

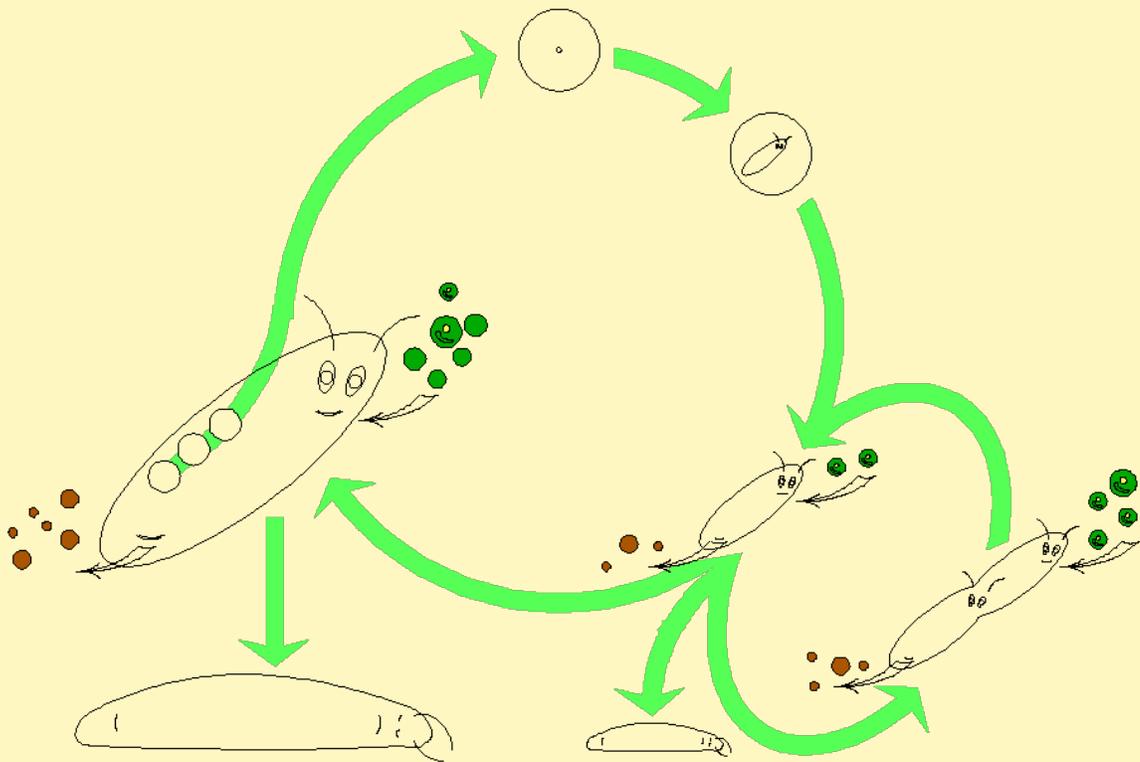
$$\frac{[E]}{[E_g] + \kappa [E]} \left(\frac{[E_g] \cdot \{ \dot{P}_{Am} \}}{[E_m]} \right)^{2/3} + \left(\frac{X_k}{X_k + X_k} \right)$$

f · V^{2/3} with f = (X_k + X_k) / (X_k + X_k)

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Notation of Dynamic Energy Budget theory

for metabolic organisation



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Notation rules for DEB theory

Some readers will be annoyed by the notation that is used in DEB theory [3], which sometimes differs from the ones that are usual in particular specialisations. One problem is that conventions in e.g. microbiology differ from those in ecology, so not all conventions can be observed at the same time. The symbol D , for example, is used by microbiologists for the (specific) dilution rate in chemostats, but by chemists for diffusivity. A voluminous literature on population dynamics exists, where it is standard to use the symbol l for survival probability. This works well as long as one does not want to use lengths in the same text! Another problem is that most literature does not distinguish structural biomass from reserve(s), which both contribute to e.g. dry weight. So the conventional symbols actually differ in meaning from the ones used by DEB theory.

Few texts deal with such a broad spectrum of phenomena as DEB theory. Moreover DEB theory has to deal with testing model predictions against measurements (which requires a careful treatment of dimensions and units), but also with the analysis of properties of implied models, which calls for scaling out all dimensions. Some core [DEBtool routines](#) also need to work with dimensionless quantities for numerical reasons (e.g. error control in numerical integration and root finding). Scaled and unscaled quantities cannot have the same symbols. Part of the reasons for the many symbols has nothing to do with DEB theory, but with the many quantities that are measured and mostly for good reasons: it is very hard to measure the dry weight of a whale, or the wet weight of a bacterium. A consequence is that any symbol table is soon exhausted if one carelessly assigns new symbols to all kinds of variables that show up.

The notation conventions are meant to aid memory for what symbols stand for what quantities and to think about dimensions more generally. It is important to distinguish symbols, which relate to quantities that have dimensions (and so units) and types, which are just labels (names) and affect the meaning of symbols as index. The notation rules stress the fundamental difference between rates and states and between relative and absolute quantities.

Symbols

- 1 Variables denoted by symbols that differ only in indices, have the same dimensions. For example M_E and M_V are both moles. This most important notation rule directly links symbols to dimension groups.
- 2 The interpretation of the leading character does not relate to that of the index character. For example, the M in M_E stands for mass in moles, but in \dot{k}_M it stands for maintenance. So the meaning of a character depends on its context.
- 3 Some lowercase symbols relate to uppercase ones via scaling: $\{e, E\}$, $\{m, M\}$, $\{j, J\}$, $\{l, L\}$, $\{u, U\}$, $\{w, W\}$ and $\{x, X\}$. It was impossible to be very strict in this rule, compare $\{d, D\}$, $\{f, F\}$, $\{\dot{k}, K\}$, or $\{\dot{p}, P\}$ for instance; here one of them is a rate, the other not and their meanings are not connected. A real exception is the time t and temperature T for consistency reasons with the almost all literature.

