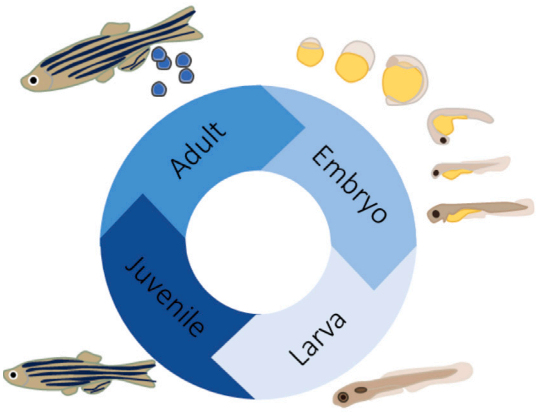

Fig. 3. Life-history and developmental milestones of zebrafish.

Modules and extensions. Temperature effects are modeled with the 1-parameter Arrhenius relationship (see Eq. (A.1)). Food intake follows a scaled functional response based on food density in the environment (see Eq. (A.2)). To predict lifespan, we also include the aging module (Kooijman, 2010). To properly model reproduction over time and the weight associated with eggs, we consider the egg-laying module of Llandres et al. (2015). This module introduces a maximum value to the reproduction buffer, adds a state variable to account for the energy in eggs and has no extra parameters.

3.2.1. Planning data collection

When planning data collection, a useful starting point is the completeness scale proposed by Lika et al. (2011b). This scale ranges from 0 to 10 and describes increasing levels of data required for DEB parameterization. At the highest level, it includes growth in length and weight, respiration, ingestion, mass and energy balances over ontogeny, data at all life stage transitions, and observations at multiple food levels. Additionally, this data should also be collected across a range of temperatures to capture thermal response effects (Cheng et al., 2025). The main objective of data collection should be to obtain all these data types. Although such completeness is yet to be achieved in practice, the scale provides a concrete reference for deciding which data should be prioritized.

Observations at major life stage transitions, such as age, length, and body mass at birth, metamorphosis, puberty, and other life stage transitions, are often accessible and are important for identifying changes in DEB dynamics. Trajectories describing growth, reproduction, feeding, and respiration over time are more difficult to obtain, but directly inform model dynamics and are therefore highly valuable for model calibration.

Several types of measurement collected under the same environmental conditions are more informative than measurements of the same type collected under different and often unknown conditions. This reduces parameter uncertainty associated to the environmental conditions and allows the datasets to provide more information on parameter values (Kooijman et al., 2008; Lika et al., 2011a; Cheng et al., 2025). Environmental conditions are also part of the measurements and should be collected alongside biological observations, particularly for field data, as this directly mitigates the issue described. Therefore, the ideal scenario is to have multiple types of data collected under different and measured environmental conditions.

DEB models describe an individual organism, but the available data may come from individuals, cohort means, populations or species-level summaries. A common assumption when building a DEB model for a species is to disregard individual variability and assume that data from one individual or averaged from a sample of individuals both adequately characterize the species' physiology (Oliveira et al., 2024). Consequently, individual variability will be a source of uncertainty and error in model predictions (Marques et al., 2019). Whether this assumption is acceptable will depend on the collected data and its degree of variability, as well as the required accuracy. On the other hand, if the objective is to model and describe inter-individual variability, then this assumption should be avoided and individual-level data and/or means and deviations can be used to estimate DEB parameters at the individual level (Palmer et al., 2024; Oliveira et al., 2024).

A data collection plan should also assume that several sources may need to be combined. Relevant data may come from literature, reports, databases, museum archives, laboratory experiments, and field observations. For long-lived species in particular, combining multiple sources is often unavoidable given that a single study rarely covers the full life cycle unless experimentally designed to do so. These sources can be used within the same model, but particular attention should be paid to the consistency of the data (see next subsection).

If major data gaps remain, data from closely related species can sometimes be used as a proxy, but it is less reliable and should be used with caution along with a deep knowledge of the life-history of both species.

3.2.2. Assessing the available data

After data have been collected, they should be evaluated as a whole for scope, reliability, and consistency. The quantity and quality of the available data influence which parameters can be estimated (see Section 3.4.2). If the research question requires estimating parameters that cannot be informed by the available data, then additional data collection is likely necessary.

When multiple data sources are combined, consistency becomes a central issue. Differences in environmental conditions are often the main cause of inconsistency. Temperature and food often differ among studies and are not always measured with sufficient detail. This is particularly relevant when laboratory and field data are included in the calibration data (Cheng et al., 2025). If some measurements are inconsistent with one another and there is insufficient information to resolve them, we recommend not including some datasets in the calibration, giving priority to higher quality datasets. Here, data quality should not be interpreted only as higher resolution or greater numerical precision. It should be assessed using explicit criteria, namely the agreement with other sources, the presence of outliers, the measurement protocol, and the completeness of the reported environmental conditions. Importantly, care should be taken to avoid modeler bias in data selection (Holländer et al., 2009; Jakeman et al., 2024).

Consistency checks should also include reporting conventions and measurement definitions. For example, body mass data should specify whether they refer to wet or dry mass and whether gonads are included; length data should specify the measurement method (e.g., standard, fork, or total length for fish); time-based data should specify the time unit and the reference point (e.g., age since fertilization or since birth).

Graphical exploration can help detect unit mismatches, apparent outliers, implausible values, and conflicts among datasets, but it cannot resolve missing experimental details, such as food conditions or measuring methods, which are crucial to obtain accurate model predictions. When such details are lacking, the resulting uncertainty should be considered during model validation. Since inconsistent data sources can increase parameter uncertainty, prediction errors may then reflect data limitations rather than model performance. As such, it should be considered when weighting datasets during the calibration process, as datasets with an increased weight coefficient will have a stronger influence on parameter estimates (Marques et al., 2019, see also Section 3.4.1).

3.3. Model implementation and usage

With a defined model structure, the next step is to implement and use the model. Here, we distinguish two paradigms: simulation and prediction. Simulation consists of solving the model differential equations under conditions specified by the modeler (Section 3.3.1). In prediction, the objective is to obtain a model output that can be compared with measured data. To get predictions, the DEB model is simulated followed by the application of auxiliary theory to translate state variables into measurement predictions. Prediction often requires dataset-specific assumptions (Section 3.3.2), and is the foundation of model calibration (Section 3.4).

3.3.1. Model simulation

The DEB model represents a life cycle as a series of functional life stages, each with its own dynamics, which can be described as a system of differential equations (see Section 3.1 and Appendix A). To implement the model, each system of differential equations is coded in a programming language and then integrated with a differential equation solver, taking care to implement the transitions between life stages. For DEB simulations, adaptive non-stiff solvers such as MATLAB's `ode45` are often sufficient (Shampine and Reichelt, 1997). Solver tolerances should be checked to ensure that numerical error does not affect model predictions or parameter estimation and consequently the derived insights (Creswell et al., 2024). To recover states at life stage transitions or other developmental milestones, event functions that check logical expressions of state variables can be used.

In practice, we recommend using established software for DEB modeling. Most modelers rely on `DEBtool` (Add-my-Pet, 2026b), a regularly maintained MATLAB package that provides a comprehensive set of functions to implement and calibrate DEB models and serves as the core software underlying the AmP database. Alternative implementations exist in other programming languages. In R, the `NicheMapR` package provides a DEB model implementation (Kearney and Porter, 2020). Parts of `DEBtool` have also been translated into Julia and are currently being developed as a Julia package (Add-my-Pet, 2025).

To simulate the model, the necessary inputs are: (1) an initial state, and (2) environmental conditions over time (e.g., food and temperature).[5] The initial states are the values of the state variables when the simulation starts and they are usually chosen to be the state at fertilization or at a life stage transition. The environmental conditions are often kept constant at pre-specified values, but variable-condition scenarios allow for studies under realistic conditions, either hindcasted or forecasted. This enables the assessment of their effect on growth, maturation, reproduction, and other life-history traits (Gourault et al., 2019; Mangano et al., 2020).

