How light and nutrients affect life in a closed bottle *

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5\textsuperscript{*} oct 1998

Abstract

We evaluate the mass and energy turnover in a canonical community that lives in a closed bottle at steady state. We use daphnids, algae and bacteria, called the DAB-community, as example of a canonical community consisting of consumers, producers and decomposers. We built up the system in four steps, starting from the Monod model for the three biota, and include reserves, maintenance and population structure for the daphnids, where the individuals follow the rules as specified by the Dynamic Energy Budget theory. This theory provides the theoretical foundation for the widely applied method of indirect calorimetry, that relates dissipating heat linearly to carbon dioxide production, oxygen consumption and ammonia production. Our evaluation illustrates the application of thermodynamical principles in a very simple, spatially homogeneous, but non-degenerated community. In the full system, we follow the fate of 16 compounds partaking in 16 chemical transformations. Dissipating heat turns out to be a useful measure for the rate of living, which increases almost proportional to light intensity when effects of temperature are excluded. We also find that dissipating heat increases for decreasing total nitrogen. We derive explicit expressions for nutrient and biomass turnover and show their relation with dissipating heat, and community structure.

1 Introduction

Figure 1 illustrates the structure of an idealized, simple, three-component ecosystem. Producers use light and nutrients to produce organic matter, which is transformed by consumers, while decomposers release nutrients from the organic matrix [73]. The system is “open” to energy flow, but closed to inputs or removal of elemental matter. The structure, which might represent a closed bottle containing daphnids, algae and bacteria, is found in many ecosystems; for example, it is very similar to the one used for material turnover in microbial flocs in sea-water plankton systems [23, 50]. It can, therefore, be regarded as a canonical community. In this chapter, we describe an approach to developing parsimonious models of the flow of energy and nutrients in the canonical community.

\textsuperscript{*}In: Jørgensen, S. E. 2000 \textit{Thermodynamics and ecological modelling}. CRC Publ., Boca Raton, FL, USA, pages 19-60
Figure 1: The canonical community consists of three components: producers that gain energy from light and take up nutrients to produce biomass, consumers that feed on producers and decomposers that recycle nutrients from producers and consumers. The community is rather closed for nutrients, but requires a constant supply of energy. Influx and efflux of nutrients largely determine the long term behaviour of the community.

Nutrient dynamics affect not only the functioning of an ecosystem, but also governs structural aspects, such as the succession of algal species in sea water plankton [76]. The main nutrients that usually affect standing crops most drastically are nitrogen compounds, phosphate, iron, and silicon for diatoms [82, 19], while light can also be limiting [14, 30, 72]. The production of organic matter by phytoplankton has been suggested to play an important role in the euphotic zone [5], and implies a coupling between carbon and mineral fluxes. Model studies and mesocosm data, however, could not confirm the importance of this ‘microbial loop’ [77, 18]. Excretion of inorganic nutrients, such as carbon dioxide and ammonia, by consumers can also be important ‘non-consumptive top-down effects’ in aquatic ecosystems [85, 74]. Andersen [4] raised the question, whether zooplankton act as a source or a sink of nutrients, and concluded that this depends on the time scale and the fate of the individuals; a set of models suggested that the fraction of nutrients locked into zooplankton initially increases with increasing nutrient loading until a maximum is reached at some intermediate loading level. The roles of bacteria as consumers of minerals (i.e. competitors of algae) versus remineralizers (symbionts of algae) is still under discussion [35, 49]. It largely depends on the composition of detritus relative to that of bacteria; bacteria must take up more ammonia from the environment if the nitrogen content of detritus is poor. Thingstad and Pengerud [80] found that coexistence of algae and bacteria is only possible if the influx of nitrogen-poor organic matter from outside the system does not exceed a threshold value.

Ecosystem modeling commonly addresses questions that relate to a much larger scale in space and time than is relevant for individuals [91, 90]. Processes on totally different space/time scales combine poorly into a single model, implying that the fate of individuals will seldom be important at the ecosystem level. Our study explores strategies of discarding detailed information without affecting the overall dynamics of the system too much.

There are many existing model studies for DAB type communities. Some “strategic” models [84, 52, 61, 33, 32, 63] focus on the relative stability of closed ecosystems versus those that exchange elemental matter with their environment. Many more practical population, community and ecosystem models incorporate nutrient flow, because the effect of nutrient availability on algal growth is well recognized [62, 7, 78, 16, 17, 6, 10, 20, 36]. The models that we will study in this contribution differ from their predecessors in being fully closed for mass flow while still recognizing more than one element, and being fully dynamic. Moreover, we will study all chemical transformations and the detailed energetic aspects of a (very much) simplified system. In contrast, many of the previous studies of closed
Table 1: Table of frequently used symbols for variables. Dots refer to rates (dimension: time$^{-1}$), not to derivatives with respect to time, which are indicated by $\frac{d}{dt}$. Index $m$ refers to the maximum value. In the dimension column, $l$ means length, $t$ time. Table 5 gives labels of compounds and transformations, which are used as indices, Table 3 gives parameters. Since volumes will here only be used for *Daphnia*, the index $D$ will be suppressed.

<table>
<thead>
<tr>
<th>symbol</th>
<th>dim</th>
<th>interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$X_j$</td>
<td>mol $l^{-3}$</td>
<td>concentration of compound (substrate) $j$</td>
</tr>
<tr>
<td>$x_{ji}$</td>
<td>-</td>
<td>scaled substrate concentration $j$ for reserve $i$: $X_i/X_{K,ji}$</td>
</tr>
<tr>
<td>$V$</td>
<td>$l^3$</td>
<td>structural body volume: $M_V/[M_V]$</td>
</tr>
<tr>
<td>$M_{Ei}$, $M_V$</td>
<td>mol</td>
<td>mass of reserve $i$, structural biomass in C-moles</td>
</tr>
<tr>
<td>$m_{Ei}$</td>
<td>mol $E_i$</td>
<td>structure-specific reserves $i$: $M_{Ei}/M_V$</td>
</tr>
<tr>
<td>$\dot{J}<em>i$, $\dot{J}</em>{i,j}$</td>
<td>mol struc $t^{-1}$</td>
<td>flux of compound $i$ (involved in transformation $j$)</td>
</tr>
<tr>
<td>$j_i$</td>
<td>mol struc $t^{-1}$</td>
<td>structure-specific flux of compound $i$: $\dot{J}_i/M_V$</td>
</tr>
<tr>
<td>$\dot{p}_i$</td>
<td>$et^{-1}$</td>
<td>power $i$</td>
</tr>
<tr>
<td>$\dot{p}_T$</td>
<td>$et^{-1}$</td>
<td>dissipating heat</td>
</tr>
<tr>
<td>$f_i$</td>
<td>-</td>
<td>scaled functional response for reserve $i$</td>
</tr>
<tr>
<td>$\dot{r}_{V*,G*}$</td>
<td>$t^{-1}$</td>
<td>specific growth rate for structural mass <em>: $\dot{J}_{V</em>,G*}/M_{V*}$</td>
</tr>
<tr>
<td>$\dot{h}$</td>
<td>$t^{-1}$</td>
<td>hazard rate</td>
</tr>
</tbody>
</table>

systems only considered one element (e.g. carbon or nitrogen), while others assume fixed grazing rates by zooplankton, or fixed production rates by phytoplankton, implying fixed population sizes, while we consider these population sizes as part of the system.

The models in this chapter are based on Kooijman’s Dynamic Energy Budget (DEB) theory [41], which is described in more detail in section 2. This theory specifies all mass transformations (feeding, growth, reproduction, etc) at the individual level, and how they change during the life cycle. The transformations at the population level directly follows via addition of fluxes. The flux of organic matter through food webs is mainly set by body size scaling relationships, which may be derived directly from the DEB theory [41]. A promising DEB-based approach to an extension to the ecosystem level is via mass conversion at the population level [42, 44], in combination with energy and mass conservation laws at the whole system level. The gist of this approach is that the link between the metabolic properties of individuals and community and ecosystem performance is still preserved. A particularly simple situation, discussed later in this chapter, arises if organisms change shape during growth in such a way that surface area is proportional to volume. For these organisms, called 1D-isomorphs, the DEB theory becomes really simple, and can be considered as a generalization of the models by Monod (no maintenance or reserves), Marr-Pirt (no reserves) and Droop (no maintenance).

To separate the community and ecosystem level questions from population dynamics, and to study the effects of different model components, we will discuss a (short) series of related models of the DAB system within the DEB-framework that span a range of levels of complexity. The extended Monod model for the three biota represents the simplest model.

A DEB model for 1D-isomorphs with one or two types of reserves for the algae takes an intermediate position, and, finally, we consider the daphnids to be 3D-isomorphs (defined in the next section), which is much more realistic, but also more complex.
Table 2: Chosen values for the mass-mass couplers $y_{i,j} = \frac{\text{mole of compound } i}{\text{mole of compound } j}$

<table>
<thead>
<tr>
<th>$y_{ED,VA}$</th>
<th>$y_{ED,E_A}$</th>
<th>$y_{ED,E_B}$</th>
<th>$y_{ED,VB}$</th>
<th>$y_{ED,EB}$</th>
<th>$y_{PA,VA}$</th>
<th>$y_{PB,VB}$</th>
<th>$y_{EB,PA}$</th>
<th>$y_{EB,PE}$</th>
<th>$y_{EB,PE}$</th>
<th>$y_{EB,VB}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3</td>
<td>0.8</td>
<td>0.8</td>
<td>0.3</td>
<td>0.8</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
<td>0.9</td>
<td>2.5</td>
<td>1.5</td>
</tr>
</tbody>
</table>

2 A DEB representation of the DAB community

A closed bottle, completely filled with water containing daphnids, algae and bacteria constitutes the DAB community, which is completely closed from its surroundings in terms of mass exchange, while dissipating heat that is generated from metabolic processes and from absorbed light can leave the bottle with such ease that the temperature in the bottle equals that of its surroundings, which is assumed to be constant.

The foundation of our representation of DAB ecosystem dynamics is a dynamic energy budget (DEB) model incorporating information on the physiology of individuals [41, and references therein]. DEB models use differential equations to describe the rates at which individual organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment, (food density, temperature, toxicant levels, etc.). Solutions of the model equations represent the life history of individual organisms in a potentially variable environment.

In Kooijman’s model, input of energy to an organism is assumed to involve transfer of material across surfaces (gut wall, membranes of cells and organelles, etc.), before it is spent on volume dependent processes, such as growth and maintenance. The geometry of the organism determines how the areas of the critical surfaces scale with size; thus organisms are characterized as ‘1D isomorphs’ (where organisms change shape during growth in such a way that surface area is proportional to volume) or ‘3D isomorphs’ (where surface area is proportional to volume $^{2/3}$. Somatic and reproductive tissues compete for available energy, and the organism aims at a stable internal environment (homeostasis), in which the relative proportions of structural tissue and energy reserves are related to the food environment. Structural material and reserves are conceived as different generalized compounds, i.e. rich mixtures of chemical compounds, mainly consisting of proteins, lipids and carbohydrates, which allows relatively simple relationships between different size measures (volumes, weights, C-moles).

Here, we shall assume that all living components of the DAB system (daphnids, algae and bacteria) have one type of structural body mass, and one type of reserves, but that the algae have two types of reserves (one with and one without nitrogen, so a protein-rich reserve and a carbohydrate/lipid-rich one). The daphnids feed on bacteria and algae, algae feed on light, carbon dioxide and ammonia, bacteria feed on feces and dead corpses of daphnids.

For simplicity’s sake, we make a series of not always extremely realistic assumptions about the DAB system. Our main purpose is not to maximize on realism, but to show which processes contribute to mass and energy turnover, and how. The less realistic assumptions can be avoided or replaced by more realistic ones, but this needs extra parameters. The assumptions are

- The volume change involved in any of the chemical transformations is negligibly small,
Table 3: Parameters and their chosen values. The mass-mass couplers are given in Table 2, chemical indices in Table 5. Length measures refer to volumetric lengths, which equal 0.526 times body lengths for *Daphnia*.

