

Supplements for:
Near-future ocean acidification impacts maintenance costs in sea-urchin larvae: identification of stress factors and tipping points using a DEB modelling approach

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1 Model description

1.1 Basic model

The basic DEBkiss model is schematically depicted in Figure 1, showing the mass fluxes J_* (in dry weight per unit of time). This model has been published in the open literature [4], but an extended version of that paper is available as a freely-downloadable e-book [3]. The e-book contains more explanation, more derivations, and more possible extensions of the basic model described here.

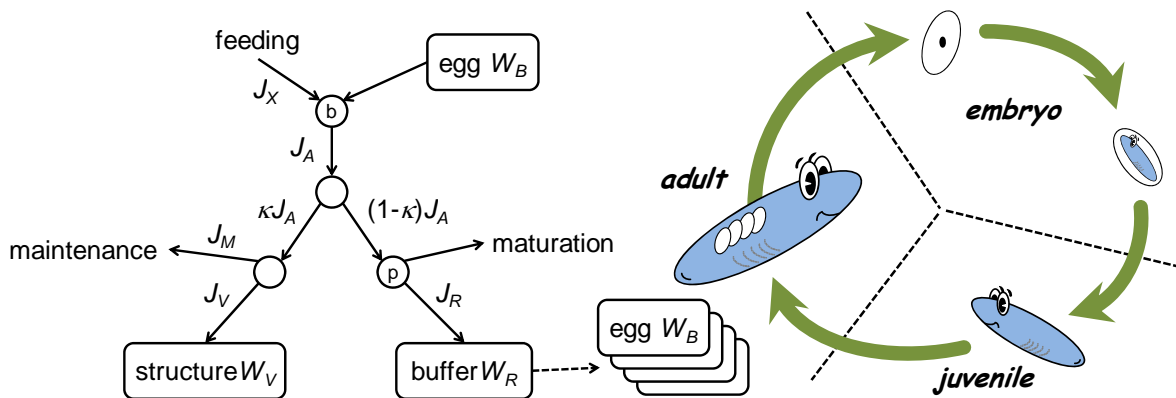


Figure 1: Schematic diagram of the energy flows and life cycle of a DEBkiss animal. The parameter symbols are explained in Table 1. The nodes b and p denote switches at birth (start of feeding; embryo to juvenile) and puberty (start of investment in the reproduction buffer; juvenile to adult). The other nodes represent a split of the assimilation fluxes.

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Table 1: Explanation of symbols, with dimensions given in mass (m for body, m_a for assimilates, and m_f for food), body length (l), numbers ($\#$), time (t). Suggested values for the yields (apart from y_{AV}) based on the typical values in [5].

Symbol	Explanation	Dimension	Sugg. value
Primary parameters			
f	Scaled functional response	f	—
J_{Am}^a	Maximum area-specific assimilation rate	$m_a/(l^2t)$	—
J_M^v	Volume-specific maintenance costs	$m_a/(l^3t)$	—
W_{B0}	Assimilates in a single freshly-laid egg	m_a	—
L_p	Volumetric length at puberty	l	—
y_{AV}	Yield of assimilates on structure (starvation)	m_a/m	0.8 mg/mg (dwt)
y_{AX}	Yield of assimilates on food	m_a/m_f	0.8 mg/mg (dwt)
y_{BA}	Yield of egg buffer on assimilates	m_a/m_a	0.95 mg/mg (dwt)
y_{VA}	Yield of structure on assimilates (growth)	m/m_a	0.8 mg/mg (dwt)
κ	Fraction of assimilation flux for soma	—	0.8
Conversions			
d_V	Dry-weight density of structure	m/l^3	
δ_M	Shape correction coefficient	—	
Fluxes and states			
J_A	Mass flux for assimilation	m_a/t	
J_M	Mass flux for maintenance	m_a/t	
J_R	Mass flux to reproduction buffer	m_a/t	
J_V	Mass flux for structure	m/t	
J_X	Mass flux of food	m_f/t	
W_B	Mass of assimilates buffer in egg	m_a	
W_R	Mass of reproduction buffer in adult	m_a	
W_V	Mass of structural body	m	
Other output			
L	Volumetric body length	l	
L_w	Physical body length	l	
ΔR	Number of eggs in a clutch	$\#$	
W_w	Physical body weight (total)	m	

The model departs from a set of assumptions, which lead to the model equations. The symbols, with their dimensions, are explained in Table 1. The first section of the table shows the primary parameters: parameters that are directly linked to a metabolic process, and that do not themselves depend on other parameters. Regarding notation, we use superscripts to indicate volume- or surface-area-specific parameters. Therefore, J_M^v is the volume-specific costs for maintenance, and J_{Am}^a is the area-specific assimilation rate at maximum food.