Simulations can also be used to understand the effects of inter-individual variability, for example by varying initial states or assigning individual-specific parameter values (Stavrakidis-Zachou et al., 2019; Accolla et al., 2019; Marn et al., 2022b; Klagkou et al., 2026a). From a broader perspective, DEB models can be embedded in population and individual-based models, allowing individual energetics to scale up to emergent population dynamics and supporting applications such as ecological risk assessment and climate-change analyses (Martin et al., 2012, 2013; Desforges et al., 2019; Donati et al., 2026).

3.3.2. Dataset predictions

When simulating a DEB model to obtain predictions for a dataset, two frameworks must be linked: the "real world", where measurements are collected, and the "abstract world", where models and theory are formulated (Lika et al., 2011a; Le Moan et al., 2024; Lagunes et al., 2026).

In the "real world", data describe the environmental conditions and life-history traits of the organism. In the "abstract world", the organism is described by the state variables which are subject to the model inputs, i.e., the environmental conditions, and parameters. To bridge these two worlds, auxiliary theory is needed (Section 2.3).

Dataset predictions can be obtained by considering four steps:

Step 1: Determine the initial state.
Step 2: Define environmental conditions over time.
Step 3: Simulate the DEB model differential equations to obtain state variable values over time.
Step 4: Apply auxiliary theory to transform state variables into dataset predictions.

Box 3 exemplifies each of these steps for a length dataset of the zebrafish estimation.

To simulate the DEB model to obtain dataset predictions, the initial state must be given. Information about the initial state can be derived from the available data based on experimental knowledge, however, in most cases assumptions must be made to fully specify the initial state. Commonly, a DEB model can be initialized in three ways:

- **Fertilization**. Under the maternal effect assumption, offspring reserve density at birth equals maternal reserve density $[E]_{maternal}$ at egg formation. For egg development, this allows the calculation of the initial reserve (E_0) at time zero, where the reserve density is also assumed to be infinite. In practice, this becomes equivalent to setting the initial structure to a very small value. In fetal development, the organism is supplied the required energy and the reserve density at birth is constant throughout development. By setting a very small value for the initial structure V_0, the initial reserve can then be derived as $E_0 = V_0[E]_{maternal}$. For the other state variables, namely maturity E_H and reproduction buffer E_R, they are initially set to 0.
- **Life stage transition**. A simulation is run until a given transition to generate the initial state variables. This requires assumptions about the environmental conditions experienced beforehand, which are often taken as constant and equal to those of the dataset being predicted. If the life stage transition is "birth", then the environmental conditions experienced by the mother will determine its state and consequently, through the maternal effect, the state of the organism at birth.
- **Initial measurement**. The model is initialized at the first observed data point (e.g., length or weight), and auxiliary theory is used to infer the corresponding state variables. This requires some assumptions on the state variables to determine their value. The most common approach is to assume that the scaled reserve

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[5] In DEBtool, the function `simu_my_pet` can be used for model simulations.

density is equal to the scaled functional response, ($e = [E]/[E_m] = f$). This hinges on food availability having remained constant long enough for the reserve density to reach equilibrium, for example, after an acclimation period to an experimental diet. The scaled reserve density can then be used to compute structure (V) and reserve (E) from the initial length or weight. The maturity E_H and the reproduction buffer E_R are inferred from the development of the organism.

We recommend simulation from fertilization or birth when early life data are available under the same environmental conditions or when a full life-history simulation is desired. For adult data, initializing at first measurement is recommended as it avoids making assumptions about past life history. If a food acclimation period was employed in the experimental setup, the reserve density assumption also becomes more accurate, as it will tend towards the food level of the experiment. However, this requires setting the maturity to its maximum (E_H^p) and inferring the value of the reproduction buffer E_R.

In the “real world” environmental conditions influence organism life-history traits, yet are often available only as snapshots rather than continuous records. Therefore, explicit assumptions are required to convert these observations into continuous environmental condition functions that can be used as inputs for model simulations. Interpolation methods, such as linear or higher order splines, can piece together sparse measurements (Lavaud et al., 2014), while Fourier transforms can be used to turn seasonal records into periodic functions (Pecquerie et al., 2009). In both cases, the simplest adequate representation should be preferred, since noise or artifacts in environmental inputs can propagate through the model and lead to unintended behavior. For sparse records, linear interpolation is often sufficient and less prone to artifacts than higher-order splines. For sparse records, linear interpolation is and less prone to artifacts than higher-order splines and for periodic records, retaining only a few dominant frequencies is often sufficient.

In the absence of data on environmental conditions, temperature and food are kept constant. Temperature is frequently controlled, so if the experiments report a constant temperature, then it should be used. Conversely, food intake is often hard to measure precisely. In these cases, a constant scaled functional response can be estimated or reconstructed from available data (Freitas et al., 2009; Pecquerie et al., 2012; Lavaud et al., 2019). Detailed recommendations for estimating dataset-specific scaled functional responses are discussed in Section 3.4.2.

To apply auxiliary theory, the key is to use the correct equation to translate state variables to dataset predictions. These equations can be found in theory descriptions (e.g., Kooijman, 2010), but can also be obtained from other AmP entries. We recommend searching for the required data type in entries with the same typified model in the AmP database,[6] and critically evaluating if what has been performed is adequate for the particular research question.

Under constant temperature and food, DEB models can sometimes be simplified, removing the need to integrate the differential equations. For example, in lifestages with isomorphic growth, the von Bertalanffy curve can be used to predict length at constant temperature and food conditions, thereby speeding up the computations. Although these simplifications are useful, care must be taken to ensure that they are applicable under the environmental conditions of the dataset and for the specific life stage being simulated.

The application of auxiliary theory can often be the source of mistakes. Below, we highlight some frequent pitfalls:

- **Unit conversions.** The parameters of the DEB model have units in joules [J], centimeters [cm], days [d], and mole [mol] (see Table A.6). Consequently, the DEB model outputs will be expressed in these units. Therefore, a final unit conversion may need to be made to match the units of the measured data.
- **Length measures.** Structural length must be converted to observed length with a shape coefficient (Eq. (1)). However, the general term length can have multiple meanings: for instance, it can refer to total length, fork length or standard length in fish; shell height, length or width in bivalves; body length or forewing length in insects; snout-vent length, tail length, or trunk length in lizards. If different methods are used to collect length measurements, then each requires a different shape coefficient. Additionally, the shape coefficient may change if isomorphism is not maintained throughout development.
- **Weight considerations.** Depending on the species, weight may be more commonly measured as ash free dry weight, dry weight, or wet weight. Predictions for these are computed with different equations and care must be taken that the correct one is employed. Moreover, weight is typically a function of just reserve and structure, but if the weight of eggs, gonads, or other reproductive reserves is relevant, the reproduction buffer (which is composed of reserve) should also be included in the weight computation.

Finally, it is often the case that multiple types of measurements (e.g., length and weight) were taken in the same environment or experiment. When this is the case, we recommend simulating the DEB model equation only once and then applying the corresponding auxiliary theory to compute predictions for each type of measurement from the simulated DEB state variables. This leads to fewer errors and assumptions and is more computationally efficient.

3.4. *Model calibration*

After model design and data collection, a DEB model is ready to be calibrated. In Section 3.4.1, we detail the AmP calibration procedure as it is the standard approach for model calibration used in the AmP collection (Lika et al., 2011a; Marques et al., 2019, 2018). Alternative calibration procedures exist, most notably Bayesian estimation (Johnson et al., 2013; Boersch-Supan et al., 2017; Palmer et al., 2024).

In addition to details on parameter estimation procedures, in Section 3.4.2, we discuss which parameters can be reliably estimated given available data. These considerations apply regardless of the estimation procedure employed and are crucial to obtain a coherent and realistic model.