<table>
<thead>
<tr>
<th>symbol</th>
<th>unit</th>
<th>value</th>
<th>interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>([M_{VD}])</td>
<td>mol/cm(^3)</td>
<td>0.04</td>
<td>structural mass density of <em>Daphnia</em>: (M_{VD}/V)</td>
</tr>
<tr>
<td>(X_{K,VA})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of algae for <em>Daphnia</em></td>
</tr>
<tr>
<td>(X_{K,VB})</td>
<td>mol/dm(^3)</td>
<td>5</td>
<td>half-saturation constant of bacteria for <em>Daphnia</em></td>
</tr>
<tr>
<td>(X_{K,L1})</td>
<td>mol/dm(^3)</td>
<td>5</td>
<td>half-saturation constant of light for algal reserves 1</td>
</tr>
<tr>
<td>(X_{K,C1})</td>
<td>mol/dm(^3)</td>
<td>1</td>
<td>half-saturation constant of CO(_2) for algal reserves 1</td>
</tr>
<tr>
<td>(X_{K,L2})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of light for algal reserves 2</td>
</tr>
<tr>
<td>(X_{K,C2})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of CO(_2) for algal reserves 2</td>
</tr>
<tr>
<td>(X_{K,N2})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of ammonia for algal reserves 2</td>
</tr>
<tr>
<td>(X_{K,PA})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of alga-faeces for bacteria</td>
</tr>
<tr>
<td>(X_{K,PB})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of bacterium-faeces for bacteria</td>
</tr>
<tr>
<td>(X_{K,PV})</td>
<td>mol/dm(^3)</td>
<td>2</td>
<td>half-saturation constant of <em>Daphnia</em>-struc. mass for bacteria</td>
</tr>
<tr>
<td>(X_{K,PE})</td>
<td>mol/dm(^3)</td>
<td>1</td>
<td>half-saturation constant of <em>Daphnia</em>-reserves for bacteria</td>
</tr>
<tr>
<td>({\dot{J}_{VA,AD,m}})</td>
<td>mol/h mm(^2)</td>
<td>1.5</td>
<td>maximum specific ingestion rate of algae by <em>Daphnia</em></td>
</tr>
<tr>
<td>({\dot{J}_{VB,AD,m}})</td>
<td>mol/h mm(^2)</td>
<td>1.25</td>
<td>maximum specific ingestion rate of bacteria by <em>Daphnia</em></td>
</tr>
<tr>
<td>(j_{E1,A,A,m})</td>
<td>mol/h mol</td>
<td>6.0</td>
<td>maximum specific synthesis rate of algal reserves 1</td>
</tr>
<tr>
<td>(j_{E2,A,A,m})</td>
<td>mol/h mol</td>
<td>4.0</td>
<td>maximum specific synthesis rate of algal reserves 2</td>
</tr>
<tr>
<td>(j_{PA,A1,B,m})</td>
<td>mol/h mol</td>
<td>3.0</td>
<td>maximum specific uptake rate of alga-faeces by bacteria</td>
</tr>
<tr>
<td>(j_{PB,A2,B,m})</td>
<td>mol/h mol</td>
<td>3.0</td>
<td>maximum specific uptake rate of bacterium-faeces by bacteria</td>
</tr>
<tr>
<td>(j_{PV,A3,B,m})</td>
<td>mol/h mol</td>
<td>2.0</td>
<td>maximum specific uptake rate of <em>Daphnia</em>-struc. mass by bacteria</td>
</tr>
<tr>
<td>(j_{PE,A4,B,m})</td>
<td>mol/h mol</td>
<td>3.0</td>
<td>maximum specific uptake rate of <em>Daphnia</em>-reserves by bacteria</td>
</tr>
<tr>
<td>(j_{ED,MD})</td>
<td>mol/h mol</td>
<td>0.8</td>
<td>specific maintenance costs for <em>Daphnia</em> reserves</td>
</tr>
<tr>
<td>(j_{E1,MA})</td>
<td>mol/h mol</td>
<td>0.5</td>
<td>specific maintenance costs for algal reserves 1</td>
</tr>
<tr>
<td>(j_{E2,MA})</td>
<td>mol/h mol</td>
<td>0.1</td>
<td>specific maintenance costs for algal reserves 2</td>
</tr>
<tr>
<td>(j_{E1,BMB})</td>
<td>mol/h mol</td>
<td>0.5</td>
<td>specific maintenance costs for bacterial reserves</td>
</tr>
<tr>
<td>(\dot{k}_{E1,A})</td>
<td>h(^{-1})</td>
<td>6.0</td>
<td>turnover rate of algal reserves 1</td>
</tr>
<tr>
<td>(\dot{k}_{E2,A})</td>
<td>h(^{-1})</td>
<td>6.0</td>
<td>turnover rate of algal reserves 2</td>
</tr>
<tr>
<td>(\dot{k}_{EB})</td>
<td>h(^{-1})</td>
<td>3.0</td>
<td>turnover rate of bacterial reserves</td>
</tr>
<tr>
<td>(V_{b}^{1/3})</td>
<td>mm</td>
<td>0.42</td>
<td>volumetric length at birth (<em>Daphnia</em>)</td>
</tr>
<tr>
<td>(V_{p}^{1/3})</td>
<td>mm</td>
<td>1.32</td>
<td>volumetric length at puberty (<em>Daphnia</em>)</td>
</tr>
<tr>
<td>(g)</td>
<td>-</td>
<td>1.0</td>
<td>energy investment ratio (<em>Daphnia</em>)</td>
</tr>
<tr>
<td>(\kappa)</td>
<td>-</td>
<td>0.3</td>
<td>fraction of catabolic flux to growth plus som. maint. (<em>Daphnia</em>)</td>
</tr>
<tr>
<td>(\kappa_R)</td>
<td>-</td>
<td>0.8</td>
<td>fraction of reproduction flux to embryonic reserves (<em>Daphnia</em>)</td>
</tr>
<tr>
<td>(\kappa_{R1})</td>
<td>-</td>
<td>0.8</td>
<td>return fraction of rejected reserves 1 (alga)</td>
</tr>
<tr>
<td>(\kappa_{R2})</td>
<td>-</td>
<td>0.7</td>
<td>return fraction of rejected reserves 2 (alga)</td>
</tr>
</tbody>
</table>
Table 4: Conversions between volume-based, molar-based and energy-based quantities of the DEB model. Coefficients \([M_*]\) convert volume to C-moles (dimension: mole volume\(^{-1}\); the brackets [] refer to volume\(^{-1}\), while the braces { } refer to surface area\(^{-1}\)). The energy-mass coupler \(\mu_{s_1s_2}\) couples energy flux \(\star_1\) to mass flux \(\star_2\) (dimension energy per mole). The chemical potential \(\mu_*\) also has dimension energy per mass, but cannot be interpreted as ratio of fluxes. The mass-mass coupler \(y_{s_1,s_2}\), also known as yield or stoichiometric coefficient, is a ratio of mass fluxes and taken to be constant, just like other couplers. We have \(y_{s_1,s_2} = y_{s_1,s_1}^{-1}\), \(y_{s_1,s_2}y_{s_2,s_3} = y_{s_1,s_3}\) and \(\eta_{s_1s_2} = \mu_{s_2s_1}^{-1}\) is a mass-energy coupler. Volumes are indicated with \(V\), masses in C-moles with \(M\), structure-specific masses with \(M_* = M/M_V\). Mass fluxes in C-moles per time are indicated with \(\dot{J}_s\) (the dot refers to time\(^{-1}\)), structure-specific mass fluxes with \(j_* = \dot{J}_s/M_V\). Energy fluxes (i.e. powers) are indicated with \(\dot{p}\). Index \(X\) refers to food, \(P\) to product (feaces). The following conversions between volume-based and mole-based quantities hold, where the dimensions are indicated with \(l\) (length), \(m\) (mass), \(e\) (energy), \(t\) (time).

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Equation</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>struc volume</td>
<td>(V = \frac{M_V}{M_V})</td>
<td>(l^3)</td>
</tr>
<tr>
<td>reserve ener</td>
<td>(E = \mu_E M_E)</td>
<td>(e)</td>
</tr>
<tr>
<td>max struc vol</td>
<td>(E_m = \mu_E [M_e])</td>
<td>(\frac{e}{l^3})</td>
</tr>
<tr>
<td>scaled length</td>
<td>(l = \left(\frac{M_V}{M_V}\right)^{1/3} = \left(\frac{V}{l^3}\right)^{1/3})</td>
<td>(\frac{e}{l^3})</td>
</tr>
<tr>
<td>max spec ass</td>
<td>(\hat{p}<em>{Am} = \mu</em>{AX} {\dot{J}_{XAm}})</td>
<td>(\frac{e}{l^3})</td>
</tr>
<tr>
<td>ener conduct</td>
<td>(\dot{v} = \frac{\hat{p}<em>{Am}}{E_m} = \frac{\dot{J}</em>{XAm}}{[M_*]})</td>
<td>(\frac{l}{t})</td>
</tr>
<tr>
<td>maint rate</td>
<td>(\dot{k}<em>M = \frac{\hat{p}<em>M}{E_G} = \frac{\dot{J}</em>{EM} y</em>{VE}}{E})</td>
<td>(\frac{l}{t})</td>
</tr>
<tr>
<td>struc mass</td>
<td>(M_V = V [M_V])</td>
<td>(m)</td>
</tr>
<tr>
<td>reserve mass</td>
<td>(M_E = \frac{E}{\mu_E} = M_V \frac{y_{VE}}{y_{EG}})</td>
<td>(m)</td>
</tr>
<tr>
<td>assim food coupl</td>
<td>(\mu_{AX} = \frac{\hat{p}<em>{Am}}{[J</em>{XAm}]} = \frac{\mu_E}{y_{XE}})</td>
<td>(\frac{e}{m})</td>
</tr>
<tr>
<td>res chem pot</td>
<td>(\mu_E = \frac{[E_m]}{[M_*]})</td>
<td>(\frac{e}{m})</td>
</tr>
<tr>
<td>prod coupl</td>
<td>(y_{PX} = \frac{\mu_E}{\mu_{AP}} = \frac{\dot{J}<em>{EA}}{\dot{J}</em>{XA}})</td>
<td>(\frac{m}{m})</td>
</tr>
<tr>
<td>struc coupl</td>
<td>(y_{XE} = \frac{\mu_E}{\mu_{VG}} = \frac{\dot{J}<em>{VE}}{\dot{J}</em>{EG}})</td>
<td>(\frac{m}{m})</td>
</tr>
<tr>
<td>spec assim fl</td>
<td>(\dot{J}<em>{EA} = \dot{J}</em>{XA} y_{EX})</td>
<td>(\frac{m}{m})</td>
</tr>
<tr>
<td>assim flux</td>
<td>(\dot{J}<em>{EA} = \dot{J}</em>{EA} M_V = \dot{J}<em>{XA} y</em>{EX})</td>
<td>(\frac{m}{m})</td>
</tr>
</tbody>
</table>

For other symbols, refer to Table 4.
which implies that the pressure in the bottle is constant.

- Although the energy content of each photon depends on its wave length, we neglect this diversity and only count photons that can be used by algae to drive their metabolism. Biochemical evidence indicates that the photosynthetic system extracts a fixed amount of energy from each usable photon, the excess energy is lost as heat. The DAB community is optically thin enough to neglect self-shading. We will not include the processes of photo-adaptation and photo-inhibition.

- Apart from light and carbon dioxide, we only consider ammonia as a possibly limiting mineral nutrient. Although nitrate would be the most frequent nitrogen nutrient in natural systems, (aquatic) animals excrete ammonia, which can block nitrate uptake by algae efficiently, even at extremely low concentrations. This interaction would complicate our analysis. Although phosphate is frequently limiting in freshwater systems [25], and its inclusion gives no theoretical complications, we again exclude it for simplicity's sake. For the same reason, we also exclude production of organic excretions by algae.

- No chemical transformations occur other than via organisms; the pH in the environment is assumed to be constant. The transformations occur within cells, which keep all chemicals that participate directly in chemical transformations at constant and low levels. Carbonates and bicarbonates are included in the variable that stands for carbon dioxide, despite the fact that these compounds are not taken up by algae. This translates into the assumption that the association/dissociations in the CO$_2$/HCO$_3^-$/$H_2$CO$_3$-complex is fast with respect to algal uptake, so CO$_2$ is a constant fraction of the complex. Oxygen and water are assumed to be non-limiting. Daphnia can survive moderate oxygen stress, by making more hemoglobin, and is probably able to ferment. Fermentation, however, comes with a considerable reduction of the energy yield of food, which would complicate our analysis.

- Aging in bacteria and algae is sufficiently slow in relation to predation by Daphnia, that these processes can be neglected, so only Daphnia ages. We need this aging process to make sure that the life span of all organisms is limited.

- Digestion of the reserves of bacteria and algae by Daphnia is complete, which means that these compounds do not contribute to faeces; faeces is considered to be a leftover of the digestion of structural body mass of algae and bacteria. This assumption does not imply a high reserve yield. A substantial fraction of structural algal biomass consists of cellulose, which cannot be digested by Daphnia. Digestion of faeces and Daphnia corpusses by bacteria is complete, and only water, carbon dioxide and ammonia is formed. The result is that the molecules of all compounds have a limited life span. This is essential to make sure that the DAB system has a finite memory. We also assume that digestion is instantaneous, which implies that only structural body mass and reserves result from Daphnia that die from aging, and we do not have to consider their partially digested gut contents.

- Apart from the feeding relationships, we exclude all other forms of interactions between organisms, such as social interactions which might reduce feeding rate at high population density.

- No spatial structure exists. The minerals and organic products (Daphnia corpses and feces) are homogeneously distributed at the molecular level, daphnids, algae and
bacteria at the individual level. Although *Daphnia* corpses and fecal pellets do not dissolve instantaneously in reality, the resulting reduction in biodegradation is partially taken into account via the transfer parameters.

- We assume that the total amounts of all compounds in the DAB system have a point attractor in the parameter region of interest, and that the number of daphnids is sufficiently large that the size distribution is close to the stable size distribution. We expect, however, that the compounds have a stable limit cycle in the case of a structured consumer population, but the mean biomass levels will probably be close to the ones that we will derive for the point attractor. This value will be helpful anyway as a reference for the dynamical results.

- Algae and bacteria behave as 1D-isomorphs, daphnids as 3D ones (see the section on the DEB model), while reproduction is continuous in time. In reality, *Daphnia* reproduction is in clutches, which are produced in synchronization with the molting cycle. All continuous-time models for allocation require a buffer for allocation to reproduction, and rules specifying how this buffer converts to new offspring. We refrain from considering these details, however, which means that reproduction in the model occurs slightly earlier than it should, and that *Daphnia* corpses have less reserves for bacteria to digest. *Daphnia* usually reproduces parthenogenetically (diploid females give birth to new ones, without interference by males), although they can reproduce sexually. We assume that they don’t do this in our bottle.

In spite of this long list of simplifying assumptions, what is left is still rather complex and involves 16 compounds and 16 chemical transformations. Four of the compounds represent reserves, so the system might seem to allow further simplification, in view of the fact that internal reserves are commonly ignored in ecosystem models. Indeed, it is one of our purposes to uncover the most relevant processes involved in mass transformations in the system. Several arguments call for an inclusion of reserves in dynamic models, the most fundamental one being for consistency reasons. Models which include maintenance, but no reserves, may have internal inconsistencies, which become apparent during transient states. Since reserve densities (amounts of reserves per unit of structural biomass) are related to food densities, reserves decrease the substrate/structural biomass conversion, which means that they are also relevant for steady state phenomena at steady state. Furthermore, reserves of algae play an essential role in *Daphnia* nutrition, as explained in the assumption about digestion; algae can accumulate large amounts of carbohydrate reserves under nitrogen limiting conditions. Total algal carbon is not necessarily an adequate quantifier of the nutritional value for daphnids and reserves of algae substantially affect the nutritional value of algae for *Daphnia* [87]. Finally, comparison of the dynamics of models with and without explicit representation of reserves shows that reserves may influence the dynamics of the system profoundly [65, 80].