Assumptions 1: There are three types of biomass: food, assimilates and structural body components. Each type has a constant composition. They can be converted in each other with a certain constant efficiency. The state variables of the organism are the masses of the structural body, the reproduction buffer for adults, and the egg buffer used by the developing embryo. Total body mass is the sum of structure and reproduction buffer in adults, and the sum of structure and egg buffer for eggs. The reproduction and egg buffer consist of assimilates.

The ‘currency’ that we are going to follow in the model is mass as dry weight (e.g., in grammes). However, we can substitute mass for energy: because we assume that each type of biomass has a strictly constant composition, the conversions between mass and energy are also constant.

The total weight of the animal is the sum of structure and buffer ($W_w = W_V + W_R$), just like the total weight of an egg ($W_w = W_V + W_B$). For some processes, we need to have access to the structural volume (L^3) of the animal. We can assume a constant density for structure (d_V):

$$L^3 = \frac{W_V}{d_V} \quad (1)$$

We can talk about L as the ‘volumetric structural length’ of the animal. If the structural biomass W_V is compressed into a cube, this will be the length of a side of that cube.

In many cases, we measure body size of an animal as some physical length measure, such as the total body length. As long as the organism does not change in shape during growth, we can translate structural weight to some physical length (L_w) and vice versa using a constant correction factor δ_M :

$$L_w = \frac{L}{\delta_M} \quad (2)$$

Assumptions 2: The animal has three life stages: an embryo that does not feed but utilises the egg buffer, a juvenile that feeds but does not reproduce, and an adult that feeds and invests into a reproduction buffer. The embryo starts with an egg buffer of assimilates and negligible structural mass. The first transition (birth) is triggered by the depletion of the egg buffer, and the second transition (puberty) by reaching a critical structural body weight.

The differential equations for the egg buffer W_B , structural body mass W_V , and reproduction buffer W_R are given by (see Fig. 1):

$$\frac{d}{dt}W_B = -J_A \quad \text{until } W_B = 0, \text{ with } W_B(0) = W_{B0} \quad (3)$$

$$\frac{d}{dt}W_V = J_V \quad \text{with } W_V(0) \approx 0 \quad (4)$$

$$\frac{d}{dt}W_R = J_R \quad \text{with } W_R(0) = 0 \quad (5)$$

Note that $t = 0$ marks the start of development in the egg.

Assumptions 3: The maximum assimilation rate is proportional to the surface area of the animal. The entire process of food searching and handling is condensed into a scaled function response (f).

Assumptions 4: Food is instantly translated into assimilates that are directly used to fuel metabolic processes. Embryos assimilate their egg buffer at the maximum rate for their structural size.

Feeding involves the transport of resources from the environment to the organism across a surface area (e.g., the area of the gut, or the area of the feeding appendages in filter feeders). As long as the organism does not change in shape (isomorphy), all surface areas scale with body volume to the power $2/3$ (and thus L^2). The assimilation flux J_A is thus given by:

$$J_A = f J_{Am}^a L^2 \quad (\text{if } W_B > 0 \text{ then } f = 1) \quad (6)$$

where f is the scaled functional response, which is the actual feeding rate at a certain food level divided by the maximum feeding rate for its current size. The scaled response f is thus between 0 (no food) and 1 (*ad libitum* food). The maximum specific assimilation rate (J_{Am}^a) is used as the primary parameter. The feeding rate (J_X) is derived from the assimilation flux using the yield of assimilates on food (y_{AX}):

$$J_X = \frac{J_A}{y_{AX}} \quad (\text{if } W_B > 0 \text{ then } J_X = 0) \quad (7)$$

If we do not need to follow feeding explicitly, we can use f as a primary model parameter. The assimilates are directly used in metabolism, and we thus do not consider any storage other than the reproduction buffer.