3.4.1. *The parameter estimation problem*

The goal in building a DEB model is to promote coherence. Within this process, we have model calibration, where the objective is to obtain DEB model predictions that best match the available data. To achieve this, the deviation between the data $\mathcal{D}$ and the predictions of the DEB model $\mathcal{P}$ is quantified with the symmetric bounded loss function $\mathcal{L}_{sb}$ (Marques et al., 2019):

$$\mathcal{L}_{sb}(\mathcal{D}, \mathcal{W}, \Theta) = \sum_{i=1}^{|\mathcal{D}|} \sum_{j=1}^{|\mathcal{D}_i|} \frac{w_{ij}}{|\mathcal{D}_i|} \frac{\left(d_{ij} - p_{ij}\right)^2}{\bar{d}_i^2 + \bar{p}_i^2}, \tag{3}$$

with $\bar{d}_i = \frac{1}{|\mathcal{D}_i|} \sum_{j=1}^{|\mathcal{D}_i|} d_{ij}, \quad \bar{p}_i = \frac{1}{|\mathcal{D}_i|} \sum_{j=1}^{|\mathcal{D}_i|} p_{ij} \quad \text{and} \quad p_{ij} = f_i(\Theta),$

where $\mathcal{D}_i$ is a dataset with $|\mathcal{D}_i|$ data points. Here, the distinction between zero- and multivariate datasets is useful. Zero-variate datasets contain a single data point ($|\mathcal{D}_i| = 1$) and often correspond to measurements at life stage transitions or maximum size. Multi-variate datasets have multiple data points and are often composed of measurement

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[6] The AmP documentation (https://amptool.debtheory.org/docs/) suggests some useful ways to query the database for data types or code snippets.

Box 3. Dataset prediction example for a length growth curve.

Dataset. Growth trajectory (length vs time since fertilization) under two different food levels is from Lawrence et al. (2008). Fig. 4 outlines the correspondence between the "real world" of data and the "abstract world" of DEB model predictions.

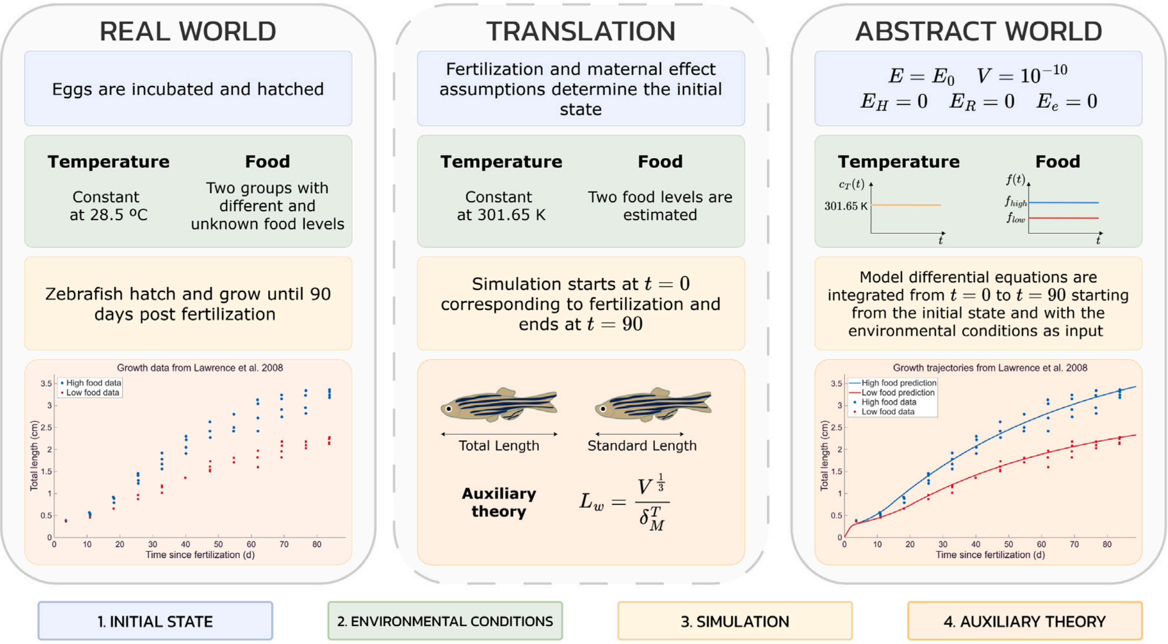

Fig. 4. Steps to obtain DEB model predictions for a growth length trajectory.

Initialization. Simulation starts at fertilization. The initial reserve E_0 is computed with the maternal effect assumption. We assume a scaled reserve density $e_{maternal} = f = 1$ for the mother because eggs are bought from a commercial supplier. The initial structure is a very small value ($V = 10^{-10}$). All other state variables (maturity E_H, reproduction buffer E_R, and egg buffer E_e) start at 0.
Environmental conditions. Temperature is kept constant at 28.5 °C. Food intake is unknown, so both scaled functional responses are estimated from post hatch data alongside organism parameters.
Simulation. The differential equations are integrated from the initial state at fertilization until the final time measurement at $t = 90$d.
Auxiliary theory. The values of structure V over time are converted to observed total length with Eq. (1). The type of length needs to be carefully considered; since the measurements are of total length, the total length shape coefficient is applied here. Length is measured in cm and time is measured in days, so no unit conversions are needed.

values either as a function of time or of others measurements (Oliveira et al., 2026).

The loss function quantifies the error of each prediction p_{ij} to its respective data point d_{ij} with the squared error $\left(d_{ij} - p_{ij}\right)^2$. Each prediction is obtained from a prediction function f_i of the parameters Θ. This function f_i, corresponds to simulating the DEB model differential equations and applying the appropriate auxiliary theory to convert the state variables to measurements, in accordance with the recommendations given in Section 3.3.2.

The prediction squared errors for all data points are normalized by dividing by the sum of the mean of the data and predictions, which bounds the loss contribution of each dataset. The normalized errors are then weighted by a set of weights $\mathcal{W}$. Weights are often set to 1 (all data points contribute equally), however they should be adjusted based on the quality or relevance of the data (see Section 3.2). Additionally, the normalized errors are divided by the size of the dataset, which results in datasets with equal weights contributing the same regardless of their size. Therefore, when using default weights of 1 for all data points, zero-variate datasets are as relevant as multi-variate datasets.

The purpose of a loss function is to quantify the deviation between the DEB model prediction and the data. This is transformed into an optimization problem with the aim of finding the parameter values Θ that minimize the loss value. The parameter values must also respect some constraints that ensure the model is biologically realistic (Lika et al., 2014a). For example, the organism simulated by the DEB model must be born and go through puberty in order to reproduce. If these conditions were not met, the organism could never exist and therefore the DEB model would not be realistic. Most constraints are a consequence of the typified model of the species, but certain datasets may require that additional constraints are satisfied. To enforce these constraints during parameter estimation, filter functions should be implemented to exclude parameter sets that do not respect the necessary conditions.

To efficiently search through parameter values, an optimization algorithm is used. In AmP estimation, the most common is the Nelder–Mead simplex algorithm (Nelder and Mead, 1965), although alternatives have been proposed (Robles et al., 2023). The Nelder–Mead method is sensitive to initial values and its performance deteriorates with increasing dimensionality, i.e., the number of parameters being estimated. To counteract these issues, the method is often serially restarted to improve convergence. An implementation of this Nelder–Mead variant is provided in the accompanying paper code.

Due to parameter constraints and numerical instabilities, the estimation may end in an execution error or get stuck being unable to solve the differential equations. Additionally, it is likely that the search stops at a local minimum where the deviation is acceptable. This is why after parameter estimation, it is crucial that model validation is performed (see Section 3.5).

Choosing the initial parameter values of the estimation helps attenuate these issues. A simple method for initialization is to look up in the AmP collection the parameters of a taxonomically close species, since it is expected that their parameter values are similar. An alternative is to use the recently proposed method of Oliveira et al. (2026) that is based on machine learning techniques. This method only works for the `s-` and `abj` typified models and it requires that zero-variate data at life stage transitions are available.