- 4 Structure V has a special role in DEB-notation. The structural volume V_V is abbreviated as V . Many quantities are expressed per structural mass, volume, or surface (see next notation rule). Likewise the energy of reserve E_E is abbreviated as E . It makes notational sense to deal with the energy of structure E_V or the volume of reserve V_E .
- 5 Analogous to the tradition in chemistry, quantities that are expressed per unit of structural volume have square brackets, $[\]$, so $[M_*] = M_*/V = M_*L^{-3}$. Quantities per unit of structural surface area have braces, $\{\}$, so $\dot{p}_* = \{\dot{p}_*\}L^2 = [\dot{p}_*]L^3 = [\dot{p}_*]V$. Quantities per unit of weight have angles, $\langle \rangle$, (with indices w and d for wet and dry weight). Likewise $m_{*1*2} = M_{*1}/M_{*2}$ is used for the amount of compound $*_1$ relative to that of compound $*_1$, all expressed in C-moles. If compound $*_1$ happens to be structure (V), the index is suppressed, so m_E is the amount of compound E (reserve) relative to that of structure. This notation is chosen to stress that these symbols refer to relative quantities, rather than absolute ones. They do not indicate concentrations in the chemical sense, because well-mixedness at the molecular level is not assumed. Likewise $j_{*1*2} = \dot{J}_{*1*2}/M_V$, where $*_1$ refers to the type of compound and $*_2$ to the process. Yield coefficients (see rule 12) are denoted by $y_{*1*2} = \dot{J}_{*1*3}/\dot{J}_{*2*3}$ and have the same dimension as m_{*1*2} , but not with the interpretation of a ratio of fluxes. Chemical indices n_{*1*2} are very similar to m_{*1*2} , but $*_1$ is now a chemical element, not a compound. So, n_{HE} is the frequency of hydrogen relative to carbon in reserve and m_{HE} the mole of water per C-mole of reserve (see section on indices).
- 6 Rates have dots, which merely indicate the dimension ‘per time’. Dots (and primes) do *not* stand for the derivative as in some mathematical and physical texts (see Subsection Expressions). Dots, brackets and braces allow an easy test for some dimensions, and reduce the number of different symbols for related variables. If time t has been scaled, i.e. the time unit is some particular value making scaled time dimensionless, the dot has been removed from the rate that is expressed in scaled time τ . Because the dimension ‘per time’ occurs frequently, several symbols are used: \dot{r} ’s mean growth, \dot{k} ’s have a neutral meaning or a decay, \dot{h} ’s a number of events per time (hazard rate). Notice that hazard rates do not necessarily relate to death, but to events more generally. Age a is a time, like t , but with the interpretation that $a = 0$ represents the moment of start of the development of the individual.
- 7 Molar values have an overbar. For example the chemical potential of reserve $\bar{\mu}_E$ is an energy per mole.
- 8 Random variables are underscored. The notation $\underline{x}|\underline{x} > x$ means: the random variable \underline{x} given that it is larger than the value x . It can occur in expressions for the probability, $\Pr\{\}$, or for the probability density function, $\phi(\cdot)$, or distribution function, $\Phi(\cdot)$.
- 9 Vectors and matrices are printed in bold face. A bold number represents a vector or matrix of elements with that value; so $\mathbf{J}\mathbf{1}$ is the summation of matrix \mathbf{J} across columns and $\mathbf{1}^T\mathbf{J}$ across rows; $\mathbf{x} = \mathbf{0}$ means that all elements of \mathbf{x} are 0.

- 10 Organic compounds are quantified in C-mole, which stand for the number of C-atoms as a multiple of Avogadro's number. So 6 C-mol of glucose equals 1 mol of glucose. Notice that for simple compounds, such as glucose we have both the option to express it in mole or C-mole, but for generalised compounds we can only express them in C-mole. So we always use C-mole. Weight (in gram) and moles are both quantifiers for mass. The difference is that an object has to consist of the single (generalised) chemical compound to quantify its mass in moles and moles of two objects can only be added or subtracted if their composition is the same. This restriction does not apply to weights.
- 11 Mass is denoted by M if expressed in moles and by W if expressed in grams. Mass expressed in moles cannot change in chemical composition, expressed in grams it can.
- 12 Mass–mass couplers y , also called yield coefficients, are constant, but yield coefficients Y can vary in time. E.g. Y_{WX} stands for the C-moles of biomass W that is formed per consumed C-mole of substrate X ; it is not constant and depends on the specific growth rate. Moreover, y is taken to be non-negative, while Y can be negative, if one compound is appearing, and the other disappearing. Yields represent ratios of fluxes expressed in moles, so $Y_{VE} = \dot{J}_{EG}/\dot{J}_{VG}$ is the ratio of the flux of reserve E (here meant to be a type) that is allocated to growth G (here meant to be a process) and the flux of structure V that is synthesised in the growth process. As a consequence we have $y_{EV} = y_{VE}^{-1}$. The indices of yield coefficients refer to types of mass, not to processes.
- 13 Energy–mass couplers $\mu_{*1*2} = \dot{p}_{*1}/\dot{J}_{*2*1}$ for process $*_1$ and mass of type $*_2$ are inverse to the mass–energy couplers $\eta_{*2*1} = \mu_{*1*2}^{-1}$. Notice that the sequence of indices changed. The mass–mass couplers $\zeta_{*1*2} = \frac{\bar{\mu}_E m_{Em}}{\mu_{*2*1}}$ are scaled energy–mass couplers, but now relative to the maximum reserve energy density $\bar{\mu}_E m_{Em}$.
- 14 Energy–energy couplers $\kappa_{*1*2} = \dot{p}_{*1}/\dot{p}_{*2}$, for process $*_1$ and process $*_2$.

coupler	mass	energy
mass	$y_{t_1 t_2}$	$\eta_{t_1 p_2}$
energy	$\mu_{p_1 t_2}$	$\kappa_{p_1 p_2}$

The different mass and energy couplers have indices that refer to types of compound t or processes p in logical ways.

In most applications \dot{p}_{*1} is part of \dot{p}_{*2} , giving the interpretation of an efficiency. If $\dot{p}_{*1} = \dot{p}_S + \dot{p}_G$ and $\dot{p}_{*2} = \dot{p}_C$, the indices are suppressed and κ gets the interpretation of the fraction of mobilised reserve energy that is allocated to soma. The fraction $\kappa_X = \kappa_{AF}$ of ingested energy is fixed in reserve (digestion efficiency), fraction $1 - \kappa_X$ is lost; fraction κ_E of rejected mobilized reserve energy returns to reserve, fraction $1 - \kappa_E$ is excreted. The same applies to fraction κ_G of energy allocated to growth that is fixed in new structure (growth efficiency) and fraction κ_R of energy allocated to reproduction that is fixed in offspring (reproduction efficiency); fractions $1 - \kappa_G$ and $1 - \kappa_R$ are lost for the individual. So κ is confined to the interval $(0, 1)$. Scaled functional response f , defined as the ingestion rate of a certain type of food as fraction of the maximum possible one of an individual of that size, differs from a κ because the maximum flux is potential, not actual; it is a scaled flux, not a fraction of an actual flux.

15 Scaled maturity v_H is called v_H because $v_H = l_b^3$ if $k = 1$, so it has the interpretation of a scaled volume. The similarity with energy conductance \dot{v} , which would become v in scaled time, is unhappy and violates the leading dimension rule in scaled time. This is less of a problem, however, because if dimensions are scaled, all are scaled and v does not occur since it would have dimension length.