Assumptions 5: The flow of assimilates is split into a constant fraction κ for maintenance and structural growth (the soma), and $1 - \kappa$ for maturation and reproduction. From the κ flow, maintenance costs are paid first. Only structural biomass requires maintenance, which is proportional to its volume. The remainder of this flow is used for growth (with certain efficiency).

A constant κ has convenient properties, which compare favourably to other possible allocation rules [6]. A constant κ , together with the assumptions for assimilation and maintenance, leads to the commonly-observed von Bertalanffy growth curve in constant environments.

Maintenance is the, rather abstract, lump sum of all the processes needed to maintain the body's integrity. Assimilate buffers are assumed not to require maintenance, which is supported by the almost-complete lack of respiration in freshly-laid eggs. The flux for structural growth (J_V) can thus be specified as:

$$J_V = y_{VA}(\kappa J_A - J_M) \quad \text{with } J_M = J_M^v L^3 \quad (8)$$

where J_M^v is the volume-specific maintenance cost, and y_{VA} is the yield of structural biomass on assimilates.

Assumptions 6: For adults, the $1 - \kappa$ flow is used to fill the reproduction buffer. For embryos and juveniles, all assimilates in this flux are burnt to increase complexity of the organism (maturation). At spawning events, the contents of the reproduction buffer are converted into eggs. The part of the buffer that was insufficient to create a single egg remains in the buffer. Transformation of buffer to egg comes with a certain (generally high) efficiency.

Before reaching 'puberty', the $1 - \kappa$ flux is used for the maturation process (which in this model definition is not associated with the build-up of biomass), which abruptly stops at puberty, when the flux is switched to the reproduction buffer. The flux into the reproduction buffer (J_R) can thus be specified as:

$$J_R = (1 - \kappa)J_A \quad (\text{if } L < L_p \text{ then } J_R = 0) \quad (9)$$

where L_p is the volumetric length at puberty. The trigger for spawning is not specified here, as this is highly species-specific. Spawning leads to a clutch of offspring ΔR , and a reset of the reproduction buffer W_R :

$$\Delta R = \text{floor} \left(\frac{y_{BA}W_R}{W_{B0}} \right) \quad (10)$$

$$W_R = W_R - \frac{\Delta R W_{B0}}{y_{BA}} \quad (11)$$

where y_{BA} is the yield for the conversion of reproduction buffer to eggs. The 'floor' function for the spawning events means rounding to the nearest integer less than the value between brackets.

Assumptions 7: If feeding is insufficient to pay somatic maintenance costs, the organism first diverts energy from the $1-\kappa$ flux of assimilates and from the reproduction buffer. If that is insufficient, structure is converted into assimilates to pay maintenance.

We need assumptions to deal with the situation of starvation, as varying food levels are common in the field, and because our animal does not have a storage of assimilates (other than the reproduction buffer). The first stage of starvation occurs when the allocated flux to the soma is insufficient to pay maintenance ($\kappa J_A < J_M$), but the total assimilation flux is enough ($J_A > J_M$), or there is still something in the reproduction buffer ($W_R > 0$):

$$J_V = 0 \quad (12)$$

$$J_R = J_A - J_M \quad (\text{if } L < L_p \text{ then } J_R = 0) \quad (13)$$

For juveniles, this means that energy is diverted from the flux to maturation, as long as $J_A > J_M$ (maturation itself is not followed as a state variable). In the second stage of starvation, the reproduction buffer is empty ($W_R = 0$) and the total assimilation flux is insufficient to pay maintenance ($J_A \leq J_M$):

$$J_V = (J_A - J_M)/y_{AV} \quad (14)$$

$$J_R = 0 \quad (15)$$

where y_{AV} is the yield of assimilates (to pay maintenance) on structure. The maximum rates of feeding, assimilation and maintenance depend on structural size, so when the animal shrinks, these rates will decrease too. Clearly, shrinking under starvation cannot continue indefinitely. If situations of prolonged starvation are analysed, it makes sense to set a limit to shrinking, e.g., to a fraction of the maximum size that the individual has reached.