3.4.2. Which parameters can be estimated?

A comprehensive DEB calibration requires multiple data types collected across life stages and environmental conditions to accurately estimate all model parameters. This amount of data is best expressed by the completeness scale: a maximum value of 10 would allow the estimation of all core parameters of the DEB model as well as detailed composition of all organic compounds (Lika et al., 2011b). However, maximum completeness has never been achieved in practice, with 6 for *Daphnia magna* being the maximum value currently in the AmP collection. As a consequence of missing data, some parameters are not estimated but are instead fixed at default values.

The parameters most commonly estimated are those strongly informed by data most commonly available: life-history, growth, and reproduction datasets: the core parameters $\{\dot{p}_{Am}\}$, $\dot{v}$, κ, $[\dot{p}_M]$, $[E_G]$, and the maturity levels (e.g., E_H^b, E_H^j, E_H^p) (van der Veer et al., 2006; Kooijman et al., 2008; Accolla et al., 2020). Appendix A shows how these parameters appear in the standard DEB model. If an aging module is included, the parameter Weibull aging acceleration $\ddot{h}_a$ can be estimated from lifespan data, while the Gompertz stress coefficient s_G can be estimated from data on survival over time.

If food conditions are uncertain, a scaled functional response f can also be estimated for a given experimental setup or environment. The reliable estimation of these scaled functional responses benefits considerably from having multiple data types measured under the same conditions. Conversely, when a scaled functional response f is estimated from a single dataset, with no other under the same conditions, its value will not be constrained by the other datasets. Predictions will be dominated by the estimated value of f, and the optimization will adjust it mainly to reduce the errors in that dataset alone. Therefore, it will distort estimates of the core parameters. Furthermore, it is also helpful to have multiple datasets of the same type across different conditions, so that changes in f predictions can be consistently attributed to changing food levels (e.g., several length curves from different sources).

For the remaining parameters, the main limitation is identifiability, both structural and practical (Marques et al., 2019; Oliveira et al., 2026). A parameter is structurally identifiable if it can be uniquely recovered, given the model equations and auxiliary theory, from ideal data (Wieland et al., 2021; Guillaume et al., 2019; Raue et al., 2010). Here, ideal data means exact, noise-free observations for a specified set of datasets and experimental conditions. Therefore, a parameter may be structurally identifiable under one set of observations but non-identifiable under another. Practical identifiability asks a different question: whether a structurally identifiable parameter can be estimated with acceptable precision from the real data available for calibration, which are finite, noisy, and often incomplete (Wieland et al., 2021; Lika and Kooijman, 2024).

If a parameter is absent from the prediction functions used to compute dataset predictions, then it cannot be estimated regardless of the optimization effort and is structurally non-identifiable. This is often the case for the digestion κ_X and defecation κ_P efficiencies. The parameter κ_X only appears in the prediction functions for food intake and in quantities related to mass and energy balances, therefore it can only be estimated it those data are included in the calibration. The same applies to κ_P, if in addition feces production data is not available. As a general rule, parameters that are not used to compute predictions are set at their default values.

Structural non-identifiability can also occur if multiple parameter combinations yield the same predictions. This frequently occurs for the maturity maintenance rate coefficient $\dot{k}_J$ and the reproduction efficiency κ_R, where life-stage timings, size trajectories, and reproduction data alone are not enough to estimate these parameters. Doing so requires reproduction data collected at multiple known food levels, ideally including ingestion, which is typically difficult to obtain Kooijman et al. (2008). As such, these parameters might also be kept at their default values.

Structural identifiability alone does not guarantee reliable estimation. A parameter may appear in the prediction functions and be identifiable in principle, while still being weakly constrained by the available calibration data, i.e., it is practically non-identifiable due to noisy or incomplete data. When these parameters are estimated, there are regions of the parameter space where the loss function, which measures deviation from the data, changes negligibly, but model behavior changes drastically for other (absent) predictions. Low practical identifiability can be mitigated through the inclusion of better data in the calibration, prior knowledge of parameter values, or in the case of AmP estimation, with the use of pseudo-data (Lika et al., 2011a; Marques et al., 2019; Oliveira et al., 2024).

Pseudo-data correspond to parameter values of a "generalized organism" and take on the form of zero-variate datasets in the loss function, i.e., they are reasonable *a priori* guesses for the parameter values. In `DEBtool`, pseudo-data are set to default values automatically (see Table A.6). Unless the estimation procedure is failing to converge, the values (and loss-function weights) of pseudo-data should be left untouched. AmP estimation guidelines recommend only one exception to changing pseudo-data: in the absence of sufficiently complete data, the maturity maintenance rate coefficient $\dot{k}_J$ should be fixed at $0.002\,\mathrm{d}^{-1}$ when the calibrated volume-specific somatic maintenance rate $[\dot{p}_M]$ is likely to be larger than $18\,\mathrm{J}\,\mathrm{d}^{-1}\,\mathrm{m}^{-3}$. If $[\dot{p}_M]$ is likely to be smaller than $18\,\mathrm{J}\,\mathrm{d}^{-1}\,\mathrm{m}^{-3}$, then $\dot{k}_J$ should be estimated and pseudo-data should be applied to the maintenance ratio $k = \dot{k}_J / \dot{k}_M = 0.3$, where $\dot{k}_M = [\dot{p}_M] / [E_G]$, and $[E_G]$ is the volume-specific cost of structure. This will tend to result in a calibrated model with predictions that better align with observed biological patterns (Kooijman, 2025; Verhille and Kooijman, 2026). When these and other modifications to pseudo-data are made, the choices for the new values should be explicitly justified.

As a general rule, a simpler calibration is usually more robust. Estimating fewer parameters that are clearly supported by the available data is preferable to estimating many parameters with low confidence. Additional parameters should only be estimated if the model predictions are consistently off, even when environmental conditions are accounted for. The choice of additional parameters to estimate should be guided by the combined knowledge of model behavior and species ontogeny, and could be aided by tools such as sensitivity analysis (Matyja, 2023). In Box 4, we exemplify the above recommendations for the two zebrafish calibrations.

3.5. Model validation

After parameter calibration, the next step is model validation. While the estimation procedure will find parameters that minimize the deviation between DEB model and calibration data, it is up to the modeler to decide whether the deviation is acceptable. Moreover, following the estimation-in-context principle, model calibration aims to ensure a coherent and realistic DEB model across ontogeny and variable environments.

With this principle in mind, model validation can be performed both quantitatively (Section 3.5.1) and qualitatively (Section 3.5.2). Quantitative validation involves assessing the quality of the estimation through error metrics and confidence intervals. Qualitative validation instead asks whether the estimated parameters are reasonable both by comparing with other estimations in the AmP collection and by checking for unrealistic model behavior.

Box 4. Parameter estimation for zebrafish.

Estimation procedure. Initial parameters were obtained with the `DEBInitNet` method (Oliveira et al., 2026). To estimate the parameters, we applied the Nelder-Mead algorithm with an initial simplex size of 0.25. The algorithm was serially restarted after 500 steps, alternating the initial simplex direction until the loss improvement after two consecutive Nelder-Mead runs was less than 10^{-4}.

Parameters estimated in each zebrafish calibration. Table 2 presents the estimated parameters. The parameters $\dot{k}_J$ and κ_R cannot be estimated because energy balances are not available. In the data-rich calibration, oxygen and feeding data allows the estimation of the efficiencies κ_X and κ_R which are connected to the assimilation transformation. The Gompertz stress coefficient s_G cannot be estimated because only lifespan informs the aging parameters. For the data-limited calibration, standard length is kept at 80% of total length due to lack of data (Augustine et al., 2011a).

Table 2. Estimated parameter values for each zebrafish calibration. Underlined values represent parameters not estimated that were set to default values.