Indices

The index of V , E and M stands for a type of compound.

The energy costs per volume of structure $[E_G]$ is an exception that violates notation rules, because G is a process. The parameter $[E_G]$ should have been omitted and replaced by $[E_V]/\kappa_G$, where $[E_V] = \bar{\mu}_V[M_V]$ is the volume-specific potential energy of structure. The notation problem results from the fact that cost for structure is basically a ratio of an energy flux and a volume flux, while E , V and M are states. Although dimension time drops out of the result, it is still present in the concept ‘cost for structure’. The mass equivalent, the yield coefficient y_{VE} , reflects that naturally as a ratio of two mass fluxes.

The index of a stands for a life history event, that of \dot{p} for a process.

Indices are catenated, but the sequence has a meaning. For example, \dot{J}_{EA} stands for a flux expressed in C-moles per time (\dot{J}) of the compound reserve (E), associated with process assimilation (A); The yield of compound V on E is denoted by y_{VE} , but that of E on V by $y_{EV} = y_{VE}^{-1}$. Some indices have a specific meaning:

*	indicates that several other symbols can be substituted. It is known as ‘wildcard’ in computer science. As superscript it denotes the equilibrium value of the variable.
'	indicates a scaling as superscript.
i, j	are counters that refer to types or species; they can take the values $1, 2, \dots$
m	stands for ‘maximum’. For example \dot{p}_{Am} is the maximum value that \dot{p}_A can attain.
+	can refer to the sum of elements, such as $V_+ = \sum_i V_i$, or to addition, such as X_{i+1} . As superscript of a flux of compound it denotes ‘accepted by the SU’.
–	as superscript of a flux of compound denotes ‘rejected by the SU’.
T	as superscript stands for transposition (interchanging rows and columns in a matrix)

Indices for compounds refer to

C	carbon dioxide	$C-$	bicarbonate	D	damage compound	E	reserve	E_+	dead reserve
H	water	\mathcal{M}	minerals	N	nitrogen-waste	N_H	ammonia	N_O	nitrate
O	dioxygen	\mathcal{O}	org. compounds	P	product (faeces)				
Q	toxicant, damage inducer	R	reprod. reserve	V	structure	V_+	dead structure	X	food

Indices for processes refer to

F	searching	X	feeding	A	assimilation	C	mobilisation
D	dissipation	E	excretion	H	maturation	G	growth
J	maturity maint.	M	vol-linked som. maint.	R	reproduction	S	somatic maint.
$T+$	dissipating heat	T	surf-linked som. maint.				

Indices for life history events refer to

0	start development	h	hatching	b	birth	s	start acceleration	j	end acceleration
x	weaning/fledging	p	puberty	e	emergence	i	‘infinite’	m	death

Indices for life stages refer to

e	embryo	j	juvenile	a	adult	n	post-natal
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Some indices can have more than one meaning, the context selects. \mathcal{M} not only denotes ‘minerals’, but also ‘morph’, relating to shape, like in shape coefficient $\delta_{\mathcal{M}}$. X stands for food as compound, but for feeding as process. The choice of the symbol relates to food type and quality being frequently poorly known in practice. The choice of the symbol F

for searching links to filtering as being a special case of searching (symbol S was already occupied). Compound C stands for the type carbon dioxide, but for mobilisation as process. (Mobilisation C has the interpretation of catabolic rate as used in the early physiological literature under particular situations at constant Respiration Quotient.) Type H not only stands the chemical element hydrogen and for the compound water, but also for maturity; the latter is also a type, but not a chemical compound (it has no mass or energy). The process maturation H is the change in the state of maturity (indicated by E_H or M_H if expressed in cumulated energy or mass of reserve invested in maturation). If maturation represents a decrease, rather than an increase in maturity, it is called rejuvenation, but the same symbols are used. Likewise, growth G is the change in the amount of structure V (typically expressed in volume V or mass M_V) and if growth is negative, it is called shrinking, but the same symbols are used. While maturation and growth can be positive or negative, rejuvenation and shrinking relate to a decrease of maturity and structure, respectively. DEB theory has no labels for the change in (total body) weight; a decrease in weight can combine with an increase in structure (as is typical for embryos).

Indices are kept as simple as possible, but for isotopes they are rather complex since we need to indicate the isotope, element, compound as well as flux as a consequence of strictly observing mass and isotope conservation.

Expressions

- 1 An expression between parentheses with an index '+' means: take the maximum of 0 and that expression, so $(x - y)_+ \equiv \max\{0, x - y\}$. The symbol ' \equiv ' means 'is per definition'. It is just another way of writing, you are not supposed to understand that the equality is true.
- 2 Although the mathematical standard for notation should generally be preferred over that of any computer language, I make one exception: the logic boolean, e.g. $(x < x_s)$. It always comes with parentheses and has value 1 if true or value 0 if false. It appears as part of an expression. Simple rules apply, such as:

$$(x \leq x_s)(x \geq x_s) = (x = x_s)$$

$$(x \leq x_s) = (x = x_s) + (x < x_s) = 1 - (x > x_s)$$

$$\int_{x_1=-\infty}^x (x_1 = x_s) dx_1/dx = (x \geq x_s)$$

$$\int_{x_1=-\infty}^x (x_1 \geq x_s) dx_1 = (x - x_s)_+$$

- 3 The following operators occur:

$\frac{d}{dt}X _{t_1}$	derivative of X with respect to t evaluated at $t = t_1$
$\frac{\partial}{\partial t}X _{t_1}$	partial derivative of X with respect to t evaluated at $t = t_1$
$\mathcal{E}g(\underline{x})$	expectation of a function g of the random variable \underline{x} : $\int_x g(x)\phi(x) dx$
$\text{var } \underline{x}$	variance of the random variable \underline{x} : $\mathcal{E}(\underline{x} - \mathcal{E}\underline{x})^2$
$\text{cv } \underline{x}$	coefficient of variation of the random variable \underline{x} : $\sqrt{\text{var } \underline{x}}/\mathcal{E}\underline{x}$
\mathbf{x}^T	transpose of vector or matrix \mathbf{x} (interchange rows and columns)
$\dot{\cdot}$ or \cdot	catenation of matrices across columns: $\mathbf{n} = (\mathbf{n}_M \dot{\cdot} \mathbf{n}_O)$
$;$	catenation across rows: $(\dot{\mathbf{J}}_1^T, \dot{\mathbf{J}}_2^T)^T = (\dot{\mathbf{J}}_1; \dot{\mathbf{J}}_2)$
$\mathbf{diag}(\mathbf{x})$	square matrix with zeros and elements of vector \mathbf{x} on the diagonal
$\det(\mathbf{A})$	determinant of matrix \mathbf{A}

Signs

Fluxes of appearing compounds at the level of the individual plus its environment are typically taken to be positive, and of disappearing compounds negative. Such fluxes are indicated with a single index for the compound. If the process is also indicated, so two indices are used, such as the mobilisation flux \dot{J}_{EC} the flux typically taken positive. The sign-problem is complex, however, and depends on the level of observation and the choice of state variables (i.e. pools). Where the sign is not obvious, I mention it explicitly. Parameters are always positive, and yield coefficients written with a lower case y are taken as parameters, but yield coefficients written with an upper case Y are ratios of fluxes (so they are variables, which might vary in time) and can be negative. The yield of structure on reserve in the growth process is $Y_{VE}^G = -y_{VE}$, with primary parameter $y_{VE} > 0$.