1.2 Link to von Bertalanffy growth

When the parameters are constant, the DEBkiss model will result in the von Bertalanffy growth pattern. The mathematical derivation is provided in [3], but is reiterated here shortly. Note that $L^3 = W_V/d_V$. We fill in the growth equation (Eq. 4 and 8) with the fluxes J_A and J_M , and use the scaled functional response f :

$$\frac{d}{dt}(d_V L^3) = 3d_V L^2 \frac{d}{dt}L = y_{VA} (\kappa f J_{Am}^a L^2 - J_M^v L^3) \quad (16)$$

$$\frac{d}{dt}L = \frac{y_{VA}}{3d_V} J_M^v \left(f \kappa \frac{J_{Am}^a}{J_M^v} - L \right) \quad (17)$$

At constant food and no stressor effects, we can obtain the von Bertalanffy growth equation, with as parameters the maximum volumetric length (L_m) and the growth rate constant (r_B):

$$\frac{d}{dt}L = r_B (f L_m - L) \quad (18)$$

$$L_m = \kappa \frac{J_{Am}^a}{J_M^v} \quad \text{and} \quad r_B = \frac{y_{VA}}{3d_V} J_M^v \quad (19)$$

1.3 Feeding rate

In DEBkiss, the feeding rate follows from the assimilation flux, compensating for the assimilation efficiency:

$$J_X = \frac{J_A}{y_{AX}} \quad (20)$$

Filling in the assimilation flux J_A leads to:

$$J_X = \frac{f}{y_{AX}} J_{Am}^a (\delta_M L_w)^2 \quad (21)$$

$$= \frac{f}{y_{AX}} J_{Am}^a \delta_M^2 L_w^2 \quad (22)$$

$$= a L_w^2 \quad (23)$$

Obviously, the compound parameter a relates to the fitted compound parameters L_{wm} and r_B . Combining the results from Eq. 19 with Eq. 22, we can make this link explicit:

$$a = L_{wm} r_B \frac{3f d_V \delta_M^3}{\kappa y_{AX} y_{VA}} \quad (24)$$

We have values for L_{wm} and r_B (from the fits on the body length data), we can set $f = 1$ (*ad libitum* food), and we might use not-unreasonable values for κ , y_{AX} and y_{VA} (Table 1). The remaining conversion factors are, however, more difficult to establish. The product $d_V \delta_M^3$ is the ratio between body dry mass (or carbon mass, when a is expressed on carbon basis) and physical body length cubed. Therefore, what is required are data on (carbon) weight at known body length.

1.4 Respiration flux

Respiration can be taken proportional to the total flux of assimilates that is dissipated. The dissipation flux is the sum of the assimilates used for maintenance (J_M) and maturation (J_H), plus the overheads for growth, reproduction and feeding. Introducing an additional subscript 'o' to specify overheads, the total dissipation flux (J_D in mg/d) is given by:

$$J_D = J_M + J_H + J_{Vo} + J_{Ro} + J_{Xo} \quad (25)$$

Animals on which respiration is measured are usually not fed, so we can ignore the overheads of feeding (also referred to as the heat increment of feeding). For larvae, we can also ignore the overheads of reproduction, thus reducing the respiration flux:

$$J_D = J_M + J_H + J_{Vo} \quad (26)$$

Next, we can fill in this equation from the fluxes as specified earlier:

$$J_D = J_M + (1 - \kappa) J_A + (1 - y_{VA}) (\kappa J_A - J_M) \quad (27)$$

$$= J_M + (1 - \kappa) J_A + (1 - y_{VA}) \kappa J_A - (1 - y_{VA}) J_M \quad (28)$$

$$= (1 - \kappa y_{VA}) J_A + y_{VA} J_M \quad (29)$$

$$= (1 - \kappa y_{VA}) f J_{Am}^a \delta_M^2 L_w^2 + y_{VA} J_M^v \delta_M^3 L_w^3 \quad (30)$$

$$= b L_w^2 + c L_w^3 \quad (31)$$

If we assume that respiration only results from somatic maintenance, we only have to consider the last term in this equation. The proportionality c links to the fitted parameter r_B . Combining the results from Eq. 19 with Eq. 30, we can make this link explicit:

$$c = r_B 3 d_V \delta_M^3 \quad (32)$$

Again, we need the product $d_V \delta_M^3$; the ratio between body dry mass (or carbon mass, when c is expressed on carbon basis) and physical body length cubed. To link dissipation in mg/d to oxygen use requires additional conversion factors (see [3]).