3 The DAB system

The chemical compounds and their transformations in the DAB community are presented in Table 5. When we replace the signs by model-dependent quantitative expressions, as discussed below, this turns Table 5 into a matrix that is known as scheme matrix [69], which will be indicated by matrix $\dot{J}$; element $i, j$ of matrix $\dot{J}$, called $\dot{J}_{i,j}$, gives the flux of
<table>
<thead>
<tr>
<th>Compounds</th>
<th>Minerals</th>
<th>Detritus</th>
<th>Daphnia</th>
<th>Algae</th>
<th>Bact</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L</td>
<td>C</td>
<td>H</td>
<td>O</td>
<td>N</td>
</tr>
<tr>
<td>Light</td>
<td>P</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
</tr>
<tr>
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<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Assim 2</td>
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<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Growth</td>
<td>A2+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Death</td>
<td>B+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 5: The chemical compounds of the DAB community and their transformations and indices. The + signs mean appearance, the − signs disappearance. The signs of the mineral fluxes depend on the chemical indices and parameter values. The labels on rows and columns serve as indices to denote mass fluxes and powers. So $\dot{J}_{C}$ denotes the vector of $C$-fluxes, while $\dot{J}_{C:GB}$ denotes the $C$-flux associated with the growth of bacteria. (Note that the table shows $\dot{J}^T$, rather than $\dot{J}$, if the signs are replaced by quantitative expressions.) The flux $\dot{J}_{C}^+$ adds all positive contributions in $\dot{J}_C$, and $\dot{J}_{C}^-$ all negative ones, so $\dot{J}_{C}^+ + \dot{J}_{C}^- = 0$. This applies to all compounds, but not for light. Index $M$ collects the 4 minerals, $O$ the 11 organic compounds; $J_{M:GB}$ denotes the 4 mineral fluxes that are associated with bacterial growth. $J_{O:GB}$ does the same for the 11 organic fluxes; $n_M$ collects the $4 \times 4$ chemical indices for minerals, $n_O$ is the $4 \times 11$ matrix of chemical indices for the organic compounds. Index $D$ refers to individual daphnids, and $+$ to the population of daphnids; Index A and B refer to individual algae and bacteria, as well as to their populations.
compound $i$ involved in transformation $j$. We quantify the compounds in terms of moles (for minerals) or C-moles (for organic compounds and biomass), and indicate the vector of moles of all compounds by $\mathbf{M}$. The concept of C-mole is a theoretical construct, where each ‘molecule’ has one C-atom and fractional amounts of the elements H, O and N. These fractions do not change in time, and other elements are neglected.

When the transformations can be written as functions of the total amount of moles of the various compounds, $\mathbf{M}$, the dynamics of $\mathbf{M}$ can be written as $\frac{d}{dt} \mathbf{M} = \mathbf{J} \mathbf{1}$, which just states that the change in masses equals the sum of the columns of the scheme matrix. This type of models are called unstructured population models, because they do not allow explicitly for differences between individuals. If individuals differ too much, and the frequency distribution of the various types of individuals changes rapidly, it becomes essential to turn to more advanced methods to quantify the processes [58, 83], but this is beyond the scope of this contribution. It is possible, however, to evaluate some properties of structured populations at steady state without resort to mathematically sophisticated techniques, because the frequency distribution of individuals among physiological states can be identified if it does not change in time.

Although we will formulate the full transient dynamics of the DAB community, the steady state dynamics is of special interest, because it is much simpler, due to the fact that a lot of information about the initial conditions becomes lost. The Jacobian $\frac{d}{dt} \mathbf{M}^T \mathbf{J} \mathbf{1}$ at steady state contains interesting information about the possible behaviour of the system close to the steady state.

### 3.1 Notation and symbols

Table 1 presents the notation and frequently used symbols, while Table 5 labels compounds and transformations. The substantial variety of compounds and processes forced us to use a rather elaborate notation that might seem clumsy at first glance, but minimizes stress on memory. The present notation allows an easy distinction between, e.g. the transformation of bacterial structural mass into faeces (by daphnids feeding on bacteria) and the backward transformation (by bacteria using faeces as substrate).

The leading symbol refers to the nature of the variable (e.g. $M$ stands for a molar mass, $\dot{J}$ for a molar flux). Dots refer to the dimension ‘per time’, and not to a time-derivative, which is indicated by $\frac{d}{dt}$. The first index identifies the compound, the second identifies the process (for fluxes). Organic compounds are coded in two characters (type and species): $V$ for structure, $E$ for reserves, $P$ for product (detritus), and $D$ for daphnids, $A$ for algae, $B$ for bacteria. Processes are also coded in two characters (type and species): $A$ for assimilation, $D$ for dissipation, $G$ for growth, $H$ for hazard, and again $D$, $A$, $B$ for daphnids, algae, bacteria. So $\dot{J}_{V,D,G,D}$ represents the molar flux ($\dot{J}$) of structural mass ($V$) of daphnids ($D$) that is involved in growth ($G$) of daphnids ($D$). If there is more than one compound or flux of the same type, they are simply numbered; $E_1A$ is the first reserve of algae, $A_2D$ is the second assimilation process for Daphnia. The sign of the flux indicates appearance (+) or disappearance (−), and can change in time. Yield coefficients $y$ have two two-character indices that refer to compounds; $y_{PA,VA}$ stands for the molar mass of algal product (faeces), $PA$, that is produced per mole of algal structural mass, $VA$, by daphnids. These yield coefficients are constants. Chemical indices $n$ have two indices as well, the first one specifies the chemical element, the second two-character index the compound; $n_{N,VA}$ stand for the number of nitrogen atoms, per carbon atom, in algal...
structural mass. These chemical indices are constants.

Table 4 gives some useful volume-mass conversions. Volumes (or lengths) are basic to the DEB model because of the assumption that uptake is proportional to surface area, molar masses are essential for mass balance equations.

## 4 The su-extended Monod model

Table 6 gives the simplest possible characterization of the compounds and transformations in the DAB-system. These are quantified in Table 7, as an introduction to the more extended discussion in the next section. The simple model results as a special case of the specification by the DEB theory, if the maintenance costs are small, the reserve turnover rates high, the reserve capacities low, while all living components can be conceived as 1D-isomorphs. The latter assumption is a realistic approximation for unicellular consumers that propagate by division, such as ciliates. The resulting model, the Monod model [38], boils down to the simple assumptions that food uptake is a hyperbolic function of food density and proportional to body mass, and growth is proportional to food uptake. The chemical composition of body mass is implicitly assumed to be constant, and the conversion from food into body mass and feaces is assumed to be fixed. Since this model basically handles just one type of food, we need to extend it to allow feeding on more than one type of food.

To apply the Monod model, we omit the 4 reserves, which leaves us with an 8-dimensional system: 2 types of minerals, 3 types of detritus and 3 populations. We also have to include growth into the process of assimilation, and assume a constant hazard rate for consumers. Oxygen and water are not included, because they are assumed to be non-limiting. They can be easily included, however, on the basis of the conservation law for elements. The prime in $y_{V_B,P_B}$ in Table 7 just indicates that, generally, $y_{V_B,P_B} \neq y_{P_B,V_B}^{-1}$, a notational rule that otherwise would apply; one conversion relates to the digestion process of daphnids, the other to the assimilation by bacteria. Figure 2 illustrates how the steady states of masses depend on the environmental parameters total carbon, total nitrogen and light.

The Monod model cannot have non-trivial steady states for $y_{P_B,V_B}^{-1} \leq y_{V_B,P_B}$. This can be seen from the system in Table 7, when we set $\frac{d}{dt} M_{P_B} = \frac{d}{dt} M_{V_B} = 0$, and try to solve the equilibrium explicitly. Such an exercise reveals that no positive solution can exist for the three detritus species, which implies cyclic non-trivial attractors (if any). The same holds for the equivalent Lotka-Volterra model, where the hyperbolic functional responses are replace by linear ones. It is not really likely, however, that $y_{P_B,V_B}^{-1} \leq y_{V_B,P_B}$, because
The extended Monod model for daphnids ($V_D$), algae ($VA$), and bacteria ($VB$) in a confined environment (no maintenance or reserves, all three components conceived as 1D-isomorphs). Detritus includes alga-feaces ($PA$), bacterium-feaces ($PB$), and dead daphnids ($PV$). Carbon dioxide ($C$) and ammonia ($N$) are obtained from the balance equation for carbon and nitrogen. The variables $x$ refer to the scaled mass densities: $x_{PA} = M_{PA}/X_{K,PA}$, $x_{PB} = M_{PB}/X_{K,PB}$, $x_{PV} = M_{PV}/X_{K,PV}$, $x_A = M_{VA}/X_{K,VA}$, $x_B = M_{VB}/X_{K,VB}$, $x_L = J_L/J_{K,L}$, $x_N = M_N/X_{K,N}$, $x_C = M_C/X_{K,C}$, where $J_L$ is the light flux that is supplied to the system to keep it going.

$$
\begin{align*}
\dot{J}_{VA,AD} &= -M_{VD} \dot{J}_{VA,AD,m} \frac{x_A}{1 + x_A + x_B} \\
\dot{J}_{PA,AD} &= -y_{PA,VA} \dot{J}_{VA,AD} \\
\dot{J}_{VB,AD} &= -M_{VD} \dot{J}_{VB,AD,m} \frac{x_B}{1 + x_A + x_B} \\
\dot{J}_{PB,AD} &= -y_{PB,VB} \dot{J}_{VB,AD} \\
\dot{J}_{VD,GD} &= -\dot{J}_{VA,AD} y_{VD,VA} - \dot{J}_{VB,AD} y_{VD,VB} \\
\dot{J}_{PV,HD} &= M_{VD} \dot{h} \\
\dot{J}_{VA,GA} &= M_{VA} \dot{J}_{VA,GA,m} f_A \text{ with for } * \in \{L, N, C\} \\
f_A &= \left(1 + \sum \frac{x_A}{\sum x_*} - \left(\sum x_*\right)^{-1} \left(\sum x_*\right)^{-1} \left(\sum x_*\right)^{-1} \left(\sum x_*\right)^{-1}\right)^{-1} \\
\dot{J}_{PA,AB} &= -M_{VB} \dot{J}_{PA,AB,m} \frac{x_{PA}}{1 + x_{PA} + x_{PB} + x_{PV}} \\
\dot{J}_{PB,AB} &= -M_{VB} \dot{J}_{PB,AB,m} \frac{x_{PB}}{1 + x_{PA} + x_{PB} + x_{PV}} \\
\dot{J}_{PV,AB} &= -M_{VB} \dot{J}_{PV,AB,m} \frac{x_{PV}}{1 + x_{PA} + x_{PB} + x_{PV}} \\
\dot{J}_{VB,GB} &= -\dot{J}_{PA,AB} y_{VB,PA} - \dot{J}_{PB,AB} y_{VB,PB} - \dot{J}_{PV,AB} y_{VB,PV} \\
\frac{d}{dt} M_{PA} &= \dot{J}_{PA} = \dot{J}_{PA,AD} + \dot{J}_{PA,AB} \\
\frac{d}{dt} M_{PB} &= \dot{J}_{PB} = \dot{J}_{PB,AD} + \dot{J}_{PB,AB} \\
\frac{d}{dt} M_{PV} &= \dot{J}_{PV} = \dot{J}_{PV,HD} + \dot{J}_{PV,AB} \\
\frac{d}{dt} M_{VA} &= \dot{J}_{VA} = \dot{J}_{VA,GA} + \dot{J}_{VA,AD} \\
\frac{d}{dt} M_{VB} &= \dot{J}_{VB} = \dot{J}_{VB,AD} + \dot{J}_{VB,GB} \\
\frac{d}{dt} M_{C} &= \dot{J}_{C} = -\dot{J}_{PA} - \dot{J}_{PB} - \dot{J}_{PV} - \dot{J}_{VD} - \dot{J}_{VA} - \dot{J}_{VB} \\
\frac{d}{dt} M_{N} &= \dot{J}_{N} = -0.1 \dot{J}_{PA} - 0.1 \dot{J}_{PB} - 0.2 \dot{J}_{PV} - 0.2 \dot{J}_{VD} - 0.2 \dot{J}_{VA} - 0.2 \dot{J}_{VB}
\end{align*}
$$
Figure 2: The steady state distribution of carbon and nitrogen in the DAB-community while increasing the total amount of carbon (upper left), nitrogen (upper right) or light (lower panels), using the extended Monod model. The non-changed amounts are 1 unit for carbon, 0.2 units for nitrogen, and 5 for light. The amounts of carbon and nitrogen are plotted cumulative, from bottom to top, across the minerals (carbon dioxide, C, or ammonia, N), detritus (P, three types, gray shaded), daphnids (i.e. consumers C), algae (i.e. producers P, gray shaded), and bacteria (i.e. decomposers D). Parameters: $j_{VA,AD,m} = 1.25$, $j_{VB,AD,m} = 1.25$, $X_{K,VA} = 2$, $X_{K,VB} = 5$, $j_{VA,GA,m} = 1.8$, $X_{K,L2} = 5$, $X_{K,C2} = 2$, $X_{K,N2} = 0.2$, $j_{PA,AB,m} = 3$, $j_{PB,AB,m} = 3$, $j_{PV,AB,m} = 2$, $X_{K,PA} = 2$, $X_{K,PB} = 2$, $X_{K,PV} = 2$, $h = 0.01$, $y_{VD,VA} = 0.2$, $y_{VD,VB} = 0.2$, $y_{PA,VA} = 0.8$, $y_{PB,VB} = 0.8$, $y_{VB,PA} = 0.35$, $y_{VB,PB} = 0.3$, $y_{VB,PV} = 0.35$. 


it would imply that daphids can extract more energy from the conversion of bacterial structural mass to feacal product, than bacteria invest to reverse the reaction.