The mass-specific fluxes, j , hazard rates, \dot{h} , and energy fluxes, \dot{p} , are always taken to be positive.

Dimensions and classes

Primary parameters are parameters that have the closest conceptual link with the underlying processes. *Compound parameters* are (simple) functions of primary parameters that typically have very simple dimensions and can (for this reason) be more easily be estimated from measurements. Many predictions only involve compound parameters, implying that it is not necessary to know all values of primary parameters to make such predictions. If the predicted variable does not have the dimension energy, for instance, we know a priori that it is not necessary to know values of primary parameters that have dimension energy. Knowledge of the value of a ratio is weaker than knowledge of numerator as well as denominator. *Environmental parameters* are parameters that relate to environmental conditions, most important being temperature and food. *Auxiliary parameters* are parameters that are not primary or environmental.

In the description of the dimensions in the list of symbols, the following symbols are used:

–	no dimension	L	length (of individual)	e	energy ($\equiv ml^2t^{-2}$)
t	time	l	length (of environment)	T	temperature
#	number (mole)	m	mass (weight)		

These dimension symbols just stand for an abbreviation of the dimension, and differ in meaning from symbols in the symbol column. The dimensions length of environment l and length of individual L differ because the sum of lengths of objects for which l and L apply does not have any useful meaning. The list below does not include symbols that are used in a brief description only.

Three classes of symbols are specified in the description in the list: constant, c, variable, v, and function, f. This classification cannot be rigorous, however. Temperature T , for example, is indicated to be a constant, but it can also be considered as a function of time, in which case all rate constants are functions of time as well. Food density X is indicated as a variable, but can be held constant in particular situations. Variables such as structural biovolume V are constant during a short period, such as is relevant for the study of the process of digestion, but not during a longer period, such as is relevant for the study of life cycles. The choice of class can be considered as a default, deviations being mentioned in the text.

List of frequently used symbols

symbol	dim	class	interpretation
a	t	v	age, i.e. time since gametogenesis or fertilisation
a_b	t	v	age at birth (start of feeding), i.e. end of embryonic stage
a_j	t	v	age at metamorphosis, i.e. change from V1- to iso-morphy
a_p	t	v	age at puberty (start of allocation to reproduction), i.e. end of juvenile stage
a_{\dagger}	t	v	age at death (life span)
A	l^2 or L^2	v	surface area
\dot{b}_{\dagger}	$l^3 \#^{-1} t^{-1}$	c	killing rate by toxicant
\dot{B}_{\dagger}^{*1*2}	$l^6 \#^{-2} t^{-1}$	c	interaction parameter for compounds $*_1$ and $*_2$ in the hazard rate
B_{*}^{*1*2}	$l^6 \#^{-2}$	c	interaction parameter for compounds $*_1$ and $*_2$ on target parameter $*$
$B_x(a, b)$	-	f	incomplete beta function
c_0	$\# l^{-3}$	c	no-effect concentration (NEC) of toxicant in the environment
c_d	$\# l^{-3}$	v	concentration of toxicant in the water (dissolved)
c_e	$\# l^{-3}$	v	scaled internal conc. of toxicant above the NEC: $(c_V - c_0)_+$
c_X	$\# l^{-3}$	v	concentration of toxicant in food
c_V	$\# l^{-3}$	v	scaled internal concentration of toxicant: $[M_Q]P_{dV}$
c_*	$\# l^{-3}$	v	scaled tolerance conc. of toxicant for target parameter $*$
d_*	$m L^{-3}$	c	density of compound $*$
d_{W_w}	$m L^{-3}$	c	density of wet mass: $W_w/V_w = d_V^w$
d_C	$m L^{-3}$	c	condition index: W_w/L_w^3
\dot{D}	$l^2 t^{-1}$	c	diffusivity
e	-	v	scaled reserve density: $[E]/[E_m] = m_E/m_{Em}$