2 Detailed plots

2.1 Growth data for the replicates

For each replicate treatment, body lengths have been determined. These individual growth curves were used in the main text to derive the stress factor on assimilation as a function of pH. Within one study, all replicates were fitted simultaneously, only differing in their stress factor (the parameters r_B , L_{wm} and L_{w0} were forced to the same value for all replicates within a study). Figure 2 shows the fits to the data of Dorey *et al.* [2], Figure 3 the data of Stumpp *et al.* [7], and Figure 4 the data of Chan *et al.* [1].

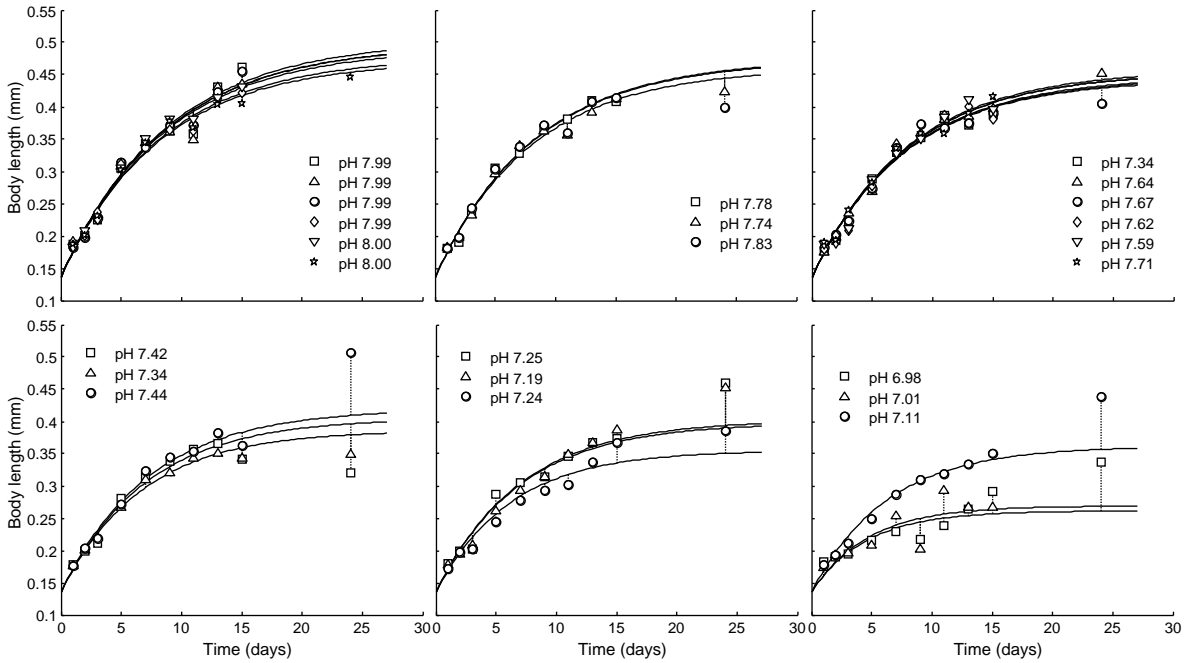


Figure 2: Model fits to the data of Dorey *et al.* [2]. All replicates are shown, grouped into their respective treatment groups.