The details of the model, such as the concept of the Synthesizing Unit, are discussed in the next section, but we shall first mention degenerated models that allow mathematical analysis.

4.1 Degenerated simplifications

A number of authors [61, 67] have studied a degenerated closed system with a single nutrient, say nitrogen, one producer and one consumer, where decomposition is instantaneous, the amount of decomposers negligibly small, and functional responses linear, as in the Lotka-Volterra model. It can be obtained from the hyperbolic functional response by increasing the maximum intake, as well as the saturation constant, such that their ratio remains constant. Rewritten in the present notation, that model reduces to

\[
\frac{d}{dt} M_{VA} = (j_{VA,GAm} M_N/X_{K,N} - j_{VA,AD,m} M_{VD}/X_{K,VA})M_{VA} \\
\frac{d}{dt} M_{VD} = (y_{VD,VA} j_{VA,AD,m} M_{VA}/X_{K,VA} - \dot{h})M_{VD} \\
\frac{d}{dt} M_{N} = -n_{N,VA} \frac{d}{dt} M_{VA} - n_{N,VD} \frac{d}{dt} M_{VD}
\]

The model is degenerated because it neglects bacteria in the mass balance, while it assumes that their action, decomposition, is infinitely fast. The equilibrium of this system can easily be calculated, for any given (constant) amount of total nitrogen in the system. The Jacobian of the system always has one eigenvalue 0 implying that the equilibrium is locally stable. As a general rule, simple prey-predator systems tend to oscillate and systems with additional degrees of freedom may exhibit a wide repertoire of exotic dynamics. The analysis of this simple model suggests that the explicit inclusion of nutrient recycling might have a stabilizing effect in more complex models. This point is explored in more detail by Gurney and Nisbet [24, pages 195-200].

5 The DEB model

The assumptions on which the DEB theory is based are listed in Table 11. This theory aspires to apply to all organisms, but the selection of assumptions listed here does not cover, inter alia endotherms, foetal development (see [41] for them), and plants (which require roots as well as shoots as types of structural biomass). Tables 9 and 10 show that the simplest version of the DEB model can be summarized in compact form, on the basis of relationships between energy fluxes and volumes (or lengths). We here need to include mineral fluxes, and introduce the DEB model stepwise on the basis of molar fluxes. To this end, we will specify all organic (i.e. non-mineral) fluxes and the mineral fluxes involved in algal assimilation as consequences of these assumptions, while the remaining mineral fluxes and dissipating heat will follow from the mass and energy conservation laws. We discuss the fluxes as if the densities of all compounds in the bottle are known, and later show how they can be obtained from mass balance considerations.

The DEB model is built on two state variables:
Table 8: The DEB model for the daphnids (VD), algae (VA), and bacteria (VB) system in a confined environment, when all three components conceived as 1D-isomorphs. The equations that replace or supplement the ones in Table 7 are given only. The additional scaled mass densities: $x_{PE} = M_{PE}/X_{K,PE}$, $x_{LA} = J_{L}/J_{K,LA}$, $x_{N} = M_{N}/X_{K,N2}$, $x_{Ci} = M_{C}/X_{K,Ci}$.

\[
\begin{align*}
\dot{J}_{E,D,A,D} &= -\sum_{*} y_{ED,*} J_{*,A,D} \quad \text{for} \ (i, *) \in \{(1, VA), (1, E_{1}A), (1, E_{2}A), (2, VB), (2, EB)\} \\
\dot{J}_{E,A,A,D} &= m_{E,A} j_{VA,A,D} \quad \text{for} \ i \in \{1, 2\}; \quad \dot{J}_{E,B,2D} = m_{EB} j_{VB,A_{2}D} \\
\dot{J}_{V,D,GD} &= M_{VD} \frac{m_{ED} k_{EB} - j_{ED,MD}}{m_{ED} + y_{VD,VD}}; \quad \dot{J}_{E,D,DD} = -j_{ED,MD} M_{VD} \\
\dot{J}_{P,V,HD} &= \dot{h}_{a} M_{VD} \frac{y_{VD,ED} m_{ED}}{1 + y_{VD,ED} m_{ED}}; \quad \dot{J}_{V,D,HD} = -\dot{J}_{P,V,HD} \\
\dot{J}_{P,E,HD} &= m_{ED} \dot{J}_{P,V,HD}; \quad \dot{J}_{E,D,HD} = -\dot{J}_{P,E,HD} \\
\dot{J}_{E_{1},A_{1},A_{1}} &= M_{VA} j_{E_{1},A_{1},AA,m} f_{A_{1}} \quad \text{with} \ f_{A_{1}} = \left(1 + \sum_{*} x_{*}^{-1} - \left(\sum_{*} x_{*}\right)^{-1}\right)^{-1} \quad \text{for} \ * \in \{L, C\} \\
\dot{J}_{E_{2},A_{2},A_{2}} &= M_{VA} j_{E_{2},A_{2},AA,m} f_{A_{2}} \quad \text{with} \ * \in \{L, N, C\} \\
\quad f_{A_{2}} = \left(1 + \sum_{*} x_{*}^{-1} - \left(\sum_{* \neq L} x_{*}\right)^{-1} - \left(\sum_{* \neq N} x_{*}\right)^{-1} + \left(\sum_{*} x_{*}\right)^{-1}\right)^{-1} \\
\dot{J}_{V,A,GA} &= \dot{r}_{V,A,GA} M_{VA} \quad \text{with} \ \dot{r}_{V,A,GA} = \left(\sum_{i} \dot{r}_{E_{i}} - \left(\sum_{i} \dot{r}_{E_{i}}\right)^{-1}\right)^{-1} \quad \text{and} \\
\dot{r}_{E_{i}} &= \frac{m_{E,A}(k_{E,A} - \dot{r}_{V,A,GA}) - j_{E,A,MA}}{y_{E,A,VA}} \\
\dot{J}_{E,A,D,A} &= -j_{E,A,MA} M_{VA} - (1 - \kappa_{R_{i}})((k_{E,A} - j_{V,A,GA}) M_{VA} - (j_{E,A,MA} + j_{V,A,GA} y_{E,A,VA}) M_{VA}) \\
\dot{J}_{E,A,GA} &= -y_{E,A,VA} \dot{J}_{V,A,GA} \quad \text{for} \ i \in \{1, 2\} \\
\dot{J}_{*,A,B} &= -M_{VB} j_{*,AB,m} \frac{1 + x_{PA} + x_{PB} + x_{PV} + x_{PE}}{x_{*}} \\
\dot{J}_{E,B,2A} &= -\dot{J}_{*,A,B} y_{EB,*} \quad \text{for} \ (i, *) \in \{(1, PA), (2, PB), (3, PV), (4, PE)\} \\
\dot{J}_{V,B,GB} &= M_{VB} \frac{m_{EB} k_{EB} - j_{EB,MB}}{m_{EB} + y_{EB,VB}}; \quad \dot{J}_{E,B,DD} = -j_{EB,MB} M_{VB} \\
\frac{d}{dt} M_{PE} &= \dot{J}_{PE} = \dot{J}_{P,E,HD} + \dot{J}_{P,E,A_{B}} \\
\frac{d}{dt} M_{ED} &= \dot{J}_{ED} = \dot{J}_{E,D,HD} + \dot{J}_{E,D,DC} + J_{ED,A_{1}D} + J_{ED,A_{2}D} \\
\frac{d}{dt} M_{E,A} &= \dot{J}_{E,A} = J_{E,A,A_{1}D} + J_{E,A,A_{2}A} + J_{E,A,GA} + J_{E,A,D,A} \quad \text{for} \ i \in \{1, 2\} \\
\frac{d}{dt} M_{EB} &= \dot{J}_{EB} = \dot{J}_{E,B,A_{C}} + J_{EB,A_{1}B} + J_{EB,A_{2}B} + J_{EB,A_{3}B} + J_{EB,A_{4}B} + J_{EB,GB} + J_{EB,DB} \\
\frac{d}{dt} M_{C} &= J_{C} = -j_{PA} - j_{PB} - j_{PV} - j_{PE} - j_{VD} - J_{E,D} - j_{E,A} - j_{E_{2}A} - j_{V,B} - j_{EB} \\
\frac{d}{dt} M_{N} &= J_{N} = -0.1j_{PA} - 0.1j_{PB} - 0.2j_{PV} - 0.2j_{PE} - 0.2j_{VD} - 0.2j_{ED} + \nonumber \\
&\quad -0.2j_{VA} - 0.4j_{E_{2}A} - 0.2j_{VB} - 0.4j_{EB}
\end{align*}
\]
Table 9: The energy fluxes as specified by the DEB model for the consumer of scaled length $l$ and scaled reserve density $e$ at scaled functional response $f$, where $X$ denotes the food density. The powers $\dot{p}_X = \dot{J}_X \mu_X$ and $\dot{p}_P = \dot{J}_P \mu_P$ for ingestion and defecation occur in the environment, not in the individual. The DEB model assumes that $\dot{J}_X \propto \dot{J}_P \propto \dot{p}_A$. The table gives scaled powers of an ectotherm, where $\mu_E$ denotes the chemical potential of the reserves. Parameters: $g$ investment ratio, $\dot{k}_M$ maintenance rate coefficient, $\kappa$ partitioning parameter for catabolic power. Dissipating power amounts to $\dot{p}_D = \dot{p}_{M_m} + \dot{p}_{M_s} + \dot{p}_{G_m} + (1 - \kappa R) \dot{p}_R$. The implied dynamics for $e > l > l_b$:
\[
\frac{d}{dt} e = f - e l \dot{k}_M g \quad \text{and} \quad \frac{d}{dt} l = \frac{\dot{e} - l}{e/g + 1} k_M^3.
\]

<table>
<thead>
<tr>
<th>power</th>
<th>embryo $0 &lt; l \leq l_b$</th>
<th>juvenile $l_b &lt; l \leq l_p$</th>
<th>adult $l_p &lt; l &lt; 1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>assimilation, $\dot{p}_A$</td>
<td>$0$</td>
<td>$f l^2$</td>
<td>$rac{f l^2}{g+e}$</td>
</tr>
<tr>
<td>catabolic, $\dot{p}_C$</td>
<td>$e l^2 g + e$</td>
<td>$e l^2 g + e$</td>
<td>$e l^2 g + e$</td>
</tr>
<tr>
<td>somatic maintenance, $\dot{p}_{M_m}$</td>
<td>$\kappa l^3$</td>
<td>$\kappa l^3$</td>
<td>$\kappa l^3$</td>
</tr>
<tr>
<td>maturity maintenance, $\dot{p}_{M_m}$</td>
<td>$(1 - \kappa) l^3$</td>
<td>$(1 - \kappa) l^3$</td>
<td>$(1 - \kappa) l^3$</td>
</tr>
<tr>
<td>somatic growth, $\dot{p}_G$</td>
<td>$\kappa l^2 e - l$</td>
<td>$\kappa l^2 e - l$</td>
<td>$\kappa l^2 e - l$</td>
</tr>
<tr>
<td>maturity growth, $\dot{p}_{G_m}$</td>
<td>$(1 - \kappa) l^2 e - l$</td>
<td>$(1 - \kappa) l^2 e - l$</td>
<td>$(1 - \kappa) l^2 e - l$</td>
</tr>
<tr>
<td>reproduction, $\dot{p}_R$</td>
<td>$0$</td>
<td>$0$</td>
<td>$(1 - \kappa) (l^2 e - l + l^3 - l_p^3)$</td>
</tr>
</tbody>
</table>

Table 10: The energy fluxes as specified by the DEB model for a decomposer of scaled length $l$ and scaled reserve density $e$ at scaled functional response $f$. We take $\dot{p}_R = 0$, so that $\dot{p}_D = \dot{p}_{M_m} + \dot{p}_{M_s} + \dot{p}_{G_m}$. An individual of structural volume $V \equiv M_V/[M_V]$ takes up substrate at rate $[\dot{J}_X] [M_V]$. The implied dynamics for $e$ and $l$:
\[
\frac{d}{dt} e = \frac{f - e l}{l} k_M g \quad \text{and} \quad \frac{d}{dt} l = \frac{\kappa l^2 e - l}{e/g + 1} k_M^3.
\]

<table>
<thead>
<tr>
<th>power</th>
<th>juvenile $2^{-1/3} l_d &lt; l \leq l_d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>assimilation, $\dot{p}_A$</td>
<td>$l^3 f / l_d$</td>
</tr>
<tr>
<td>dissipating, $\dot{p}_D$</td>
<td>$l^3$</td>
</tr>
<tr>
<td>somatic growth, $\dot{p}_G$</td>
<td>$l^3 e l_d - 1$</td>
</tr>
</tbody>
</table>

|}$
Table 11: The assumptions, in their simplest form, that lead to the DEB model.

**General**

1. Structural body mass and one or more reserves are the state variables of the individual and they do not change in composition (strong homeostasis).

2. Substrate (food) is converted into faeces and these compounds do not change in composition at steady state (just convenience, not essential).

3. Assimilates derived from food are added to reserves, which fuel all other metabolic processes: synthesis of structural body mass, of (embryonic) reserves (i.e. reproduction), and processes that are not associated with synthesis of biomass.

4. If the individual propagates via reproduction (rather than via division), it starts in the embryonic stage that initially has a negligibly small structural body mass (but a substantial amount of reserves)

**Specific**

4a. The reserve density of the hatchling equals that of the mother at egg formation.

5. The transition from embryo to juvenile initiates feeding, and from juvenile to adult initiates reproduction, which is coupled to ceasing maturation. The transitions occur when the cumulated energy invested in maturation exceeds a threshold value. Unicellulars divide a fixed time after initiation of DNA duplication, which occurs when the cumulated energy invested in maturation exceeds a threshold value.

6. Somatic and maturity maintenance are proportional to structural volume, but maturity maintenance does not increase after a given cumulated investment in maturation.