e_b	-	v	scaled reserve density at birth: $[E_b]/[E_m] = m_E^b/m_{Em}$
e_H	-	v	scaled maturity density: $gu_H/l^3 = [E_H]/[E_m]$
e_H^b	-	c	scaled maturity density at birth: $gu_H^b/l_b^3 = [E_H^b]/[E_m]$
e_H^p	-	c	scaled maturity density at puberty: $gu_H^p/l_p^3 = [E_H^p]/[E_m]$
e_R	-	v	scaled energy in the reproduction buffer: E_R/E_m
E	e	v	non-allocated energy in reserve
E_0	e	v	energy costs of one egg/foetus
E_H	e	v	accumulated energy investment into maturation
E_H^b	e	c	maturity at birth
E_H^j	e	c	maturity at metamorphosis
E_H^p	e	c	maturity at puberty
E_m	e	c	maximum reserve: $[E_m]V_m = [E_m]L_m^3$
E_R	e	v	energy in the reproduction buffer
$[E]$	eL^{-3}	v	reserve density: E/V
$[E_b]$	eL^{-3}	v	reserve density at birth
$[E_G]$	eL^{-3}	c	volume-specific costs of structure; better replaced by $[E_V]/\kappa_G$
$[E_H]$	eL^{-3}	v	maturity density: E_H/V
$[E_m]$	eL^{-3}	c	maximum reserve density: $\{\dot{p}_{Am}\}/\dot{v}$
$[E_V]$	eL^{-3}	c	volume-specific potential energy of structure: $\bar{\mu}_V[M_V]$
E_W	e	c	total potential energy (reserve + structure + reprod. buffer)
E_W^b	e	c	total potential energy (reserve + structure) at birth
f	-	v	scaled functional response: $f = \frac{X}{K+X} = \frac{x}{1+x}$
\dot{F}	$l^{2 \text{ or } 3}t^{-1}$	v	searching (filtering) rate
\dot{F}_m	$l^{2 \text{ or } 3}t^{-1}$	v	maximum searching (filtering) rate
$\{\dot{F}_m\}$	$l^{2 \text{ or } 3}L^{-2}t^{-1}$	c	specific searching (filtering) rate
g	-	c	energy investment ratio: $\frac{[E_G]}{\kappa[E_m]}$
g_H^b	-	c	energy divestment ratio at birth: $\frac{[E_H^b]}{(1-\kappa)[E_m]}$
g_H^p	-	c	energy divestment ratio at puberty: $\frac{[E_H^p]}{(1-\kappa)[E_m]}$
\dot{h}	t^{-1}	v	specific death probability rate (hazard rate)
\dot{h}_a	t^{-1}	c	ageing rate for unicellulars: $\frac{[E_G]}{\kappa\mu_{QC}} \frac{k_E+k_M}{g+1}$
\dot{h}_G	t^{-1}	c	Gompertz ageing rate
\dot{h}_m	t^{-1}	c	maximum throughput rate in a chemostat without complete washout
\dot{h}_N	t^{-1}	c	hazard rate for clutches
\dot{h}_W	t^{-1}	c	Weibull ageing rate
\dot{h}_X	t^{-1}	v	feeding rate in particles per time
\ddot{h}_a	t^{-2}	c	Weibull ageing acceleration
\bar{h}_*	$e\#^{-1}$	c	molar enthalpy of compound *
i_Q	$l^3L^{-3}t^{-1}$	c	uptake rate of toxicant
\dot{j}_*	$\#\#\#^{-1}t^{-1}$	v	structure-specific flux of compound *: \dot{J}_*/M_V
\dot{J}_*	$\#t^{-1}$	v	flux of compound *
$\dot{J}_{*,*2}$	$\#t^{-1}$	v	flux of compound * ₁ associated with process * ₂
$\dot{\mathbf{J}}$	$\#t^{-1}$	v	matrix of fluxes of compounds $\dot{J}_{*,*2}$
$\dot{J}_{W_w^b}$	mt^{-1}	v	neonate mass production: $\dot{R}W_w^b$
$\{\dot{J}_{XAm}\}$	$\#L^{-2}t^{-1}$	c	surface-area-specific maximum ingestion rate

$[\dot{J}_{XAm}]$	$\#L^{-3}t^{-1}$	c	volume-specific maximum ingestion rate: $\{\dot{J}_{XAm}\}/L_d$
k	-	c	maintenance ratio: \dot{k}_J/\dot{k}_M
k'	-	c	rejuvenation ratio: \dot{k}'_J/\dot{k}_M
\dot{k}_e	t^{-1}	c	elimination rate of toxicant
\dot{k}_E	t^{-1}	c	specific-energy conductance: \dot{v}/L_d
\dot{k}_J	t^{-1}	c	maturity maintenance rate coefficient
\dot{k}'_J	t^{-1}	c	rejuvenation rate
\dot{k}_M	t^{-1}	c	somatic maintenance rate coefficient: $[\dot{p}_M]/[E_G]$
K_*	$\#l^{-3}$ or -2	c	(half) saturation coefficient: $\{\dot{J}_{*Am}\}/\{\dot{F}_m\}$
l	-	v	scaled structural length: $(V/V_m)^{1/3} = L/L_m$
l_b	-	v	scaled structural length at birth: $(V_b/V_m)^{1/3} = L_b/L_m$
l_d	-	v	scaled structural length at division: $(V_d/V_m)^{1/3} = \dot{k}_M g/\dot{k}_E$
l_j	-	v	scaled structural length at metamorphosis: $(V_j/V_m)^{1/3} = L_j/L_m$
l_T	-	c	scaled heating length: L_T/L_m
l_p	-	v	scaled structural length at puberty: $(V_p/V_m)^{1/3} = L_p/L_m$
l_∞	-	v	ultimate scaled structural length: $(V_\infty/V_m)^{1/3} = L_\infty/L_m$
L	L	v	structural length: $V^{1/3}$
L_b	L	v	structural length at birth: $V_b^{1/3}$
L_d	L	v	structural length at division: $V_d^{1/3}$
L_j	L	v	structural length at metamorphosis: $V_j^{1/3}$
L_m	L	c	maximum structural length: $V_m^{1/3} = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]} = \frac{\dot{v}}{g\dot{k}_M}$
L_p	L	v	structural length at puberty: $V_p^{1/3}$
L_T	L	c	heating length: $V_T^{1/3} = \{\dot{p}_T\}/[\dot{p}_M]$
L_F	L	v	structural length of foetus
L_w	L	v	physical length: $L/\delta_{\mathcal{M}}$
L_∞	L	v	ultimate structural length: $V_\infty^{1/3}$
m_{*1*2}	$\#\#\^{-1}$	v	mass of compound $*_1$ in moles relative to that of compound $*_2$: M_{*1}/M_{*2}
m_*	$\#\#\^{-1}$	v	mass of compound $*$ in moles relative to M_V : M_*/M_V
m_{Em}	$\#\#\^{-1}$	c	maximum molar reserve density: $M_{Em}/M_V = [M_{Em}]/[M_V]$
M_*	$\#$	v	mass of compound $*$ in moles
$\mathcal{M}(V)$	-	f	shape (morph) correction function: $\frac{\text{real surface area}}{\text{isomorphic surface area}}$
$[M_{Em}]$	$\#L^{-3}$	c	maximum reserve density in non-embryos in C-moles $[E_m]/\bar{\mu}_E$
$[M_{sm}]$	$\#L^{-3}$	c	maximum volume-specific capacity of the stomach for food
$[M_V]$	$\#L^{-3}$	c	number of C-atoms per unit of structural body volume V : d_V/w_V
$[M_Q^0]$	$\#L^{-3}$	c	(internal) no effect concentration of compound Q ; see c_0
n_{*1*2}	$\#\#\^{-1}$	c	number of atoms of element $*_1$ present in compound $*_2$
n_{*1*2}^0	$\#\#\^{-1}$	v	number of isotopes 0 of element $*_1$ present in a pool of comp. $*_2$
n_{*1*2}^{0k}	$\#\#\^{-1}$	v	number of isotopes 0 of element $*_1$ present in comp. $*_2$ in process k
\mathbf{n}	$\#\#\^{-1}$	c	matrix of chemical indices n_{*1*2}
N	$\#$	v	(total) number of individuals: $\int_a \phi_N(a) da$
\dot{p}_*	et^{-1}	v	energy flux (power) of process $*$
\dot{p}_{T+}	et^{-1}	v	total dissipating heat
\dot{p}_{TT}	et^{-1}	v	radiation and convection heat
$\dot{\mathbf{p}}$	et^{-1}	v	vector of basic powers: $(\dot{p}_A \dot{p}_D \dot{p}_G)$