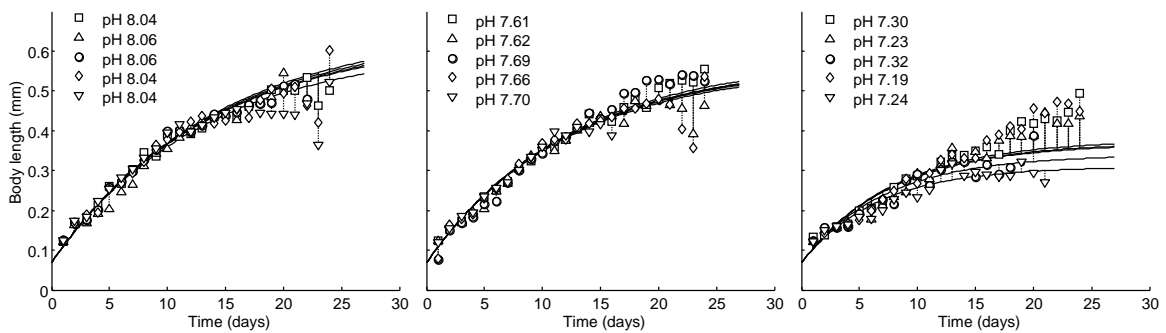


Figure 3: Model fits to the data of Stumpp *et al.* [7]. All replicates are shown, grouped into their respective treatment groups.

Figure 5 shows how the growth pattern in the reference treatment differs between the studies of [2], [1] and [7]. A model fit was made, assuming that the only parameters that are different in the latter study are the initial size and the maintenance costs (as a factor

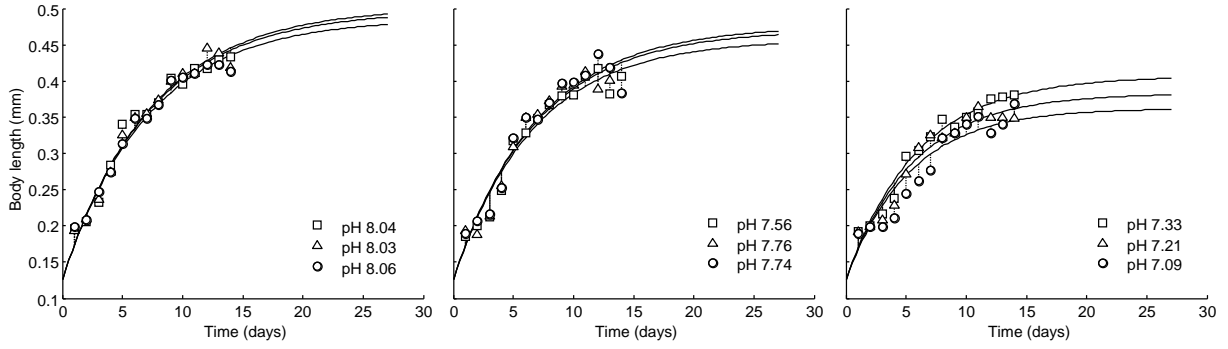


Figure 4: Model fits to the data of Chan *et al.* [1]. All replicates are shown, grouped into their respective treatment groups.

F_M on the maintenance in the other two studies). The difference in maintenance costs leads to differences in the parameters of the growth curve (r_B and L_{wm}).

Table 2: Parameter estimates for the fit in Figure 5, with 95% confidence intervals.

Symbol	Explanation	Value
L_{w0}	Initial body length in [2, 1] (mm)	0.15 (0.13-0.16)
	Initial body length in [7] (mm)	0.059 (0.042-0.075)
L_{wm}	Maximum body length in [2, 1] (mm)	0.51 (0.48-0.53)
r_B	Von Bertalanffy growth rate constant in [2, 1] (d^{-1})	0.11 (0.099-0.12)
F_M	Factor by which maintenance is lower in [7] (-)	1.07 (1.03-1.11)