7. The feeding rate is proportional to surface area and depends on food density according to the rules for synthesizing units.

8. The reserves must be partitionable, such that the dynamics is not affected, and the energy density at steady state does not depend on structural body mass (weak homeostasis).

9. A fixed fraction of energy, utilized from the reserves, is spent on somatic maintenance plus growth, the rest on maturity maintenance plus maturation or reproduction (the $\kappa$-rule).

9a. If more than one reserve contributes to growth, the growth rate follows the rules of a fast Synthesizing Unit, while fixed fractions of the rejected reserves fluxes are returned to the reserves from which the fluxes are mobilized, the remainder being excreted.

10. Under starvation conditions, individuals always give priority to somatic maintenance and follow one of two possible strategies:

They do not change the reserve dynamics (so continue to reproduce).

They cease energy investment in reproduction and maturity maintenance (thus changing reserves dynamics).

Most unicellulars and some animals shrink during starvation, but do not gain energy from this.

11. Death by ageing follows a hazard rate that is proportional to the cumulated concentration of modified proteins, that accumulate at a rate proportional to the amount of changed DNA; The increase in changed DNA is proportional to the catabolic rate.
Figure 3: A diagram of the structure of the DEB model for a consumer, producer and a decomposer. The boxes represent state variables, the rounded ones sources or sinks. The circles indicate SuS, the triangle indicates allocation. The substrates for the decomposer and the consumer are mixtures of substrates.

- structural biomass, quantified as volume $V$ (maximum volume $V_m$), mass $M_V$ (maximum mass $M_{Vm}$) or scaled length $l \equiv (V/V_m)^{1/3}$ (maximum scaled length 1)
- reserves, quantified as energy density $[E]$ (maximum energy density $[E_m]$), mass $M_E$ (maximum mass $M_{Em}$), or scaled reserve density $e \equiv [E]/[E_m]$

Diagrams for mass fluxes through the three types of organisms in the DAB community are presented in Figure 3; Table 9 gives the basic powers for each individual, which can be classified into three groups for each reserve, that organize all mass fluxes:

\[
\dot{p} \equiv \left( \begin{array}{c}
\dot{p}_A \\
\dot{p}_D \\
\dot{p}_G
\end{array} \right) = \begin{array}{c}
\text{assimilation power (coupled to food intake)} \\
\text{dissipating powers (no net synthesis)} \\
\text{anabolic power (somatic growth)}
\end{array}
\]

Most of the maintenance power, and part of the growth and assimilation power will end up as dissipating heat, because of the overhead costs; growth and assimilation do not occur with 100% efficiency. Dissipating heat can be written as a weighted sum of the three organizing energy fluxes.

5.1 Feeding and time budgets

Uptake of algae and bacteria by *Daphnia* and of the four types of organic compounds by bacteria are sequential processes for substitutable compounds, while the uptake of light, carbon dioxide and ammonia by algae are parallel process for complementary compounds. Uptake rates for sequential and parallel processing can be derived with reference to time budgets.
The uptake system (a receptor in the outer membrane of bacteria, or the whole food grabbing/mouth/gut-system of animals) can be in a substrate (food) ‘binding’ stage, or in a substrate processing stage. When it is in the latter stage, it cannot bind other substrate items, which sets an upper limit to the substrate uptake capacity. The system cannot do two things at the same time, which means that we use the conservation law for time at this place. This mechanism directly leads to a hyperbolic functional response for a single substrate, if the substrate ‘particles’ arrive randomly with a certain intensity, and if the length of the processing stage does not depend on the intensity of the substrate arrival process (e.g. this length is constant, or exponentially distributed, or proportional to the size of the substrate ‘particle’ that arrived). Substrate rejection is, therefore, an essential feature of biological uptake systems.

We assume that the handling time is proportional to cell size, which implies that the food densities of algae and bacteria, $x_A$ and $x_B$, for Daphnia, can be taken proportional to their structural biomasses, $M_{VA}$ and $M_{VB}$, because the volume of the bottle remains constant; All other choices would involve the cell size structure of algae and bacteria populations in the feeding rates of daphnids.

If uptake of different types of substrate is by the same uptake system, uptake is sequential and directly interferes because this system has some maximum capacity. Each substrate has its own substrate product (reserves) conversion efficiency. (We think of reserves as generalized compounds, i.e. rich mixtures of carbohydrates, lipids, proteins, ribosomal RNA etc, that do not change in chemical composition.) If each type of substrate has its own uptake system, and uptake is parallel, rather than sequential, such as nutrients in algae, the interaction of the uptake rates is more complex, if a single generalized compound has to be produced, due to stoichiometric constraints.

The Synthesizing Unit (SU) is a simple concept [43] that can be conceived as an enzyme, or set of enzymes (or more abstract generalizations thereof), that follows classical association/dissociation kinetics, except that the dissociation rates of the substrate-SU complex are taken to be small in comparison with the dissociation of the product-SU complex. The maximum production rate is then set by the product-SU dissociation rate. This leads to very simple quantitative expressions for the production rate of the SU. While the full description of the association/dissociation kinetics of an enzyme that binds one molecule of A and one molecule of B to produce one molecule of C requires 9 parameters, this SU only requires 3: two saturation constants and one maximum production rate. For a single substrate, the SU follows the Michaelis Menten kinetics, and uptake is a hyperbolic function of substrate concentration (Holling type II functional response).

The saturation constant (for nutrients) combines the process of transportation and acceptance (i.e. binding probability, if the SU is in the binding stage). Transportation is required to bring molecules in the environment to the SU, and converts a concentration to an arrival flux, which is frequently taken to be proportional to concentration. The conceptual separation of the transportation from the acceptance process is essential to combine nutrient and light inputs, which must be in comparable units (arrival frequency of ‘particles’: molecules and photons). The saturation constant for light reflects acceptance only, since the process of transportation is already included in the nature of light. Light can be quantified in different ways, all relating to the number of photons that pass a unit of surface area that is perpendicular to the direction of the photons (assuming parallel light). Differences in light measures relate to differences in the way the energy contents of the photons are weighted. Solar radiation peaks between wavelength of 400 and 700 nm.
Photons with wavelength between 550 and 720 nm can be used for photosynthesis. When these photons are coming in, part of them is reflected, and most of them are absorbed by compounds that cannot extract useful work from light. Ignoring photochemical reactions other than those involving photo pigments, this light energy only affects temperature. A (small) part of the photons that can be used by the photo pigments actually reaches the pigments. We here assume that this part represents a fixed fraction of incoming light per unit of structural algal mass, when changing the light intensity; the relative frequency distribution of wavelengths among photons is thus taken to be independent of the intensity. We here quantify light as number of incoming photons times this fraction.

Note the fundamental difference between substitutable (as for bacteria and daphnids) and complementary (as for algae) substrates. If substrates are substitutable, $f \rightarrow 1$ if one of the substrates becomes abundant, which does not hold for complementary substrates, due to stoichiometric constraints on product (reserve) formation. At high light, $f_{A1} \rightarrow (1 + x_{C1}^{-1})^{-1}$, for instance; $f_{A1}$ only approaches 1 if both light and carbon dioxide are abundant. Tilman [81] gives a classification of substrates.

Substrate (food) uptake is proportional to surface area, according to the DEB model, which means that it is proportional to squared length for organisms that do not change in shape during growth. Such organisms are called 3D-isomorphs. If organisms do change in shape during growth, surface area can be a complex function of volume. If it is proportional to volume, the organism is called a 1D-isomorph. Since maintenance is also assumed to be proportional to volume, size structure is irrelevant to much of the dynamics, and we arrive at an attractive simplicity, where the population behaviour of a few large individuals is identical to that of many small ones, if the total biovolumes are equal[60]. It can be argued that size structure is of minor importance for organisms that reset their volume when it increased by a factor two since birth, which is the reason that we assume 1D-isomorphism for bacteria and algae. Detailed change in shape of growing bacteria resembles a mixture of a 1D and a 0D-isomorph (surface area does not change during growth of a 0D-isomorph, where increase in maintenance-requiring structural biomass is at the expense of internal vacuoles, see [41]), while algae are approximately 3D (green algae) or 0D (diatoms, [51]) isomorphs. We assume 3D-isomorphism for Daphnia only, because the ratio of the maximum length and the length at birth is about a factor 6, so the ratio of the corresponding volumes is about $6^3 = 216$, which would deviate too much from 1D-isomorphism.

The feeding process has, in an ecosystem setting, two aspects: the disappearance of substrate, and the increase of reserves. These processes are quantified in Table 7, 8 and 12, and will be briefly discussed in the following sections.

**Daphnia**

Embryonic Daphnia does not feed; it maintains, grows and develops at the expense of reserves. The scaled functional response for juvenile and adult Daphnia amounts to

$$f_D = \left(1 + (x_A(1 + \epsilon_{E1}m_{E1} + \epsilon_{E2}m_{E2}) + x_B(1 + \epsilon_{EB}m_{EB}))^{-1}\right)^{-1}$$

where $x_\ast = X_\ast/X_{K\ast}$, for $\ast \in \{A, B\}$, are the scaled densities of the structural body mass of algae and bacteria, and $X_{K\ast}$ the corresponding saturation constants, so $X_\ast = M_\ast/V_{env}$, for a bottle of volume $V_{env}$. The parameters $\epsilon_\ast$ quantify the extension of the prey-handling time by the reserves of the prey, e.g. by elongating the time required for digestion. The
quantities \( m_{E_1A}, m_{E_2A} \) and \( m_{EB} \) denote the molar densities of the reserves of algae and bacteria.

Since feeding is assumed to be proportional to surface area, and \( Daphnia \) is a 3D-isomorph, we have that \( J_{s,AD,m} = \{J_{s,AD,m}\}V^{2/3} \), for \( * \in \{VA, VB\} \), where the surface area-specific maximum ingestion rate \( \{J_{s,AD,m}\} \) is treated as a parameter (i.e. a constant), and \( V = M_{VD}/[M_{VD}] \) is the structural biovolume, where \([M_{VD}]\) is treated as a parameter. Since the nutritional value of algae and bacteria for \( Daphnia \) does not need to be the same, \( Daphnia \) might have a preference for one of them. Such preferences turn up in the values for the saturation constants, which are hidden in the scaled food densities \( x_A \) and \( x_B \).

Let \( \dot{J}_{VA,AD,m} \) and \( \dot{J}_{VB,AD,m} \) denote the maximum ingestion rates of algae and bacteria by \( Daphnia \), \( y_{ED,*} \) the food-reserve coupling, and \( y_{P*,V*} \) the food-faeces coupling on the basis of C-moles. We give the maximum ingestion rates positive values, which means that the feeding fluxes have negative signs, because food disappears. The feeding rates for \( Daphnia \) amount to

\[
\dot{J}_{VA,A,D} = -f_D \frac{x_A \dot{J}_{V*,AD,m}}{x_A(1 + \epsilon_{E_1A}m_{E_1A} + \epsilon_{E_2A}m_{E_2A}) + x_B(1 + \epsilon_{EB}m_{EB})}
\]

for \((i,*) \in \{(1,A),(2,B)\}\). As a first approximation, we might neglect the effect of reserves on the prey-handling time and set \( \epsilon_* = 0 \). Note that the ingestion of prey reserves is coupled to preys structural body mass via the reserve densities. Although daphnids are feeding on two types of prey, the chemical composition of the prey can change in time and depends on the nutritional condition of the prey. The feacal production is taken to be proportional to the ingestion of structural mass.

**Alga**

As explained in [43, 51, 45], the scaled functional responses that are presented in Table 8 directly follow from the dynamics of the Synthesizing Unit. It has the property of being numerically close to a minimum model: if a nutrient exceeds others in availability, relative to the needs, it hardly affects assimilation. The concentration ranges where several nutrients limit assimilation simultaneously is rather small.

The maximum assimilation rates \( \dot{J}_{E_i,A,A,m} \) are proportional to the total structural body mass of the algae, as a consequence of the assumption of 1D-isomorphism, so \( \dot{J}_{E_i,A,A,m} = \dot{J}_{E_i,A,A,m}M_{VA} \), where the mass-specific maximum assimilation rates \( \dot{J}_{E_i,A,A,m} \) are treated as parameters. Nutrients and light are complementary, rather than substitutable, which urges the specification of synthesis of reserves in terms of nutrient densities (and light availability), and evaluate uptake rates of nutrients from synthesis of reserves via stoichiometric couplings. We assume that the assimilation process of nutrients do not involve overhead costs, other than paid from light, which implies that the mass-mass couplers equal the chemical coefficients, so \( y_{C,E_1A} = y_{C,E_2A} = 1 \) and \( y_{N,E_2A} = n_{N,E_2A} \). We conceive \( y_{L,E_iA} \) as a parameter, which indirectly specifies the heat loss that is associated with assimilation via the energy difference between light plus nutrients and reserves.

**Bacterium**

The scaled functional response for the bacterium follows from the assumption that substrates are fully substitutable and are converted into reserves. Since mineral fluxes are
obtained from mass balance equations, they can become negative, meaning that minerals are taken up from the environment. Depending on the C/N ratio of substrate relative to reserves, ammonia is taken up from or excreted into the environment, for instance. Minerals do not occur in the expression for the assimilation flux, which implies that they must be available *ad libitum*. If this is actually not the case, mineral masses can become negative in the expressions for the change of the system. This unrealistic situation can only occur with unusual combinations of parameter values and mass distributions within the DAB system. If in any particular system, the assumption of *ad lib* minerals for bacteria is not realistic, model modification is required.

The maximum assimilation rates \( \dot{J}_{*,A,B,m} \) are proportional to the total structural body mass of the bacteria, as a consequence of the assumption of 1D-isomorphism, so \( \dot{J}_{*,A,B,m} = j_{*,A,B,m} M_{VB} \), where the mass-specific maximum assimilation rates \( j_{*,A,B,m} \) are treated as parameters.