$\{\dot{p}_{Am}\}$	$e L^{-2}t^{-1}$	c	surface-area-specific maximum assimilation rate
$[\dot{p}_{Am}]$	$e L^{-3}t^{-1}$	c	volume-specific maximum assimilation rate: $\{\dot{p}_{Am}\}/L_d$
$[\dot{p}_M]$	$e L^{-3}t^{-1}$	c	specific volume-linked somatic maintenance rate: \dot{p}_M/V
$[\dot{p}_S]$	$e L^{-3}t^{-1}$	v	volume-specific somatic maintenance rate: $\dot{p}_S/V = [\dot{p}_M] + \{\dot{p}_T\}/L$
$\{\dot{p}_T\}$	$e L^{-2}t^{-1}$	c	specific surface area-linked somatic maintenance rate: $\dot{p}_T V^{-2/3}$
P_{*1*2}	-	c	partition coeff. of a compound in matrix $*_1$ and $*_2$ (moles per volume)
P_{ow}	-	c	octanol/water partition coefficient of a compound
P_{PX}	-	c	faeces/food partition coefficient of a compound
P_{Vd}	$l^3 L^{-3}$	c	biomass/water (dissolved fraction) partition coefficient of a compound
P_{VW}	-	c	structural/total body mass partition coefficient of a compound
$q(c, t)$	-	v	survival probability to a toxic compound
\ddot{q}	t^{-2}	v	ageing acceleration (scaled density of damage inducing compounds m_Q)
\dot{r}	t^{-1}	v	specific growth rate of structure
\dot{r}_m	t^{-1}	c	(net) maximum specific growth rate (of structure)
\dot{r}_m°	t^{-1}	c	gross maximum specific growth rate (of structure)
\dot{r}_j	t^{-1}	v	specific growth rate during acceleration: $\dot{k}_M \frac{f L_m/L_b - 1}{1+f/g}$
\dot{r}_B	t^{-1}	v	von Bertalanffy growth rate: $\frac{\dot{k}_M/3}{1+f/g}$
\dot{r}_N	t^{-1}	v	specific population growth rate
\dot{r}_N^m	t^{-1}	v	maximum specific population growth rate
\dot{R}	$\# t^{-1}$	v	reproduction rate, i.e. number of eggs or young per time
\dot{R}_∞	$\# t^{-1}$	c	ultimate reproduction rate
\dot{R}_m	$\# t^{-1}$	c	maximum reproduction rate, i.e. \dot{R}_∞ at $f = 1$
s	-	v	stress value
s_0	-	c	stress value without effect
s_d	-	v	demand stress: $4/27 - s_s$
s_E^0	-	c	yolkiness: E_0^{\max}/E_0^{\min}
s_G	-	c	Gompertz stress coefficient
s_H	-	c	rejuvenation stress coefficient
s_H^{bp}	-	c	maturity ratio: $\frac{E_H^b}{E_H^p}$
s_{HL}^{bp}	-	c	maturity density ratio: $\frac{E_H^b L_p^3}{E_H^p L_b^3}$
s_M	-	c	acceleration factor at $f = 1$: L_j/L_b
s_R	-	v	up-regulation of mammalian assimilation: $1 + \delta L_F^2/L^2$
s_R^b	-	v	overall reproduction efficiency: $\kappa_R L_b^3 ([M_V]\mu_V + [E_m])/E_0$
s_s	-	v	supply stress: $\frac{\dot{p}_J [\dot{p}_M]^2}{f^3 s_M^3 \{\dot{p}_{Am}\}^3} = \frac{\dot{p}_J \dot{p}_M^2}{\dot{p}_A^3}$
\bar{s}_*	$e T^{-1} \#^{-1}$	c	molar entropy of compound $*$
t	t	v	time
t_d	t	v	inter division period
t_D	t	c	DNA duplication time
t_E	t	v	mean reserve residence time
t_{Em}	t	c	maximum reserve residence time: $(g\dot{k}_M)^{-1} = L_m/\dot{v}$
t_g	t	v	gut residence or gestation time
t_h	t	v	food handling interval
t_j	t	v	time since birth at metamorphosis
t_p	t	v	time since birth at puberty

t_R	t	v	time at spawning or at first brood
t_s	t	v	mean stomach residence time
T	T	c	temperature
T_A	T	c	Arrhenius temperature
T_b	T	c	body temperature
T_e	T	c	environmental temperature
u_E	-	v	scaled reserve: $U_E \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E\kappa}{[E_G]V_m} = \frac{e l^3}{g}$
u_E^0	-	v	initial scaled reserve: $U_E^0 \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E_0 \kappa}{[E_G]V_m}$
u_H	-	v	scaled maturity: $U_H \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E_H \kappa}{[E_G]V_m}$
u_H^b	-	c	scaled maturity at birth: $U_H^b \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E_H^b \kappa}{[E_G]V_m}$
u_H^j	-	c	scaled maturity at metamorphosis: $U_H^j \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E_H^j \kappa}{[E_G]V_m}$
u_H^p	-	c	scaled maturity at puberty: $U_H^p \frac{g^2 k_M^3}{\dot{v}^2} = \frac{E_H^p \kappa}{[E_G]V_m}$
U_E	tL^2	v	scaled reserve: $\frac{M_E}{\{J_{EA_m}\}} = \frac{E}{\{\dot{p}_{Am}\}}$
U_E^b	tL^2	c	scaled reserve at birth: $\frac{M_E^b}{\{J_{EA_m}\}} = \frac{E_b}{\{\dot{p}_{Am}\}}$
U_E^p	tL^2	c	scaled reserve at puberty: $\frac{M_E^p}{\{J_{EA_m}\}} = \frac{E_p}{\{\dot{p}_{Am}\}}$
U_H	tL^2	v	scaled maturity: $\frac{M_H}{\{J_{EA_m}\}} = \frac{E_H}{\{\dot{p}_{Am}\}}$
U_H^b	tL^2	c	scaled maturity at birth: $\frac{M_H^b}{\{J_{EA_m}\}} = \frac{E_H^b}{\{\dot{p}_{Am}\}}$
U_H^j	tL^2	c	scaled maturity at metamorphosis: $\frac{M_H^j}{\{J_{EA_m}\}} = \frac{E_H^j}{\{\dot{p}_{Am}\}}$
U_H^p	tL^2	c	scaled maturity at puberty: $\frac{M_H^p}{\{J_{EA_m}\}} = \frac{E_p}{\{\dot{p}_{Am}\}}$
\dot{v}	$L t^{-1}$	c	energy conductance (velocity)
v_H	-	v	scaled maturity: $\frac{E_H}{[E_G]V_m} \frac{\kappa}{1-\kappa} = \frac{u_H}{1-\kappa}$
v_H^b	-	c	scaled maturity volume at birth: $\frac{E_H^b}{[E_G]V_m} \frac{\kappa}{1-\kappa} = \frac{u_H^b}{1-\kappa}$
v_H^j	-	c	scaled maturity volume at metamorphosis: $\frac{E_H^j}{[E_G]V_m} \frac{\kappa}{1-\kappa} = \frac{u_H^j}{1-\kappa}$
v_H^p	-	c	scaled maturity volume at puberty: $\frac{E_H^p}{[E_G]V_m} \frac{\kappa}{1-\kappa} = \frac{u_H^p}{1-\kappa}$
V	L^3	v	structural volume: L^3
V_b	L^3	v	structural volume at birth (transition embryo/juvenile): L_b^3
V_d	L^3	v	structural volume at division: L_d^3
V_j	L^3	v	structural volume at metamorphosis: L_j^3
V_T	L^3	c	structural volume reduction due to heating: $\{\dot{p}_T\}^3 [\dot{p}_M]^{-3} = L_T^3$
V_m	L^3	c	maximum structural volume: $L_m^3 = (\kappa \{\dot{p}_{Am}\} / [\dot{p}_M])^3 = (\dot{v} / \dot{k}_{Mg})^3$
V_p	L^3	v	structural volume at puberty (transition juvenile/adult): L_p^3
V_w	L^3	v	physical volume
V_∞	L^3	v	ultimate structural volume: L_∞^3
w_*	$m \#^{-1}$	c	molar weight of compound *
W_d	m	v	dry weight of (total) biomass
W_w	m	v	wet weight of (total) biomass
W_w^b	m	v	wet weight of (total) biomass at birth
x	-	v	scaled biomass (cq food) density in environment: X/K
x	-	v	transformed reserve density (used for embryos): $\frac{g}{e+g}$