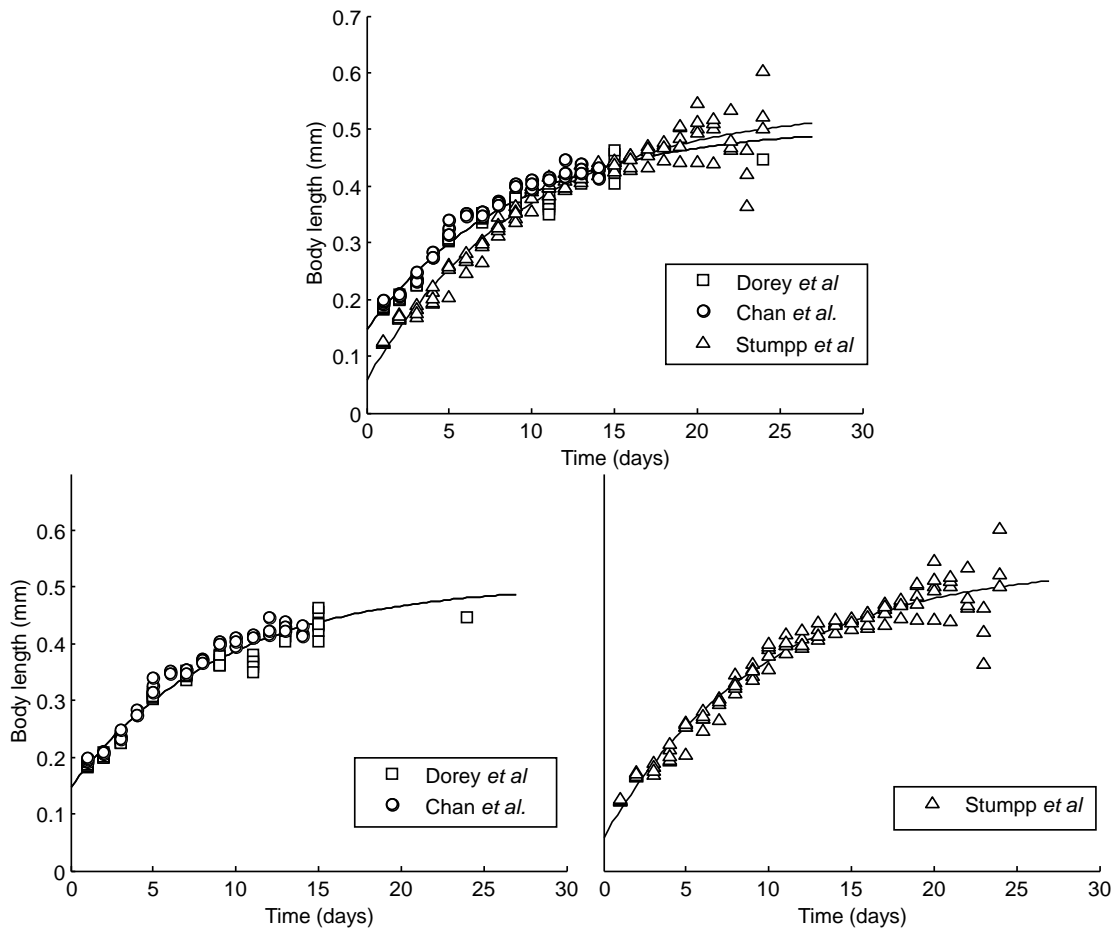


Figure 5: Model fits for the reference treatment of the data in [2], [1] and [7]. Top plot shows all data together; the bottom two plots provide the two fits separately. The fit to the data of [7] only differs in initial size and in maintenance costs.

2.2 Feeding and respiration

Figure 6 shows the feeding data from Stumpp *et al.* [7], with the three treatment groups in separate panels.

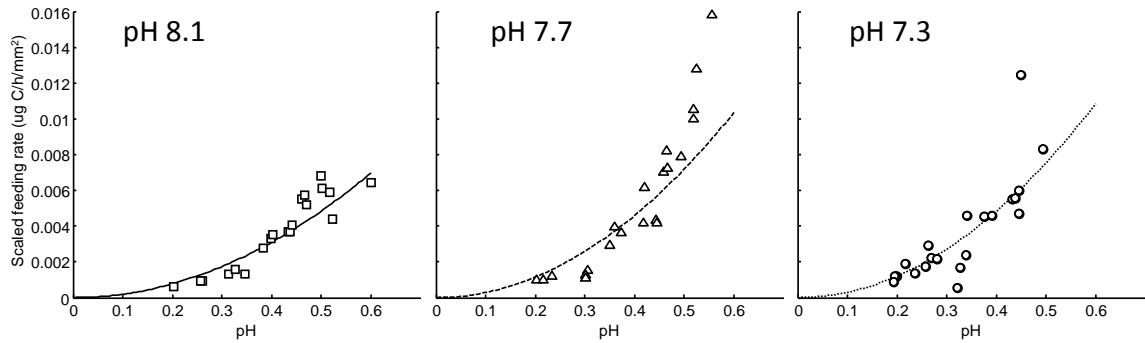


Figure 6: Feeding data from Stumpp *et al.* [7]. Line represents the average proportionality constant a (see Eq. 23).