### 5.2 Dissipating power

Somatic maintenance is used to fuel protein turnover, to maintain concentration gradients of ions and compounds in cells and in the body, to fuel behaviour, movements, and other forms of activity. It is conceived as an energy drain, or a drain of reserves, that eventually is fully mineralized and leaves the body in the form of dissipating heat, carbon dioxide, ammonia and water, without fueling any net synthesis. Overhead costs in growth and/or reproduction account for processes that directly relate to synthesis. Maintenance has priority over growth, which is ceased as soon as the allocation to growth plus maintenance matches the maintenance costs.

Somatic maintenance costs are taken proportional to structural mass, and the specific maintenance costs \( j_{E*,M,*} \) are considered as parameters. The dissipating power for bacteria equals the maintenance power. Algae excrete a fraction \( (1 - \kappa_{Ri}) \) of the reserves that are rejected by the growth \( su \), which contribute to dissipating power as well. Daphnids invest in development and have overhead costs for reproduction, which also contribute to dissipating power (see later).

Dissipating power should not be confused with dissipating heat; it stands for the power involved in metabolic processes that are not directly related to processes of synthesis. Dissipating power, assimilation power and growth power all contribute to dissipating heat. The overhead costs of assimilation and growth contribute to dissipating heat, but not to dissipating power. This is just a matter of book keeping and largely relate to convenience, rather than being fundamentally different.

### 5.3 Growth and reserve kinetics

The weak homeostasis assumption (# 8 in Table 11) and the partitionability requirement for reserves imply that the reserve density, i.e. the ratio of the reserves and the structural mass follows first order kinetics, at a rate that is inversely proportional to length for a 3D-isomorph, or constant for a 1D one. The DEB model assumes that a constant fraction of the catabolic flux, i.e. the flux that is released from the reserves, is spent on somatic maintenance plus growth, the rest on maturity maintenance plus the increase in the state of maturity (development) or reproduction (if the state of full maturity is reached). Since both somatic and maturity maintenance are taken proportional to structural mass, the
Table 12: The specification of fluxes when the consumer is considered as a 3D-isomorph, rather than a 1D one. Index \( D \) now relates to individuals and index + to the population of daphnids. These equations replace the corresponding ones in Table 8.

\[
\begin{align*}
\dot{J}_{V^*, A_D} &= \{\dot{J}_{V^*, A_D}\}V^{2/3} \quad \text{for} \quad * \in \{A, B\} \\
\frac{d}{dt}M_{ED} &= \dot{J}_{ED, AD} - \dot{J}_{ED, CD} = \dot{J}_{ED, AD} - (\dot{V}V^{-1/3} - j_{VD, GD})M_{ED} \\
\frac{d}{dt}M_{VD} &= \dot{J}_{VD, GD} = \frac{\kappa \dot{J}_{ED, CD} - \dot{J}_{ED, MD}}{\dot{y}_{ED, VD}} \\
\dot{J}_{VD, GD} &= \frac{\kappa (\dot{V}V^{-1/3} - j_{VD, GD})m_{ED} - \dot{J}_{ED, MD}}{\dot{y}_{ED, VD}} = \frac{\kappa m_{ED}\dot{V}V^{-1/3} - \dot{J}_{ED, MD}}{\kappa m_{ED} + \dot{y}_{ED, VD}} \\
\dot{J}_{ED, CD} &= \frac{\dot{m}_{ED}\dot{y}_{ED, VD} \dot{V}V^{-1/3} + \dot{J}_{ED, MD}}{\kappa m_{ED} + \dot{y}_{ED, VD}} \\
\dot{J}_{ED, DD} &= \dot{J}_{ED, MD} + (1 - \kappa)\dot{J}_{ED, CD} \quad \text{for embryos and juveniles} \\
\dot{J}_{ED, DD} &= \dot{J}_{ED, MD} + (1 - \kappa_R)\dot{J}_{ED, RD} + \frac{1 - \kappa}{\kappa}j_{ED, MD}V_p[M_{VD}] \quad \text{for adults} \\
\dot{J}_{ED, RD} &= (1 - \kappa)\dot{J}_{ED, CD} - \frac{1 - \kappa}{\kappa}j_{ED, MD}V_p[M_{VD}] \\
\dot{h}(a) &= \frac{h_{\infty}V(a)}{1 - \kappa} + \frac{\dot{h}_{\infty}(1 - V_b/V_{\infty} + \dot{k}_{MD}(a_{\infty}V_a/V_{\infty} + 0.5(a - a_{\infty}))(a - a_{\infty}))}{(a - a_{\infty})} \\
\dot{J}_{*, A_D} &= N_\varepsilon \dot{J}_{*, AD} \quad \text{for} \quad * \in \{V, A, E, A, VB, EB, PA, PB\} \\
\dot{J}_{PV, H^+} &= N_\varepsilon \dot{h}M_{VD} \quad \text{and} \quad \dot{J}_{PE, H^+} = m_{ED}\dot{J}_{PV, H^+} \\
\dot{J}_{ED, D^+} &= N_\varepsilon \varepsilon \dot{J}_{ED, DD} + N_\varepsilon \dot{J}_{ED, DD} \\
\dot{J}_{*, G_D^+} &= N_\varepsilon \varepsilon \dot{J}_{*, GD} + N_\varepsilon \dot{J}_{*, GD} \quad \text{for} \quad * \in \{V, D, E\} \\
M_{*, +} &= N_\varepsilon \varepsilon m_{*, D} + N_\varepsilon M_{*, D} \quad \text{for} \quad * \in \{V, E\}
\end{align*}
\]

two maintenance fluxes and the two growth fluxes can be taken together in the juvenile stage, where feeding occurs, but reproduction not. This means that for unicellulrals (algae, bacteria), allocation can be simplified to the simple rule: maintenance is subtracted from the catabolic flux, the rest is invested into growth.

Since uptake and maintenance are both proportional to structural mass in 1D-isomorphs, the distinction between the individual and the population vanishes. For algae and bacteria \( M_{Vs} \) can stand for the structural mass of a single cell, as well as for the sum of these structural masses of all cells in the bottle; the specific growth rate equals the population growth rate: \( j_{V^*, G^*} = r_{V^*, G^*}, * \in \{A, B\} \). This does not hold for 3D-isomorphs, where \( M_{VD} \) stands for the structural mass on an individual \textit{Daphnia}. We need the frequency distribution of these masses in the populations, to evaluate the population performance. This will be done in the section on mass turnover.
Daphnia

When daphnids are considered to be 1D-isomorphs, and we do not have to distinguish the individual and population levels, growth is proportional to the difference between the catabolic and maintenance rates, and the catabolic rate follows from the first order dynamics of the reserve density. The parameter $k_{ED}$ stands for the reserve turnover, and $j_{ED,EM}$ for the specific maintenance costs (see Table 8). 1D-isomorphic growth is commonly an acceptable idealization for dividing organisms, such as ciliates; if substrate density is constant, mass (or volume) increases exponentially in time, but it is reset to the volume at ‘birth’ as soon as it increased by a factor two. Realism is lost at the level of the individual if it does not divide. The dynamics for the consumers in Table 8 is supposed to be realistic at the individual level for e.g. ciliates, rather than daphnids. The main reason for its presentation is to reveal the link of physiologically structured populations with the better known unstructured ones [60] for conceptual reasons, as well as to study the trade-off between realism and model complexity. It is commonly true that the structured populations hardly differ from the much simpler unstructured ones [59].

Aging in unicellulars differs from that of multicellulars, according to the DEB theory, because it is a binary process at the cellular level; multicellulars consist of a mixture of cells that are and are not hit by the aging process. Because unaffected cells grow and divide, if energetics allows, the fraction of affected cells can vary in time. For unicellulars the aging rate works out to be proportional to the oxygen consumption that is associated with the catabolic rate. If the elemental composition of reserves and structural mass are identical, oxygen consumption is proportional to the catabolic rate.

Daphnia individuals

The daphnids are considered to be reproducing multicellular 3D-isomorphs, we also have to distinguish the life stages embryo, juvenile and adult. The equations in Table 12 now apply, but these flux specifications cannot be used for time-integrations; they only specify the steady state on the assumption that the age-distribution among individuals in the population is that at steady state.

During the embryonic stage, we set $J_{AD,AD} = 0$ as only difference from the juvenile and adult stages. Juveniles do not differ from adults in reserve kinetics and growth.

The balance equation for reserves is the difference between assimilation and catabolism. The reserve density follows a first order process with rate $\dot{V}^{-1/3}$, which decreases for increasing size as a consequence of the assumption of weak homeostasis. The parameter $\dot{V}$ is an energy conductance, which can be interpreted as the ratio of the maximum surface area-specific assimilation rate and the (maximum) volume-specific reserve density. The expression for maximum assimilation can easily be obtained in the case of feeding on one chemical compound, but we now have to consider five compounds, a complication that will be discussed below.

The investment in growth is a fixed fraction of the catabolic flux minus the somatic maintenance costs, which gives the growth rate and the catabolic flux. The role of $k_{ED}$ for 1D-isomorphs is now taken over by $\dot{V}^{-1/3}$, which changes in time during growth.

At steady state we have $\frac{d}{dt}M_{ED} = j_{V,D,GD}M_{ED}$, or $\dot{J}_{ED,AD} = \dot{V}^{-1/3}M_{ED}$, or

$$m_{ED} = \frac{\{\dot{J}_{ED,AD}\}}{[M_{VD}]\dot{V}}$$

(3)
In other words: assimilation balances catabolism, and the reserve density does not change during growth at steady state.

The structural mass settles ultimately at 

\[ M_{V,\infty} = \frac{\kappa J_{ED,AD}}{J_{ED,MD}} \]

which gives

\[ V_{1/3} = \frac{\dot{e}v}{gk_M} = \left( \frac{M_{V,\infty}}{[M_V]} \right)^{1/3} = \frac{\kappa J_{ED,AD}}{J_{ED,MD}} = \frac{\kappa J_{ED,AD}}{[J_{ED,MD}]} \] (4)

The energy conductance is given by 

\[ \dot{v} = \frac{\kappa g y_{V,ED}}{k_M} \left( J_{ED,AD,m} \right) \frac{1}{[M_V]} \]

with \( J_{ED,AD,m} = \max \{ \{ J_{ED,A_1D,m} \}, \{ J_{ED,A_2D,m} \} \} \) being the maximum value of \( \{ J_{ED,AD} \} \) for all possible combinations of food intake, leading to \( J_{ED,AD,m} = \max \{ \{ J_{ED,A_1D,m} \}, \{ J_{ED,A_2D,m} \} \} \). The maximum assimilation from bacteria occurs when bacteria have maximum reserves, which leads to

\[ \{ J_{ED,A_2D,m} \} = \{ J_{V,B,AD,m} \} \left( y_{V,B} + \frac{J_{EB,AB,m}}{k_E} y_{E,B} \right) \] (5)

with \( J_{EB,AB,m} = \max \{ y_{EB,*A,B,m} \}, (*,i) \in \{(PA,1),(PB,2),(PV,3),(PE,4)\} \). The maximum assimilation from algae is more complex, because the reserves of the algae are coupled; depending on parameter values, one reserve can be maximal if the other is limiting growth to the extent that growth is ceased. It can be written as

\[ \{ J_{ED,A_1D,m} \} = \max \{ J_{V,A,AD,m} \} \left( y_{E,A} + m_{E_1A} y_{E,B} + m_{E_2A} y_{E,D} \right) \] (6)

The maximum is likely to be reached in one of three possible combinations of nutrient inputs for the algae: minimal for CO\(_2\) and maximal for NH\(_3\), maximal for CO\(_2\) and minimal for NH\(_3\), and maximal both both CO\(_2\) and NH\(_3\). Minimum reserves correspond to the situation where growth has completely ceased, and the full catabolic flux from that reserve is spend on maintenance. The section on reserve kinetics for algae will explain why the minimum reserve density 1 and corresponding reserve density 2 are given by

\[ m_{E_1A} = \frac{j_{E_1A,MA}}{k_{E_1A}} \quad \text{and} \quad m_{E_2A} = \frac{j_{E_2A,A_2A,m} - \kappa R_2 j_{E_2A,MA}}{(1 - \kappa R_2)k_{E_2A}} \] (7)

The role of reserves 1 and 2 can be interchanged, but the reserves at maximum CO\(_2\) and NH\(_3\) input must be obtained numerically. Growth is asymptotic, and the aging process makes sure that expression (4) sets an upper bound on body volume, that no individual can reach.

Apart from somatic maintenance costs, Daphnia invests into maturity maintenance, increases its state of maturity, and pays overhead costs for reproduction, which are all processes that so not directly relate to increase in mass, and should be combined with somatic maintenance to arrive at a dissipative flux. We will evaluate the dissipating flux in the section on reproduction.

Daphnia reproduction and aging

Stage transitions, from embryo to juvenile, and from juvenile to adult, occur if investment
into maturation exceeds some threshold value. If maturity maintenance equals \( \kappa \) times the somatic maintenance, these transitions occur at fixed amounts of structural body mass, or structural body volume, \( V_b \) and \( V_p \), say (the indices refer to birth and puberty, conceived at point events). At other values for the maturity maintenance, the threshold values for structural mass depend on food history, and we have to make use of these relationships to estimate the maturity maintenance costs. We here choose for the simple option, because we do not expect that small deviations affect the results.

The investment of reserves into maturity maintenance plus increase in maturity for embryos and juveniles, and into maturity maintenance plus reproduction for adults equals \((1 - \kappa) J_{ED, CD}\).

The maturity maintenance costs for adults equals \( 1 - \kappa \kappa_{MD} V_p [M_{VD}] \), while a fraction \((1 - \kappa_R)\) of the investment into reproduction is dissipated as overhead costs. The total investment into reproduction equals the difference of \((1 - \kappa)\) times the catabolic flux, minus the maturity maintenance costs, while the flux to embryonic reserves equals \( J_{ED, RD} = \kappa_R J_{ED, RD} - J_{ED, RD}^2 \).