x_b	-	v	transformed reserve density (used for embryos): $\frac{g}{c_b+g}$
X_*	# l^{-3} or l^{-2}	v	density of compound * in environment; default: food
X_r	# l^{-3}	c	substrate density in feed of chemostat
y_{*1*2}	# # $^{-1}$	c	yield coefficient that couples mass flux * ₁ to mass flux * ₂
Y_{*1*2}^k	# # $^{-1}$	v	yield coefficient that couples flux * ₁ to flux * ₂ in process k : $\dot{J}_{*1k}/\dot{J}_{*2k}$
z	-	v	zoom factor to compare body sizes inter-specifically; $z = 1$ for $L_m = 1$ cm
α	-	v	function of reserve and structure (used for embryos): $3gx^{1/3}/l$
α_b	-	v	function of reserve and structure (used for embryos): $3gx_b^{1/3}/l_b$
α_{*1*2}^{*3}	-	c	reshuffle coefficient for element * ₁ of compound * ₂ in process * ₃
β_{*1*2}^{0*3}	-	c	odds ratio of isotope 0 of element * ₁ of compound * ₂ in process * ₃
γ_{*1*2}^0	-	c	$\frac{\text{number of isotopes } 0}{\text{number of atoms}}$ of element * ₁ in comp. * ₂
$\Gamma(x)$	-	f	gamma function
δ	-	c	aspect ratio
δ_l	-	c	shape parameter of generalised logistic growth
$\delta_{\mathcal{M}}$	-	c	shape (morph) coefficient: L/L_w
δ_X	-	c	maximum shrinking fraction
ζ_{*1*2}	# # $^{-1}$	c	coefficient that couples mass flux * ₁ to energy flux * ₂ : $\bar{\mu}_E m_{Em} \mu_{*2*1}^{-1}$
η_{*1*2}	# e^{-1}	c	coefficient that couples mass flux * ₁ to energy flux * ₂ : μ_{*2*1}^{-1}
η	# e^{-1}	c	matrix of coefficients that couple mass to energy fluxes
θ	-	v	fraction of a number of items: $0 \leq \theta \leq 1$
κ	-	c	fraction of mobilised reserve allocated to soma
κ_A	-	c	fraction of assimilation that originates from well-fed-prey reserves
κ_E	-	c	fraction of rejected flux of reserves that returns to reserves
κ_G	-	c	fraction of growth energy fixed in structure: $\frac{[E_V]}{[E_G]} = \frac{\mu_V [M_V]}{[E_G]} = \frac{\mu_V}{\mu_E} y_{VE}$
κ_P	-	c	fraction of food energy fixed in faeces
κ_R	-	c	fraction of reproduction energy fixed in eggs
κ'_R	-	c	modified reproduction efficiency: $(1 - \kappa)\kappa_R$
κ_X	-	c	fraction of food energy fixed in reserve
κ_V	-	c	fraction of energy in mobilised larval structure fixed in pupal reserve: y_{EV}^l/y_{EV}
$\bar{\mu}_*$	e # $^{-1}$	c	specific chemical potential of compound *
$\bar{\mu}_{T*}$	e # $^{-1}$	c	yield of heat on *
μ_{*1*2}	e # $^{-1}$	c	coefficient that couples energy flux * ₁ to mass flux * ₂ : η_{*2*1}^{-1}
$\bar{\mu}_{\mathcal{M}}$	e # $^{-1}$	c	vector of specific chemical potentials of ‘minerals’
$\bar{\mu}_{\mathcal{O}}$	e # $^{-1}$	c	vector of specific chemical potentials of organic compounds
$\bar{\mu}_*$	e # $^{-1}$	c	molar Gibbs energy of compound *
ξ_E^W	e m^{-1}	c	energy density of dry mass (excluding reproduction buffer)
ρ	-	c	binding probability of substrate
ρ_h	-	c	specific handling rate
$\dot{\sigma}$	e $T^{-1}t^{-1}$	v	rate of entropy production
τ	-	v	scaled time or age: typically $t\dot{k}_M$ or $a\dot{k}_M$
τ_b	-	v	scaled age at birth: $a_b\dot{k}_M$
τ_{Em}	-	c	scaled maximum reserve residence time: $t_{Em}\dot{k}_M = g^{-1}$
τ_h	-	v	scaled food handling interval: $t_h\dot{k}_M$
τ_j	-	v	scaled age at metamorphosis: $a_j\dot{k}_M$
τ_p	-	v	scaled age at puberty: $a_p\dot{k}_M$
$\phi_{\underline{x}}(x)$	$\text{dim}(x)^{-1}$	f	probability density function of \underline{x}