Figure 7 shows the respiration data from Dorey *et al.* [2], with the six treatment groups in separate panels.

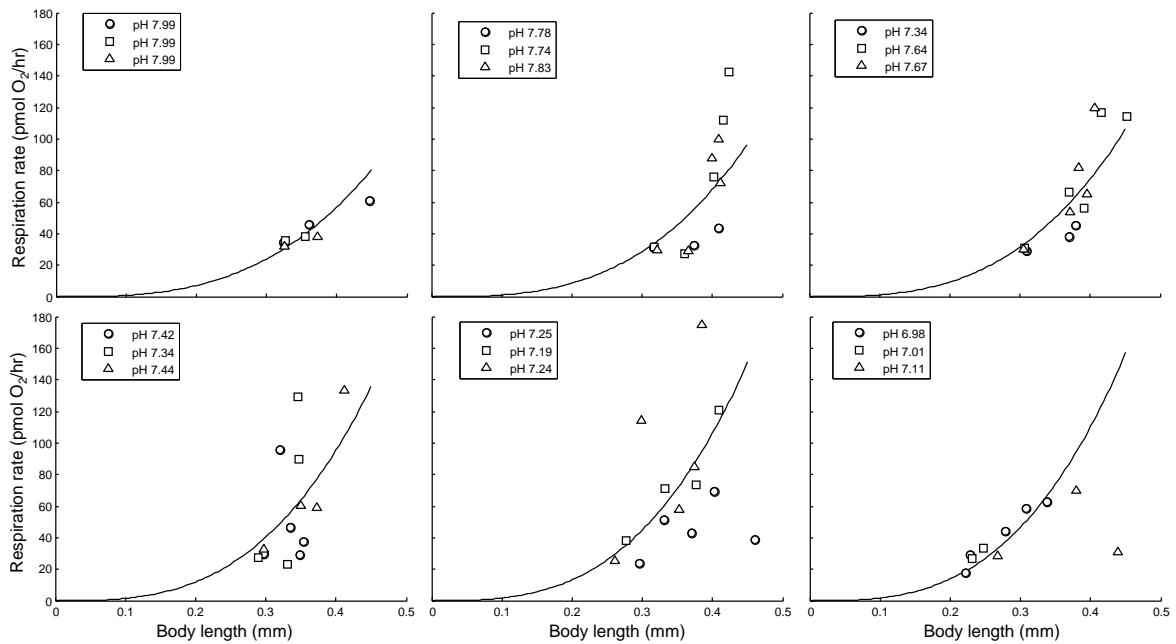


Figure 7: Respiration data from Dorey *et al.* [2]. Line represents the average proportionality constant b (see Eq. 31).

2.3 Stress factors

Figure 8 shows the stress factors as derived from the fits in Section 2.1, for each of the three studies.

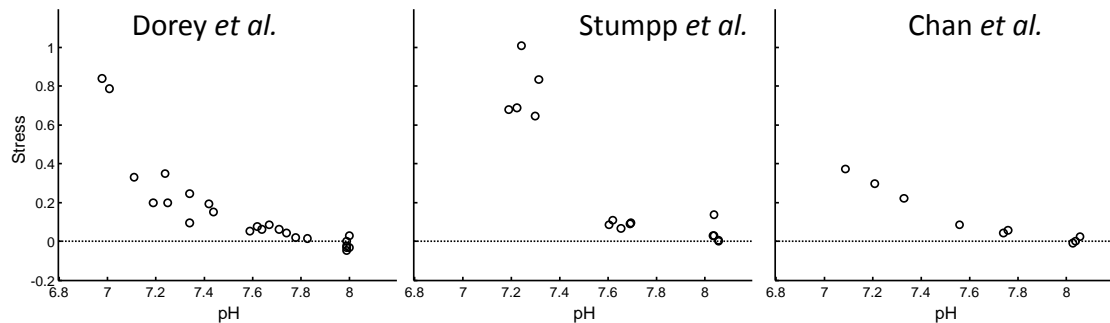


Figure 8: Stress factors versus pH as derived for each replicate in the three studies.

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