If the respiration ratio does not depend on the state of the individual, the oxygen flux that is not associated with feeding is proportional to the catabolic flux \[42\]. If oxygen is converted to free radicals with a fixed efficiency, \( dna \) change is proportional to the oxygen flux, the accumulation rate of transformed proteins is proportional to the amount of changed \( dna \), and the hazard rate is proportional to the concentration of transformed proteins, the hazard rate equals for \( a > a_0 \). The aging acceleration \( \dot{h} \) and the maintenance rate coefficient \( \dot{k}_{MD} = J_{ED, MD} Y_{VD, ED} \) are treated as fixed parameters. The approximative expression for the hazard rate in Table 12 holds for the situation where growth becomes negligibly small after some age \( a_\infty \) and the volume becomes arrested at \( V_\infty \), with \( V_\infty = a_\infty^1 \int_0^{a_\infty} V(a) da \). If the growth period is short with respect to the life span, and mortality builds up after growth has been ceased, this relationship reduces to \( \dot{h}(a) = 0.5 \dot{h}_a \dot{k}_{MD} \).

Growth of the embryo is of importance to evaluate its structural mass and reserves, which needs to be done to construct the full mass balance of the DAB community. As derived in \[41\], the change in scaled length \( l \) and scaled reserve density \( e \) is given by

\[
\frac{d}{da} e = -\dot{k}_{MD} g \frac{e}{l} \quad \text{and} \quad \frac{d}{da} l = \dot{k}_{MD} g \frac{e - l}{3e + g}
\]

(8)

where the conversions of \( e \) and \( l \) to masses is given in Table 4.

At steady state, where food density does not change, the volume at age \( a \) since birth can be obtained explicitly

\[
V(a)^{1/3} = V_\infty^{1/3} - (V_\infty^{1/3} - V_b^{1/3}) \exp(-\dot{r}_B a)
\]

(9)

where the von Bertalanffy growth rate is given by \( \dot{r}_B = (3/\dot{k}_{MD} + 3V_b^{1/3}/\dot{v})^{-1} \).

Dilution by growth ensures that transformed proteins hardly build up during the embryonic period, which means that birth initializes the aging process. Derivation and backgrounds of the model for aging are given in \[41\], together with tests against experimental data, including an evaluation of effects of energetics and mutagenic compounds on aging.

_Daphnia population structure_
We now evaluate the fluxes to and from the population of *Daphnia*, assuming the age and size distributions are close to the stable ones.

At steady state, the easiest approach is to relate the states of the individuals to age. We introduce the relative density $\phi(a) = \phi(a)/N$, where $N$ denotes the number of juveniles plus adults, and $\phi_{e}(a) = \phi_{e}(a)/N_{e}$ for embryos. These relative densities no longer depend on time at steady state, so we omit the reference to time. We will write $J_{1D,2D}(a)$ for the flux of compound *1* linked to transformation *2* in an individual of age $a$, where $a_{b}$ is the age at birth and $a_{p}$ the age at puberty (the transition from juvenile to adult). The DEB model obtains these ages from $V(a_{b}) = V_{b}$ and $V(a_{p}) = V_{p}$.

The characteristic equation applies at steady state:

$$M_{E0} = \int_{a_{p}}^{\infty} \exp\{-\int_{a_{b}}^{a} \dot{h}(a) \, da_{1}\} \dot{J}_{ED, RD}(a) \, da$$  \hspace{1cm} (10)

where $M_{E0}$ refers to the reserves of an embryo of age 0. Given that reserve density at birth equals that of the mother, it can most easily be obtained from the backwards integration of the $\frac{d}{dt} e$ and $\frac{d}{dt} l$, starting from $e = e_{b}$ and $l = l_{b}$. This integration has to be done anyway, to evaluate the expected masses of embryo reserves and structure, and the growth and dissipating fluxes for embryos.

The characteristic equation simply states that each individual is expected to replace itself exactly during its lifespan. This is only possible if $V_{\infty} > V_{p}$, but the difference between $V_{\infty}$ and $V_{p}$ should be really small if the life span is much larger than $a_{p}$. In practice, this difference is expected to be temporally larger, because of the intrinsic oscillations.

The constraint on the ultimate volume translates into a constraint on the specific assimilation, $\{\dot{J}_{ED, AD}\} > V_{p}^{1/3}[M_{VD}] J_{ED, MD}/\kappa$, which can be related to a constraint on food densities. We use the characteristic equation to solve the required assimilation rate for the replacement of daphnids; given the assimilation rate, the trajectories of the state variables (reserves and structural mass) are fixed.

Since embryos do not feed (remove algae or bacteria, or produce faeces) or die (produce dead biomass), we separate embryos from juveniles and adults. The number of individuals in the two groups are denoted by $N_{e}$ and $N$. The embryonic period $a_{b}$ is of no relevance, at steady state. Embryos are still important, because they represent a mass that plays a role in the mass balance, and they contribute to mineral fluxes. Their role is much more important in transient situations.

The age distributions of embryos and juveniles plus adults are given by

$$\phi_{e}(a) = a_{b}^{-1} \text{ for } a \in [0, a_{b}]$$ \hspace{1cm} (11)

$$\phi(a) = \frac{\exp\{-\int_{a_{b}}^{a} \dot{h}(a) \, da_{1}\}}{\int_{a_{b}}^{\infty} \exp\{-\int_{a_{b}}^{a} \dot{h}(a) \, da_{1}\} \, da_{2}} \text{ for } a \in [a_{b}, \infty)$$ \hspace{1cm} (12)

Since $\phi_{e}(a_{b}) = \phi(a_{b})$, the number of embryos relates to that of juveniles plus adults as $N_{e}^{-1} N = a_{b}^{-1} \int_{a_{b}}^{\infty} \exp\{-\int_{a_{b}}^{a} \dot{h}(a) \, da_{1}\} \, da$. The step from individuals to the population is most easily made via the concept of ‘randomly selected individual’, and multiplication by the number of individuals. To this end, we introduce the expectation operators $E_{e}$ and $E$, i.e. $E_{e} Z = \int_{a_{b}}^{\infty} Z(a) \phi_{e}(a) \, da$ and $E Z = \int_{a_{b}}^{\infty} Z(a) \phi(a) \, da$, for any function $Z(a)$ of age.

At steady state, the dead biomass production must balance the consumption by bacteria

$$\dot{J}_{VD, H+} = -\dot{J}_{PV, AB} \quad \text{and} \quad \dot{J}_{ED, H+} = -\dot{J}_{PE, AB}$$
Alga

The process of growth in algae is complicated by the fact that two reserve fluxes $\dot{J}_{E,A,GA}$ that are allocated to growth must be integrated to produce the structural biomass flux $\dot{J}_{V,A,GA}$, which implies the existence of rejected fluxes of reserves due to stoichiometric constraints. The rejected fluxes are partially returned to the originating reserves, and partially mineralized and excreted into the environment.

The growth of structural algal mass follows the kinetics of a fast $su$, while the flux allocated to growth equals the difference between the catabolic flux, which is proportional to the reserve density, and the maintenance flux $\dot{J}_{E,A,MA}$. The parameters $\dot{k}_{E,A}$ have the interpretation of the algal reserve turnover rates. The specific maintenance fluxes $j_{E,A,MA}$ are treated as parameters, and combine both somatic and maturity maintenance. Since the increase in the state of maturity is combined with somatic growth, and leads to an increase of the value for $y_{E,A,V A}$. The dissipating flux for algae equals the maintenance flux plus the excreted flux of mineralized reserves. The growth equation is implicit, due to the phenomenon of dilution by growth. The numerical evaluation of the specific growth rate from the reserve densities can be done following a Newton-Raphson scheme, starting from value 0. Two iterations already result in a high accuracy. Similar to the process of assimilation, the sink of reserves into growth is quantified via the specification of growth, and the (fixed) coupling between reserves and structural biomass.

At steady state, the reserve densities do not change, so $\frac{d}{dt}M_{E,A} = \dot{r}_{V,A,GA}M_{E,A}$, which implies for $j_{E,A,A,A} = \dot{J}_{E,A,A,A}/M_{V A}$

$$j_{E,A,A,A} = \dot{r}_{V,A,GA}m_{E,A} + (1 - \kappa_R)(\dot{k}_{E,A} - \dot{r}_{V,A,GA})m_{E,A} + \kappa_R(j_{E,A,MA} + y_{E,A,V A}\dot{r}_{V,A,GA})$$

(13)

The removal of reserves by grazing is obviously directly coupled to the removal of structural mass, because cells are grazed, which combine the compounds. At steady state, the growth rate must equal the consumption rate by daphnids: $\dot{J}_{V,A,GA} = \dot{J}_{V,A,AD}$.

Bacterium

The growth of bacterial structural biomass is proportional to the difference between the catabolic rate and the maintenance costs. The dynamics of the reserve density is a first order process, again, and the parameter $\dot{k}_{EB}$ represents the turnover rate of bacterial reserves. The specific maintenance flux $j_{EB,MB}$ is treated as a parameter, and the maintenance flux represents the dissipating flux.

At steady state, the reserve densities do not change, so $\frac{d}{dt}M_{EB} = \dot{r}_{V,B,GB}M_{EB}$, which implies for $j_{EB,AB} = \dot{J}_{E,B,AB}/M_{V B}$

$$j_{EB,AB} = \dot{k}_{EB}m_{EB}$$

(14)

At steady state, the growth rate must equal the consumption rate by daphnids: $\dot{J}_{V,B,GB} = \dot{J}_{V,B,AD}$, while the sink of bacterial reserves due to grazing is directly coupled to that of structural mass.

5.4 Mineral fluxes and mass balance

The mineral fluxes follow from the organic fluxes and the uptake of minerals by algae, as a direct result of the conservation law for chemical elements. Since this law has to apply for
each transformation, it is possible to decompose the total mineral fluxes into those involved in each of the transformations. This is even possible to decompose the mineral fluxes into contributions of each individual, but we will confine the analysis to the community level.

Let us partition the scheme matrix $\dot{J}$ into two submatrices that correspond with the minerals and the organic compounds, respectively: $\dot{J}^T = \left( \dot{J}_M^T : \dot{J}_O^T \right)$. The mineral fluxes $\dot{J}_M$ can be linked linearly to the organic fluxes $\dot{J}_O$, using the chemical indices $\mathbf{n}$ (see Table 5), by

$$\dot{J}_M = -n_M^{-1}n_O \dot{J}_O$$  \hspace{1cm} (15)

The change in mass $M$ can be compactly written as $\frac{d}{dt}M = \dot{J}_1$. At steady state, we have by definition $\frac{d}{dt}M = 0$. As for the organic compounds, all mineral fluxes must balance at steady state, so $0 = \dot{J}_M^T 1 = \dot{J}_H^T 1 = \dot{J}_O^T 1 = \dot{J}_N^T 1$.

The equations that have been discussed above fully specify mass turnover and, indirectly, the structure in the DAB community. One way to obtain the masses at steady state, is to evaluate the time trajectories, starting from appropriate initial values, and follow them till they stabilize. The total amounts of the elements do not change in time, only the distribution of the elements among the compounds, so this information about the initial condition is conserved.

6 Mass turnover

Some interesting physiological quantities follow directly from the composition of reserves relative to structural mass. If reserves and structural mass have identical compositions in terms of element frequencies, it can be shown [42] that the Respiration Quotient (RQ), the Urination Quotient (UQ) and the Watering Quotient (WQ) are constant, i.e. they do not depend on the states of the individual. The RQ is defined as the ratio of the carbon dioxide production and the oxygen consumption, excluding the contributions from feeding and assimilation. The UQ and WQ are defined as similar ratios for ammonia (N-waste) and water production over oxygen consumption. These quotients are given by

$$\text{RQ} = \frac{1 - n_{NE}}{1 + \frac{n_{HE}}{2} - \frac{n_{OE}}{2} - \frac{n_{NE}}{2}} = \left( \frac{n_{NN}}{n_{NE}} - \frac{n_{CN}}{2} \right) \text{UQ}$$  \hspace{1cm} (16)

$$\text{UQ} = \frac{n_{HE}}{1 + \frac{n_{HE}}{2} - \frac{n_{OE}}{2} - \frac{n_{NE}}{2}} = \left( \frac{n_{NN}}{n_{NE}} - \frac{n_{HN}}{2} \right) \text{UQ}$$  \hspace{1cm} (17)

$$\text{WQ} = \frac{n_{HE}}{1 + \frac{n_{HE}}{2} - \frac{n_{OE}}{2} - \frac{n_{NE}}{2}} = \left( \frac{n_{NN}}{2n_{NE}} - \frac{n_{HN}}{2} \right) \text{UQ}$$  \hspace{1cm} (18)

where $n = 4n_{CN} + n_{HN} - 2n_{ON}$. The interest in the RQ is in its information about the relative contributions of carbohydrates, lipids and proteins in the fueling of metabolism, while UQ and WQ are the logical counterparts of the RQ, which did not yet found their way into physiological applications. The can become valuable in the study of protein turnover and the measurement of respiration with the technique of double labelled water. The RQ, UQ and WQ are only constant if the elemental composition of reserves and structure are identical. For $n_{HE} = 1.8$, $n_{OE} = 0.5$ and $n_{NE} = 0.2$, and ammonia as N-waste, the quotients are RQ = 0.952, UQ = 0.19 and WQ = 0.571.
The Specific Dynamic Action (SDA) stands for the food-specific oxygen consumption that is associated with feeding, which is also known as the heat increment of feeding, although it has only an indirect relationship with heat flux. It can be shown [42] that the SDA amounts to

\[
\frac{J_{OA}}{J_X} = (n_{M}^{-1})_{O \ast} n_{O} \begin{pmatrix}
1 \\
0 \\
- y_{EX} \\
- y_{PX}
\end{pmatrix} = \begin{pmatrix}
1 & 1 & \frac{3}{4} \\
0 & n_{CX} & n_{CE} & n_{CP} \\
- y_{EX} & - n_{OE} & - n_{OP} \\
- y_{PX} & - n_{NE} & - n_{NP}
\end{pmatrix} \begin{pmatrix}
1 \\
y_{EX} \\
y_{PX}
\end{pmatrix}
\]

(19)

where \((n_{M}^{-1})_{O \ast}\) stands for the row of \(n_{M}^{-1}\) that corresponds with oxygen, which amounts to \((-1 - \frac{1}{4} \frac{3}{2} \frac{3}{4})\) in the present case. The SDA can be calculated for daphnids feeding on algae and bacteria, but the variable reserves of these food items makes that the SDA is variable as well. This problem disappears when the SDA is calculated for the structural mass of algae and bacteria.