$\Phi_{\underline{x}}(x)$	-	f	distribution function of \underline{x} : $\int_{-\infty}^x \phi_{\underline{x}}(y) dy = \Pr\{\underline{x} \leq x\}$
ω_*	-	c	contribution of reserve to body weight or physical volume: $\omega_w = \frac{[E_m]}{d_V} \frac{w_E}{\mu_E}$
ω_j	-	c	contribution of larval structure to reserve at pupation: $\frac{\kappa_V}{\kappa} \frac{[M_V]\mu_V}{[E_G]} = \frac{\kappa_V}{\kappa} \frac{\mu_V}{\mu_{GV}}$

Notational elaborations

Since conservation of atoms gives $\mathbf{0} = \mathbf{n}_M \dot{\mathbf{J}}_M + \mathbf{n}_O \dot{\mathbf{J}}_O$ or $\dot{\mathbf{J}}_M = -\mathbf{n}_M^{-1} \mathbf{n}_O \dot{\mathbf{J}}_O$, we can write $\dot{\mathbf{J}}_M = \mathbf{y}_{MO} \dot{\mathbf{J}}_O$ with

$$\mathbf{y}_{MO} = -\mathbf{n}_M^{-1} \mathbf{n}_O = \begin{pmatrix} y_{CX} & y_{CV} & y_{CE} & y_{CP} \\ y_{HX} & y_{HV} & y_{HE} & y_{HP} \\ y_{OX} & y_{OV} & y_{OE} & y_{OP} \\ y_{NX} & y_{NV} & y_{NE} & y_{NP} \end{pmatrix}$$

in the case of the standard DEB model. This relationship links chemical indices to yield coefficients conceptually and clearly shows that yield coefficients are ratios of mass fluxes.

Notation differences between [1] and [2]

Some notational differences between first and second editions of the DEB book exist.

[1]	[2]	interpretation
m	k_M	maintenance rate coefficient
-	m_*	structure-specific molar mass of compound *
\dot{M}	\dot{p}_M	energy flux allocated to maintenance
\dot{H}	\dot{p}_T	energy flux allocated to heating
\dot{p}	\dot{h}	individual-specific predation probability rate
K	X_K	half saturation constant
$[G]$	$[E_G]$	energy requirement to grow a unit volume of structure
\dot{v}	\dot{k}_E	specific energy conductance (in V1-morphs)
\dot{D}	\dot{h}	dilution rate of chemostat
-	\dot{D}	diffusivity
\dot{I}	\dot{J}_X	ingestion rate
W_1	X_W	total biomass density in C-moles per volume

The motivation behind these changes was that the second edition deals more elaborately with masses and mass fluxes, which involves many new symbols. This made it necessary to link the symbol more closely to its dimension group.

Notation differences between [2] and [3]

Some notational differences between second and third editions of the DEB book exist.

The heating length is now called L_T rather than L_h to make a better link to \dot{p}_T . The (half) saturation coefficient is now called K , rather than X_K to simplify the notation.

L now means volumetric structural length, and L_w some physical length, in analogy with V_w . Since structure is an abstract concept, it has no shape, the label ‘volumetric’ in structural volumetric length is suppressed and L is called structural length. The use of physical length only makes sense if the length measure is defined and if growth is isomorphic.

Since the theory has been substantially extended, and new variables needed to be considered, quite a few new symbols appeared. Since the comments on DEB3 build on DEB3, the notation of DEB3 is followed, and new symbols are added in the list above.

Units

Where possible, the SI system for units of measurement is used:

A	ampere of electric current	At	ampere-turn of magnetomotive force
C	coulomb of electrical charge (1 C = 1 A S)	°C	degree Celsius (0 °C = 273.15 K)
cd	candela of luminous intensity	d	day of time (1 d = 24 h = 86.4 ks)
F	farad of electric capacitance (1 F = 1 C V ⁻¹)	g	gram of mass
h	hour of time (1 h = 3600 s)	H	henry of inductance (1 H = 1 Wb A ⁻¹)
Hz	hertz of frequency (1 Hz = 1 s ⁻¹)	J	joule of energy (1 J = 1 N m)
K	kelvin of temperature	l	liter of volume (1 l = 1 dm ³)
lm	lumen of luminous flux (1 lm = 1 cd sr ⁻¹)	lx	lux of illumination (1 lx = 1 lm m ⁻²)
m	meter of length	mol	mole of compound (1 mol = 6.02 10 ²³ molecules)
nt	nit of luminance	N	newton of power (1 N = 1 kg m s ⁻²)
Ω	ohm of resistance (1 Ω = 1 V A ⁻¹)	Pa	pascal of pressure (1 Pa = 1 N M ⁻²)
rad	radian of plane angle	s	second of time
S	siemens of electrical conduction (1 S = 1 Ω ⁻¹)	sr	steradian of solid angle
T	tesla of magnetic flux density (1 T = 1 Wb m ⁻²)	V	volt of potential difference (1 V = 1 W A ⁻¹)
W	watt of power (1 W = 1 J s ⁻¹)	Wb	weber of magnetic flux (1 Wb = 1 V s)

Standardized prefixes that can be used in combination with SI units:

10 ⁻¹⁸	a	atto-	10 ⁻¹⁵	f	femto-	10 ⁻¹²	p	pico-	10 ⁻⁹	n	nano-
10 ⁻⁶	μ	micro-	10 ⁻³	m	milli-	10 ⁻²	c	centi-	10 ⁻¹	d	deci-
10 ¹	da	deka-	10 ²	h	hecto-	10 ³	k	kilo-	10 ⁶	M	mega-
10 ⁹	G	giga-	10 ¹²	T	tera-	10 ¹⁵	P	peta-	10 ¹⁸	E	exa-

The unit ‘year’ is not part of the SI system. Modern tradition is followed to use the symbol ‘a’ (annum of time: 1 a ≈ 365.25 d = 31.56 Ms) for geohistorical dates before present and ‘yr’ for geohistorical periods. Both symbols can be combined with prefixes.

Preferred units

At the level of individuals, preferred units in DEB theory are

d	time	d ⁻¹	rate
cm	length	cm d ⁻¹	conductance
J	energy	J d ⁻¹	energy flux (1 J d ⁻¹ = 11.574 μW)
mol	mass	mol d ⁻¹	mass flux

Gram as unit for mass is only used if changes in chemical composition are possible, such as total body mass, otherwise mole or C-mole is used. All generalised compounds (i.e.

mixtures of a large number of chemical compounds that do not change in chemical composition) are quantified in C-mole and denoted as mole (since confusion can be excluded). Only for pure chemical compounds, such as urea, the full notation C-mole is essential.

Bibliography

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