Parameter		Data-limited	Data-rich	Units
Core parameters				
$\{\dot{p}_{Am}\}$	Surface-specific maximum assimilation rate	169.42	138.59	$\mathrm{J\,d^{-1}\,cm^{-2}}$
κ_X	Digestion efficiency	0.8000	0.7154	–
κ_P	Defecation efficiency	0.1000	0.2094	–
$\dot{v}$	Energy conductance	0.0157	0.0276	$\mathrm{cm\,d^{-1}}$
κ	Allocation fraction to soma	0.2833	0.3093	–
$[\dot{p}_M]$	Volume-specific somatic maintenance rate	251.98	155.96	$\mathrm{J\,d^{-1}\,cm^{-3}}$
$[E_G]$	Specific cost for structure	5217.4	5272.5	$\mathrm{J\,cm^{-3}}$
$\dot{k}_J$	Maturity maintenance coefficient	0.0020	0.0020	$\mathrm{d^{-1}}$
E_H^b	Maturity at birth	0.3577	0.8756	J
E_H^j	Maturity at metamorphosis	9.4048	19.394	J
E_H^p	Maturity at puberty	1243.9	3808.9	J
κ_R	Reproduction efficiency	0.95	0.95	–
Aging parameters				
$\ddot{h}_a$	Weibull aging acceleration	2.341e–9	1.995e–9	$\mathrm{d^{-2}}$
s_G	Gompertz stress coefficient	1e–4	1e–4	–
Auxiliary theory parameters				
δ_M^T	Shape coefficient for total length	0.0933	0.1406	–
δ_M^S	Shape coefficient for standard length	0.1166	0.2163	–

3.5.1. Quantitative validation

The estimation procedure finds parameters that minimize the overall deviation between the DEB model and the data, therefore it is important to assess the errors for each dataset individually. The most common error metric used is the mean relative error (RE):

$$\mathrm{RE}(\mathcal{D}_i, \mathcal{P}_i) = \sum_{j=1}^{|\mathcal{D}_i|} \frac{|d_{ij} - p_{ij}|}{|d_{ij}|} \tag{4}$$

Similarly to the loss function, the relative error is less sensitive to the scale of the data. The mean relative error (MRE) for all calibration data is a useful metric of the quality of the estimation. In the AmP collection, most estimations have an MRE between 0.05 and 0.15. However, relative errors should be analyzed carefully when data values (d_{ij}) are close to zero, since small denominators can dominate the metric. In such cases, model evaluation can be complemented with symmetric and scale-independent metrics, such as the symmetric mean squared error (SMSE), the symmetric mean absolute percentage error (SMAPE), or with logarithmic difference metrics for strictly positive quantities (Oliveira et al., 2026).

Interpreting relative errors must be done with care as to how parameters affect the predictions of calibration data. A low relative error for a dataset does not necessarily imply that the parameters in the corresponding prediction function have been accurately estimated. If a parameter only appears in the prediction function of a single dataset, then it is likely that it will be adjusted mainly to minimize the error in that dataset. This should reduce confidence in the parameter estimate, since it may yield unrealistic predictions under different environmental conditions.

Additionally, the distinction between zero-variate (single data point) and multi-variate datasets (multiple data) is central for interpreting quantitative errors (see Section 3.4.1). For zero-variate datasets, it is more likely that relative errors are small because they consist of a single data point, particularly in the poorly constrained situations where a parameter only affects the prediction for one dataset. A common example is when the Weibull aging acceleration $\ddot{h}_a$ only appears in the prediction of the lifespan a_m, resulting in a near zero relative error (see Box 5).

For multivariate datasets, a low relative error may still yield unrealistic model behavior. It is therefore important to visually compare the DEB model simulation with the data to assess whether there are any patterns in the residuals. Additionally, data scatter can dominate error metrics and should also be taken into consideration when comparing errors between datasets.

Deviations between model and data should be quantified and linked to reasons as to why they occur. Only by doing so can the magnitude of the errors be put into perspective and help to judge whether any of the previous modeling steps need to be revisited. In general, the deviations between the DEB model and the data can be attributed to one of the following factors, in decreasing order of importance (Marques et al., 2019):

1. **Unknown environmental conditions**. When conditions are not measured, they must either be guessed or estimated. Both of these choices introduce assumptions that can lead to errors.
2. **Unknown experimental procedures**. Without knowledge of how measurements were made, the appropriate auxiliary theory

Box 5. Quantitative validation of data-limited estimation.

Lifespan prediction. Table 3 presents the relative errors for each dataset included in the data-limited estimation. The mean relative error of the estimation is of 0.127, while the prediction for the lifespan has a very low relative error of 0.0014. This is the only dataset informing the parameter $\ddot{h}_a$, which means that this parameter can be adjusted until the prediction for lifespan is equal to the data and the relative error approaches 0. To obtain a better estimate of $\ddot{h}_a$, survival data would need to be added to the estimation.

Table 3. Relative errors for each dataset in the data-limited estimation.

Dataset	Value	Prediction	RE	Units	Source
Age at birth a_b	5.00	4.55	0.0896	d	Best et al. (2010)
Age at puberty a_p	75.00	70.03	0.0662	d	Eaton and Farley (1974a)
Lifespan a_m	1642.5	1642.4	0.0001	d	Gerhard et al. (2002)
Total length at birth L_b	0.400	0.311	0.2231	cm	Schilling (2002)
Standard length at puberty L_p	2.60	2.87	0.1047	cm	Eaton and Farley (1974a)
Ultimate total length L_∞	5.00	5.82	0.1642	cm	Spence et al. (2008)
Ultimate wet weight W_∞^w	1.00	1.01	0.0149	g	Augustine et al. (2011a)
Ultimate reproduction rate R_∞	240	213	0.1098	$\# \mathrm{d}^{-1}$	Eaton and Farley (1974b)
Time-length curve $t - L$	–	–	0.0918	d–cm	Best et al. (2010)

Prediction tradeoffs. The largest errors are for the datasets age at birth a_b, length at birth L_b, and ultimate reproduction rate R_∞. Here, a tradeoff occurs: if birth occurred later, the length at birth would increase. This would require more energy for each egg, which would in turn reduce an already underestimated reproduction rate. A possible explanation for why this occurs is different environmental conditions between datasets, a hypothesis that is supported by each of these datasets having a different source. Estimating scaled functional responses for each dataset would be possible, but given that most sources only provide a single datapoint, it would likely lead to worse estimates of the core parameters.

may not be applied. Moreover, assumptions regarding the initial state will likely be incorrect.

3. **Individual variability**. Even within controlled experimental setups, individual variability will play a role and introduce scatter into the data. Individual parameters can be estimated, but assumptions associated with this procedure will still cause errors (Oliveira et al., 2024; Palmer et al., 2024).
4. **Stochasticity of physiological and ecological processes**. Standard DEB theory does not fully consider the underlying stochasticity of biological processes, so some data scatter can be attributed to this.
5. **Misalignment between model structure and biology**. DEB theory strives for the best compromise between realism and complexity (Kooijman, 2018, 2020b), but reality is often not simple and therefore detailed life-history processes may not be captured accurately by the model.
6. **Measurement errors**. All measurements have an associated error, which will contribute to the deviation between model and data. Scatter often depends on the type of data being measured; for respiration data, it tends to be large (Verhille and Kooijman, 2026).

A common situation is to have prediction tradeoffs for a group of datasets (Box 5). These are characterized by (1) larger relative errors than for the rest of the estimation and (2) an inability to improve the prediction for one dataset without worsening it for another. They are often caused by not accounting for different environmental conditions in the estimation, incorrect model structures, low practical identifiability of parameters, or even inconsistent data (e.g. due to incompatible measurements from different individuals). As such, they may require revisiting model structure, dataset modeling assumptions or the choice of parameters being estimated.

Uncertainty quantification provides an additional layer of quantitative validation. Confidence intervals help diagnose parameter identifiability issues and reveal which parameters are strongly informed by the data and which are effectively fixed by pseudo-data (Marques et al., 2019; Stavrakidis-Zachou et al., 2019; Lika and Kooijman, 2024). Bayesian estimation methods also offer a natural framework to propagate measurement uncertainty and prior information (including pseudo-data) into posterior distributions of parameters and predictions, and the associated likelihood formulation can also be used for post-calibration uncertainty analyses such as profile likelihood methods (Johnson et al., 2013; Boersch-Supan et al., 2017).

3.5.2. Qualitative validation

A first and important step in qualitative validation is to compare the estimated parameters with those of taxonomically and ecologically similar species. The AmP collection can be used to search for similar species and `AmPtool` provides tools to perform this comparison programmatically.[7] Several patterns in DEB parameter values have been observed across taxa, hinting that similar species should have similar values, so it is expected that the estimated parameters fall within the cloud of parameters for the species' family or order (Marques et al., 2018; Kooijman et al., 2021).

While this step is crucial, its reliability depends on the quality of the estimates for the similar species used for comparison. If those have low completeness or their parameter estimates are uncertain, deviations in parameter values may not be informative. However, if their calibration is robust, then parameter deviations may suggest that some assumptions or model structure choices should be reconsidered.

Finally, the DEB model should be simulated under different environmental conditions and model outputs, beyond the calibration data, should be computed. Although data may not be available, a modeler familiar with the species should be able to evaluate the predictions for realism and plausibility.

We also recommend not including all available data in the estimation. If multiple datasets of the same type are available, some may not be included in the estimation and can be saved for external validation. Obtaining predictions for these external validation datasets requires simulating the model with the appropriate environmental conditions. If these are unavailable, they can be inferred from other datasets or estimated from the data (e.g., a scaled functional response for the data) whilst keeping the core parameters fixed. The goal is to assess

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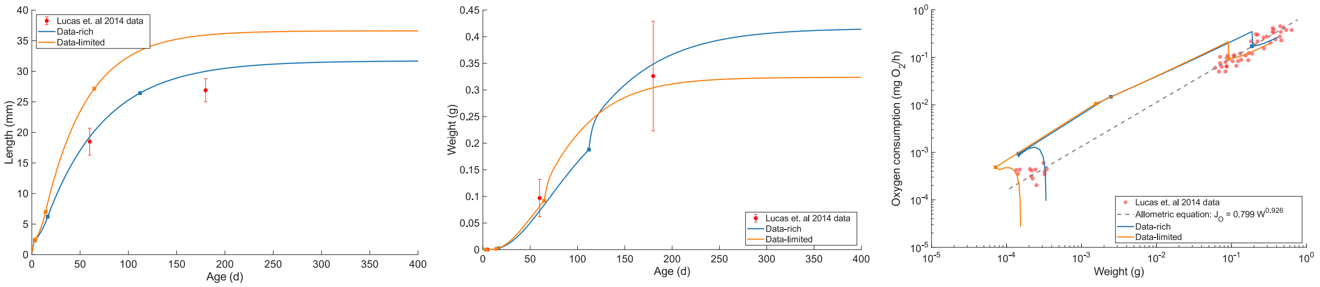
[7] The `AmPtool` MATLAB package can be found at https://github.com/add-my-pet/AmPtool.

Box 6. Qualitative validation with external data.

External validation data and simulations. Length, weight and oxygen data are digitized from Lucas et al. (2014). Model trajectories correspond to DEB simulations from fertilization until 400 days of age, at constant temperature ($T = 28\,°\mathrm{C}$) and food ($f = 0.75$). The scaled functional response f was not estimated but instead inferred from similar growth trajectories.



Length and weight. The data-limited calibration reaches maximum size earlier and underestimates maximum weight while overestimating length. Comparatively, the data-rich estimation captures the relationship between length and weight better throughout ontogeny, as the trade-off in prediction error is smaller. The data-rich calibration included several experiments where weight and length were both recorded, whereas the data-limited calibration only has data on the relationship between weight and length for the maximum size.

Oxygen consumption. Although the data-limited calibration does not have oxygen data, the predictions are very similar to those of the data-rich estimation. Both are an order of magnitude larger until adulthood, which could likely be resolved by including oxygen data for the egg phase. The drop in oxygen consumption is due to the onset of puberty and the low κ of the calibrations. Although it is not realistic, it is a consequence of a sudden transition to allocation in reproduction. Depending on the level of detail required, this behavior could promote a change in model structure.

whether the model predictions are similar to the external validation data, whilst considering the reasons for deviations described previously. The analysis should focus on assessing whether prediction tradeoffs exist and if they lead to an unacceptable mismatch between model and data. See Box 6 for a showcase of this recommendation.

3.6. Model publication

Model publication is the final step in the development of a DEB model. FAIR (Findable, Accessible, Interoperable, Reusable) and CARE (Collective Benefit, Authority to Control, Responsibility, Ethics) principles should guide both what is shared and how it is shared so that the model can be independently reused, audited, and extended. Code and metadata should be openly versioned and archived in citable releases whenever possible (Lemmen and Sommer, 2024), while keeping authorship through appropriate (open source) license. All of this should be planned from the start of the workflow, so that data, assumptions, code, and calibration choices remain traceable.

DEB model publication can be organized into three main dimensions: data, implementation, and calibration. We provide guidance for each of these below.

Data. For each dataset, the model entry should describe where the data came from, how the values were obtained, and how they were transformed before being used for model calibration. Here, the data includes not only the measurements, but also the environmental conditions whenever they are available.

The description should include a full citation to the original source whenever possible. It should distinguish between acquisition methods: direct measurements, digitized values, transformed records, or inferred quantities. All transformations from source data to model inputs should be documented, including unit conversions, temperature corrections, aggregations, filtering, and imputation choices. Moreover, if the transformations were performed programmatically, the accompanying code should be shared.

Implementation. The model publication should describe the model structure and whether any extra modules were included. Relevant model assumptions should be documented so that future users can understand modeling choices and potentially expand upon them. For model calibration, dataset-specific assumptions should be given, namely which environmental-condition assumptions and initialization methods were employed. Other relevant considerations, such as dataset-specific parameter infeasibility filters, should also be reported.

Given that DEB models are software outputs, they should follow standard practice recommendations. Scripts should be commented to explain code decisions and non-obvious implementation details. Software versions and dependencies should be explicit and usage instructions should be given.

Calibration. Calibration reporting begins with the initial parameter set for the calibration and why it was chosen (Marques et al., 2019; Oliveira et al., 2026). Authors should report the full configuration of the calibration problem, including objective function, dataset weights, stopping criteria, and any algorithm-specific parameters. Pseudo-data values and weights should be reported explicitly, and any deviation from defaults should be justified. Simulations used for independent model validation should be described, and the simulation code should be shared. The goal of this step is to provide model users with the full sequence of steps used to estimate and validate parameters so that it can be easily reproduced from initial to calibrated parameters.

The AmP workflow is a strong example of these publication standards (Marques et al., 2018; Kooijman, 2025). In this workflow, datasets used for calibration are always linked to original sources. The typified model and other model assumptions are often documented. The parameter estimation code is versioned, and many AmP entries are updated over time, with previous versions remaining accessible through the corresponding entry page.. The DEB models developed for this manuscript are an example of this and were only possible because these principles are cornerstones of the AmP collection. We therefore strongly encourage users who develop their own DEB models to submit their entries to the Add-my-Pet collection, contributing to a comprehensive and openly accessible repository of species data and DEB parameters that facilitates cross-species comparisons and the advancement of DEB theory, whilst benefiting from quality control by experienced maintainers.

Despite this, we believe that further improvements are still necessary for full reproducibility across entries. In the data dimension, the majority of entries still store values directly in MATLAB files, and the way those values were obtained is not always documented in sufficient detail. In the implementation dimension, model structure is sometimes implicit beyond the typified model label, and dataset-specific assumptions are not always reported despite strong recommendations and the existence of a dedicated discussion section. In the calibration dimension, reproducibility is often limited because initial parameter sets and calibration algorithmic details (e.g., the number of Nelder–Mead restarts) are not yet systematically described. These omissions hamper reproducibility and slow the progress of parameter-estimation algorithms. Another limitation for reproducibility is the absence of formal versioned releases for DEBtool. Implementing versioned releases, and linking each model publication to the release number used for simulation and calibration, would make the computational workflow more traceable and reproducible. In the absence of versioned releases, we recommend referencing the DEBtool Git commit used during development. To ensure preservation and sharing, other archives that provide unique identifiers such as Zenodo or Software Heritage[8] could be used to store parameter calibrations, including past versions (Di Cosmo, 2020).

The code accompanying this paper provides a `DEBtool`-compatible example aligned with these recommendations. The repository `README.md` file provides an overview of the code structure and the choices made during its development.

4. Concluding remarks

Fitting DEB models involves high levels of abstraction. Because these models represent the life-cycle of an individual, building them might require reasoning beyond a particular research question, extensive amount of data and a clear understanding of the theoretical framework and assumptions. In this paper we provide practical guidelines to help DEB users in facing the three major challenges when developing a DEB model: process representation, data collection and evaluation, and calibration.

Using the zebrafish case study, we showed how model calibration and validation should yield a fitted model that provides biologically coherent predictions across multiple physiological processes (Marques et al., 2019; Lika et al., 2011a). Since estimating DEB parameters goes beyond simple curve fitting (Kooijman et al., 2024), answering a specific research question is often only one outcome. We stress how a reliable DEB parameter estimation requires comprehensive life-cycle data and consistency among datasets, for which underlying conditions should be explicitly modeled. We also showed how varying levels of data completeness influence parameter estimation. Lastly, ensuring that model predictions are consistent with life-history data is a key modeling practice: this may seem beyond the original research question, but it is essential to prevent achieving a good fit for the wrong reasons.

Implementing DEB theory differs from implementing phenomenological models, which might achieve good fits, but lack the explanatory power needed to integrate dynamics across molecular, individual, and ecosystem levels (Kooijman et al., 2024). The focus on theoretical consistency makes DEB theory a powerful tool to connect knowledge across different scientific disciplines and levels of organization. Yet, it is only by providing a realistic set of coherent parameter values that one is able to explore its full functionality. Because of this very effort in ensuring consistency, DEB provides a strong quantitative and integrated lens on biology, which can be useful for predicting ecological outcomes and is crucial for systemically understanding life in a changing world.

CRediT authorship contribution statement

Diogo F. Oliveira: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Formal analysis, Conceptualization. **Anna Sulc:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Eline Le Moan:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Elisa Donati:** Writing – review & editing, Writing – original draft, Conceptualization. **Evridiki Klagkou:** Writing – review & editing, Validation, Software, Methodology, Formal analysis, Conceptualization. **María-José Lagunes:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Urban Dajčman:** Writing – review & editing, Writing – original draft, Conceptualization. **Tjui Yeuw Tan:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology, Formal analysis, Conceptualization.

Code availability

The code developed for this paper is archived in Zenodo (Klagkou et al., 2026b). The repository follows the structure of AmP entries and is based on the `DEBtool` MATLAB package. In addition to model implementation and calibration scripts, it also includes code to reproduce the analyzes presented here.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

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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[8] SWHID for `DEBtool_M`: swh:1:dir:a05e5053d3c381cef16e6fb8c582e81e40d4a316.

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Appendix A. Standard DEB model equations

The assumptions in Table A.4 are sufficient to mathematically define the standard DEB model. The derivation and a detailed treatment of each component of the model is given in Kooijman (2010), Chapter 2, pp. 24–78, with the assumptions being discussed in detail in Chapter 1.

The dynamic equations for the standard DEB model are presented in Table A.5, with the core parameters of the model presented in Table A.6. The state equation for each state variable is a function of powers that describe how the energy intake of an organism is allocated to each metabolic process. The model takes as input a temperature T with units K, via a correction factor $c_T(T)$ (Eq. (A.1)), and an ingestion power $\dot{p}_X$, with units $\mathrm{J\,d^{-1}}$.

Temperature affects all metabolic rates such as growth and maintenance. The effect of temperature is incorporated into the model via the temperature correction factor c_T:

$$c_T(T) = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right), \tag{A.1}$$

where T_A is the Arrhenius temperature (in K) and $T_{ref} = 20\,^{\circ}\mathrm{C} = 293.15\,\mathrm{K}$ is a reference temperature. This formulation only describes how rates change with temperature and cannot be used to model the temperature tolerance range of a species. For that, data at the lower and/or higher extreme temperatures is required, which can then be used to estimate the parameters of a more complex temperature correction function (see Kooijman (2010), p. 22). Temperature is assumed to affect all metabolic rates in the same way (Sousa et al., 2008), and the same correction factor is therefore applied to all powers. Consequently, temperature influences the timing of life-stage transitions (higher temperatures lead to higher metabolic rates and faster progression) but not body size[9] (Kearney, 2021).

Table A.4
The assumptions that specify the standard DEB model. Common terms for assumptions are given in italics. Adapted from Table 2.4 in Kooijman (2010), p. 77.

1. The amounts of reserve, structure and maturity are the state variables of the individual; reserve and structure have a constant composition (*strong homeostasis*) and maturity represents information.
2. Food uptake is initiated at birth. Allocation to maturity is redirected to reproduction at puberty. Both birth and puberty occur when maturity reaches certain threshold values.
3. Food is converted into reserve, which is mobilized to fuel all other metabolic processes. The rate at which reserve is mobilized depends on the state variables of the organism and on temperature.
4. The embryo stage has initially a negligibly small amount of structure and maturity, but a substantial amount of reserve. The reserve density at birth equals that of the mother at egg formation (*maternal effect*).
5. The feeding rate is proportional to the surface area of the individual and the food–handling time is independent of food density.
6. The equilibrium reserve density at constant food density does not depend on the amount of structure (*weak homeostasis*).
7. Somatic maintenance is proportional to structural volume, but some components, such as osmosis in aquatic organisms or heating in endotherms, are proportional to structural surface area.
8. Maturity maintenance is proportional to the level of maturity.
9. A fixed fraction of mobilized reserves is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation or reproduction (*the κ–rule*). Maintenance costs take priority over growth and reproduction.
10. The individual does not change in shape during growth (*isomorphism*).

Table A.5
Equations for state variables in the standard DEB model, life stage definitions, and powers associated to each process.

State Variable	Dynamics Equation	Name
E [J]	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	Reserve
V [cm^3]	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$	Structure
E_H [J]	$\frac{dE_H}{dt} = \begin{cases} \dot{p}_R & E_H < E_H^p \\ 0 & \text{otherwise} \end{cases}$	Maturity
E_R [J]	$\frac{dE_R}{dt} = \begin{cases} 0 & E_H < E_H^p \\ \kappa_R \dot{p}_R & \text{otherwise} \end{cases}$	Reproduction Buffer
Powers [$\mathrm{J\,d^{-1}}$]	Equation	Name
$\dot{p}_A$	$\dot{p}_A = \begin{cases} 0 & E_H < E_H^b \\ \kappa_X \dot{p}_X & \text{otherwise} \end{cases}$	Assimilation
$\dot{p}_P$	$\dot{p}_P = \begin{cases} 0 & E_H < E_H^b \\ \kappa_P \dot{p}_X & \text{otherwise} \end{cases}$	Feces production
$\dot{p}_C$	$\dot{p}_C = c_T E \frac{[E_G]\dot{v}V^{-1/3} + [\dot{p}_M]}{\kappa E/V + [E_G]}$	Mobilization
$\dot{p}_S$	$\dot{p}_S = c_T \left[\dot{p}_M\right] V$	Somatic maintenance
$\dot{p}_G$	$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_S$	Growth
$\dot{p}_J$	$\dot{p}_J = c_T \dot{k}_J E_H$	Maturity maintenance
$\dot{p}_R$	$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$	Maturation/Reproduction
Life stage	Start	End
Egg	Egg formation; $E_H = 0$	$E_H = E_H^b$ (birth)
Juvenile	$E_H = E_H^b$ (birth)	$E_H = E_H^p$ (puberty)
Adult	$E_H = E_H^p$ (puberty)	∞

Table A.6
Core parameters of the standard DEB model and default values for a "generalized organism".

Symbol	Parameter	Default value	Units
$\{\dot{p}_{Am}\}$	Surface-specific maximum assimilation rate	–	$\mathrm{J\,d^{-1}\,cm^{-2}}$
κ_X	Digestion efficiency	0.8	–
κ_P	Defecation efficiency	0.1	–
$\dot{v}$	Energy conductance	0.02	$\mathrm{cm\,d^{-1}}$
κ	Allocation fraction to soma	0.8	–
$\left[\dot{p}_M\right]$	Volume-specific somatic maintenance rate	18	$\mathrm{J\,d^{-1}\,cm^{-3}}$
$\left[E_G\right]$	Specific cost for structure	2800	$\mathrm{J\,cm^{-3}}$
$\dot{k}_J$	Maturity maintenance coefficient	0.002	$\mathrm{d^{-1}}$
E_H^b	Maturity at birth	–	J
E_H^p	Maturity at puberty	–	J
κ_R	Reproduction efficiency	0.95	–

Food quality and quantity affects development time and size. Often, the availability of food is quantified through a scaled functional response $f(X)$, which is defined by a Michaelis–Menten or Holling type II equation of the density of food in the environment X.

$$f(X) = \frac{X}{X+K}, \tag{A.2}$$

where K is the half-saturation coefficient. This function expresses the feeding rate as a fraction of the maximum feeding rate that an individual of a given size can achieve when consuming the same type of food. Due to lack of detailed data, $f(X)$ is typically treated as a parameter, independent of the density of food X, therefore it is often referred to simply as f. Its values range between 0 (no food intake) and 1 (*ad libitum* feeding). Values greater than 1 can be used to account

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[9] As such, standard DEB model assumptions cannot reproduce the Temperature-Size Rule (Verberk et al., 2021). Alternatively, Richard et al. (2024) propose that the food searching, a physical rather than physiological process, may scale differently with temperature.

Table B.7
Typified DEB models and functional life stages. The Sources column provides references with more details on each typified model. For a curated selection of papers on animal groups, see https://debportal.debtheory.org/docs/DEBpapers.html.

Model	Description	Functional life stages	Taxa	Sources
s–models				
`std`	standard DEB model	$\mathcal{E} \to \mathcal{J} \to \mathcal{A}$	Most animal species without larval phases; reptiles (lizards, snakes); birds; some crustaceans	Kooijman (2010), pp. 76–78
`stf`	`std` with fetal development	$\mathcal{F} \to \mathcal{J} \to \mathcal{A}$	Some sharks	Kooijman (2020a)
`stx`	`stf` with baby stage until weaning	$\mathcal{F} \to \mathcal{B} \to \mathcal{J} \to \mathcal{A}$	Mammals	Desforges et al. (2019)
`ssj`	`std` with programmed shrinking stage	$\mathcal{E} \to \mathcal{J} \to \mathcal{S} \cdots \mathcal{J} \to \mathcal{A}$	Eels (Anguilliformes); sea urchins, starfish (Echinodermata)	van der Meer and Kooijman (2015)
`sbp`	`std` with growth ceasing at puberty	$\mathcal{E} \to \mathcal{J} \to \mathcal{A}^{=}$	Copepods; some hemimetabolous insects	Koch and De Schamphelaere (2019)
a–models				
`abj`	`std` with acceleration between birth and metamorphosis	$\mathcal{E} \to \mathcal{J}^{\uparrow} \to \mathcal{J} \to \mathcal{A}$	Most fish species; amphibians (frogs, salamanders); marine invertebrates	Kooijman et al. (2011) and Lika et al. (2014b)
`asj`	`abj` with delayed acceleration	$\mathcal{E} \to \mathcal{J} \to \mathcal{J}^{\uparrow} \to \mathcal{J} \to \mathcal{A}$	Some bivalve mollusks	Stechele et al. (2022)
`abp`	`abj` with growth ceasing at puberty	$\mathcal{E} \to \mathcal{J}^{\uparrow} \to \mathcal{J} \to \mathcal{A}^{=}$	Some copepods and insects; possibly ostracods, spiders, scorpions	Koch and De Schamphelaere (2019)
h–models				
`hep`	`abj` with larval stage after acceleration behaving as an adult	$\mathcal{E} \to \mathcal{J} \to \mathcal{A} \Rightarrow \mathcal{I}$	Mayflies (Ephemeroptera); dragonflies and damselflies (Odonata)	Klagkou et al. (2026a)
`hex`	`hep` with accelerating larval stage behaving as an adult and pupal phase	$\mathcal{E} \to \mathcal{A} \Rightarrow \mathcal{P} \to \mathcal{I}$	Beetles (Coleoptera); butterflies and moths (Lepidoptera); flies (Diptera); bees and wasps (Hymenoptera)	Llandres et al. (2015)
`hax`	hybrid between `hep` (until pupation) and `hex`	$\mathcal{E} \to \mathcal{J} \to \mathcal{A} \Rightarrow \mathcal{P} \to \mathcal{I}$	Some holometabolous insects with extended larval stages	Klagkou et al. (2024b)

Life stages: $\mathcal{E}$ - Egg, $\mathcal{F}$ - Fetus, $\mathcal{B}$ - Baby, $\mathcal{J}$ - Juvenile, $\mathcal{S}$ - Programmed shrinking, $\mathcal{A}$ - Adult, $\mathcal{P}$ - Pupa, $\mathcal{I}$ - Imago.
Superscripts: ↑ - Acceleration, = - Non-growing.
Transitions: → - Maturity threshold, ⋯ - Time delay, ⇒ - Reproductive reserve density threshold.

for different diets and experimental protocols when in reference to a baseline value.

Using the scaled functional response, the ingestion power can be written as:

$$\dot{p}_X = c_T \{\dot{p}_{Xm}\} f V^{2/3}, \tag{A.3}$$

where $\{\dot{p}_{Xm}\}$ is the surface-specific maximum ingestion rate. The assimilation power $\dot{p}_A$ then becomes:

$$\dot{p}_A = c_T \{\dot{p}_{Am}\} f V^{2/3}, \quad \{\dot{p}_{Am}\} = \kappa_X \{\dot{p}_{Xm}\} \tag{A.4}$$

The equations presented here are based on the energy formulation of the standard DEB model, however, other formulations exist. Some formulations consider reserve density $[E] = E/V$ instead of reserve E as a state variable, which leads to different dynamics equations. Other formulations reformulate the model in terms of mass instead of energy or even in a dimensionless form. All of these formulations are mathematically equivalent and can be transformed into each other by applying the appropriate transformations (Kooijman, 2010).

Appendix B. Typified DEB models

Currently, the AmP collection contains entries for 11 typified models, including the standard DEB model. Each typified model is referred to as a 3-letter acronym, e.g., the standard DEB model is known as `std`. The first letter of the acronym also defines to which of the three classes of typified DEB models it belongs: `s`–, `a`–, or `h`–models.

The `std` model belongs to the `s`–models and is the basis for the models in this class. The `s`–models can then differ in embryonic development (e.g., fetal instead of egg development), by having a baby stage until weaning, programmed shrinking, or growth ceasing at puberty. `a`–models assume metabolic acceleration at or soon after birth, and like `s`–models, can have growth ceasing at puberty . Lastly, `h`–models are used for insects. They assume acceleration in certain stages and have additional life stages such as pupa and imago. The pupa life stage is similar in dynamics to the fetal life stage as it is non-feeding and not fully mature, however energy is obtained from existing reserves and structure. The transition to the pupa stage is based on a threshold value of reproductive reserve density $[E_R] = E_R/V$, instead of a threshold on maturity E_H. The imago life stage is a non-growing and non-feeding stage where the organism reproduces using energy saved from previous stages.

Table B.7 provides an overview of each typified model, with a brief description of its characteristics and the progression between functional life stages. The table also includes the most common taxa for each model as well as sources with more details on the equations of each model. Species from similar taxa can often be modeled with the same typified model, however, as discussed in Section 3.1, the choice of a typified model requires evaluating whether the functional life stages are in agreement with the species biology and ontogeny.

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