The dynamics of the DAB system has some interesting properties. If the consumers go extinct, the bacteria will follow and the algae grow to a density where assimilation just balances maintenance, which occurs when

\[
j_{E,A,A,m} f_{A} = (1 - \kappa_{R_{i}}) k_{E,A} m_{E,A} + \kappa_{R_{i}} j_{E,A,MA}.
\]

Together with the carbon and nitrogen balances, this equation defines the biomass and reserves of the algae. An infinite number of trivial steady states exist, consisting of distributions of elements over minerals and detritus, without living components.

The conservation law for elements makes sure that the Jacobian of the equilibrium \(\frac{d}{dT} J_{1}\), if it exists, has two eigenvalues that are zero; a property known as neutral stability: A (small) shift in the state results in a (small) shift in the point or cyclic attractor, because the total amounts of elements is conserved in a closed system. This information from the initial conditions does not become lost in a closed system. This property can only be removed by supplying the system with a mass input and leak. These two eigenvalues can also be removed by omitting the equations for change in carbon dioxide and ammonia, and expressing their amounts as the difference between total carbon and nitrogen and the carbon and nitrogen locked in biota and detritus.

The Jacobian of the equilibrium that has been selected in Tables 3 and 2, and Figure 5 has a very small positive eigenvalue. This means that the equilibrium is not stable. The system moves very slowly towards extinction for daphnids and bacteria after perturbation into the direction of the corresponding eigenvector and for extinction of all biota into the opposite direction. The equilibrium does attract trajectories form a large part of the state space towards its direct neighbourhood, however, and extinction is really slow, which makes that the unstable equilibrium is still of interest for the analysis of the temporary behaviour of the DAB community. Several parameters can be used to decrease the value of the real positive eigenvalue, but when it becomes almost zero, the equilibrium point disappears. Algae can escape grazing and force consumers into extinction if the conversion from structural mass of algae to reserves of consumer is too low to pay consumers’ maintenance costs, in combination with alga’s ability to survive on low reserves.

A simple experiment with a DAB community in a real bottle in the window shows that such a community can function for quite some time, but ultimately goes extinct. Another reason for ultimate extinction is that nutrient recycling is not as perfect as modelled here,
and organic matter builds up that cannot be readily degraded by bacteria that managed to survive; although bacteria in a rich sample from the field are metabolically extremely versatile, each species can use a very much restricted set of substrates. Intra-specific competition among bacteria leads to a decline of species diversity in spatially homogeneous experimental units. Nitrogen locked into poorly degradable organic matter is found to be the largest nitrogen pool in oceans, next to N$_2$ gas. Peptidoglycan constitute the major component of ultrafiltered dissolved organic matter, and originates from cell walls of Gram-negative bacteria [53], with a C/N ratio of 17.

Trying to understand the steady state behaviour of the community in the bottle, it helps to realize that, when we change light, or total carbon or nitrogen, while all other parameters are not changed, we know a priori that, at steady state, the consumer grows at a rate that is not effected by these three variables. This is because growth must balance death, which is set by aging. The reserve density of the consumer directly relates to growth, and is also not affected by the three variables.

Figure 4 shows the effect of maintenance and reserves, when compared to Figure 5, on the way the stable steady state for masses depends on changes in total carbon, total nitrogen and light. The Jacobian in this steady state has two eigenvalues zero, two pairs of conjugated complex ones with negative real parts, and seven real negatives ones. This implies that the steady state is stable, indeed. A detailed comparison with the Monod model is complicated by freedom in the choice of parameter values. Bacteria can now also feed on reserves of dead daphnids, algae have two nutrient uptake routes, reserve kinetics can be changed via turnover rates and recovery fractions. For this reason, the presented results can only be preliminary, and this presentation just aims to identify the processes that need to be considered in the study of the dynamics of closed systems.

Apart from the stable steady state at low total carbon and nitrogen, an interesting unstable steady state exists at high C and N levels. Figure 5 illustrates that an increase of total nitrogen, starting from a situation where nitrogen is limiting, shifts carbon proportionally from detritus and algae to carbon dioxide, consumers and decomposers, till it ceases to be limiting. A similar increase in carbon also results in a proportional increase in biomass of all three living components, but ammonia is decreasing linearly, till it hits a threshold at which the community goes extinct. An increase of light has a more complex effect on biomass. It results in a peak for the consumers and the decomposers, and a dip for the producers, while an increase beyond the level where light ceases to be limiting has no effect at all. Assimilated light, in the lower panels of Figure 5 quantifies ‘the rate of living’. It is curious to not that is decreasing for increasing nitrogen, as long as nitrogen is limiting. Coupled to this phenomenon is that ammonia is practically absent if nitrogen is strongly limiting, all nitrogen is then fixed into the biota. This corresponds well with widely known qualitative observations; nitrogen minerals are extremely low in oligotrophic systems (lakes, oceans as well as rain forests).

7 Energy turnover and dissipation heat

We used fixed stoichiometries in all chemical transformations. It is only fair to point to some implicit assumptions here, which is basic to all complex biochemical transformations, such as the transformation of reserves into structural mass.

Some of the reserve ‘molecules’ are used as building blocks for structure, part is used to
Figure 4: The steady state distribution of carbon and nitrogen in the DAB-community while increasing the total amount of carbon (upper left), nitrogen (upper right) or light (lower panels), using the DEB model. The non-changed amounts are 1 unit for carbon, 0.2 units for nitrogen, and 5 for light. The amounts of carbon and nitrogen are plotted cumulative, from bottom to top, across the minerals (carbon dioxide, C, or ammonia, N), detritus (P, three types, gray shaded), daphnids (i.e. consumers C), algae (i.e. producers P, gray shaded), and bacteria (i.e. decomposers D). Parameters: $j_{V,AD,m} = 1.5$, $j_{V,B,AD,m} = 1.25$, $X_{K,VA} = 2$, $X_{K,VB} = 5$, $j_{E_1,AA,m} = 6$, $j_{E_2,AA,m} = 4$, $X_{K,L1} = 5$, $X_{K,C1} = 1$, $X_{K,L2} = 2$, $X_{K,C2} = 2$, $X_{K,N2} = 2$, $j_{PA,AB,m} = 3$, $j_{PB,AB,m} = 3$, $j_{PV,AB,m} = 2$, $j_{PE,AB,m} = 3$, $X_{K,PA} = 2$, $X_{K,PB} = 2$, $X_{K,PV} = 2$, $X_{K,PE} = 1$, $j_{ED,MD} = 0.1$, $k_{ED} = 1.5$, $j_{E_1,MA} = 0.05$, $j_{E_2,MA} = 0.025$, $k_{E_1} = 6$, $k_{E_2} = 6$, $\kappa_{R1} = 0.8$, $\kappa_{R2} = 0.7$, $k_{EB} = 3$, $j_{EB,MB} = 0.15$, $h = 0.01$, $g = 1$, $y_{ED,VA} = 0.3$, $y_{ED,E1A} = 0.8$, $y_{ED,E2A} = 0.8$, $y_{V,VB} = 0.3$, $y_{VD,EB} = 0.8$, $y_{PA,VA} = 0.7$, $y_{PB,VB} = 0.7$, $y_{C,E1A} = 1$, $y_{C,E2A} = 1$, $y_{L,E1A} = 0.5$, $y_{L,E2A} = 0.2$, $y_{N,E2A} = 1$, $y_{EB,PA} = 0.7$, $y_{EB,PB} = 0.7$, $y_{EB,PV} = 0.7$, $y_{EB,PE} = 0.9$, $y_{ED,VD} = 2.5$, $y_{E1A,VA} = 1.5$, $y_{E2A,VA} = 1.5$, $y_{EB,VB} = 1.25$. 
Figure 5: The steady state distribution of carbon and nitrogen in the DAB-community while increasing the total amount of carbon (upper left), nitrogen (upper right) or light (middle panels), using the DEB model. The lower panels present the amounts of assimilated light (by the algae), which is proportional to the amount of dissipating heat. The non-changed amounts are 1000 units for carbon, 500 units for nitrogen, and 1000 for light. The amounts of carbon and nitrogen are plotted cumulative, from bottom to top, across the minerals (carbon dioxide, $C$, or ammonia, $N$; the amount of carbon dioxide is very small with respect to carbon in living matter), detritus (four types, gray shaded, but the band is too narrow to be visible), daphnids (i.e. consumers $C$, structure and reserve), algae (i.e. producers $P$; structure, $C$- and $N$,C-reserves, gray shaded), and bacteria (i.e. decomposers $D$, structure and reserve). The algae have three carbon components, and two for nitrogen, because one reserve lacks nitrogen. An increase of light above 4 units has no effect (so all lines proceed horizontally).
generate power to drive the synthesis through combustion, which relates to the production of carbon dioxide and ammonia. The power that is required to drive this transformation depends on the chemical potentials of the compounds that are involved, while the chemical potentials themselves depend, generally, on the local chemical environment, i.e. the set of concentrations of all compounds. If the chemical potentials of any compound involved in the transformation from reserve ‘molecules’ to structural mass ‘molecules’ plus combustion products would vary, the stoichiometric coefficients will vary, as consequence of the dual role of reserves (fuel and building blocks). The use of fixed stoichiometries, and, therefore, constant chemical potentials, translates into the assumption that the chemical environment does not change, despite of the transformation. This odd assumption can be justified by the realistic assumption that the actual transformation is via monomers, which concentrations are kept low and constant by the cells in which this transformation occurs, while the bulk of mass in reserves and structure is present in the form of polymers that do not partake in transformations in that form. As a consequence, the entropy of reserves and structure is assumed to be negligibly small, which implies, via Gipps’ relationship between free energy and enthalpy, that their numerical values become almost the same. This results when pushing the implications of homeostasis into the extreme. It is obviously a very simplified and idealized point of view, which nevertheless seems to work.

The empirical evidence for this point of view is in the success of the empirical method of indirect calorimetry, which relates dissipation heat linearly to carbon dioxide production, oxygen consumption and N-waste production. Mathematically, this method is based on

$$\dot{p}_T = J_{\mu}^T \mu_T,$$

where

$$\mu_T = \begin{pmatrix} \mu_{TC} & \mu_{TH} & \mu_{TO} & \mu_{TN} \end{pmatrix}^T \simeq \begin{pmatrix} 60 & 0 & -350 & -590 \end{pmatrix} \text{kJ mol}^{-1}$$

is the vector of coefficients that are obtained via multiple regression [11, 9]. The fact that these coefficients are fixed directly supports the assumption that the chemical potentials are constant, which implies that the entropy is zero (or at least small enough to be neglected). The empirical weight coefficients could, in principle, be species dependent, but practice learns that they vary little. The method is well tested for a wide variety of animals over the many years of use, but (as far as we know) not for autotrophic systems.

Thus the DEB model offers a theoretical underpinning of the method of indirect calorimetry [42], which rests on the work of Crawford [15] and Lavoisier and de Laplace [47], in the 18th century [55]. All mass fluxes in the DEB model for feeding on a single food source can be written as weighted sums of three powers: assimilation, dissipation and growth, so can the dissipating heat, as an implication of the chemical potentials being constant. The consequence is that dissipating heat can be written as a sum of three mass fluxes (linear functions of linear functions are again linear functions). The selection of oxygen, carbon dioxide and ammonia is very convenient, because they can be measured easily. The fact that the empirical method of indirect calorimetry is based on three mineral fluxes directly relates to the three organizing powers behind the DEB structure: assimilation, dissimilation and growth.

Reproduction power is not part of the short list of organizing powers because reserves of the mother are converted into reserves of the embryo in the egg, which must have an identical chemical composition due to the strong homeostasis assumption. From a strict chemical perspective, there is no transformation, only a reduction of reserves, that is related to the overhead costs for reproduction, which included in the dissipating power. The transformation involved in reproduction has big kinetic consequences, but no for the relationship
between mass and energy. Development power is also not part of the list of organizing powers, because it does not involve the synthesis of compounds that are abundant enough to affect the whole body. The state of maturity should be treated as information rather than matter, although this cannot be quantified in the entropy of biomass, because it is zero. Development power should, therefore, be treated as a dissipating flux. The class of models that is consistent with the method of indirect calorimetry is quite small.

The addition of assimilation fluxes, as in Table 8, should not affect the weight coefficients, because we could repeat the thought experiment for different food sources, one at a time, while the different experiments have growth and dissipating powers in common, that should not depend on food composition, if the organism uses the same reserves. The coefficients can be species dependent, but we will not implement that for simplicity’s sake.

The respiration ratio (RQ), i.e. the ratio between carbon dioxide production and oxygen consumption, usually varies little, while ammonia production is small. This have led to the common practice to take respiration (i.e. carbon dioxide production or oxygen consumption) proportional to dissipating heat, and consider respiration as a measure for metabolic work. If the composition of reserves, relative to structural mass, obeys certain constraints, the RQ is constant indeed, within the context of the DEB model [42]. The simplified relationship between respiration and heat will not be used here, because the flux of ammonia is essential.

The dissipating heat \( \dot{p}_T \) directly follows from the energy balance equation. The reasoning is as follows. Let \( \mathbf{J}_L \) denote the vector of photon fluxes that are involved in the various transformations, which is zero for all transformations, except for the two algal assimilation processes. So

\[
\mathbf{J}_L = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}^T
\]

so \( \mathbf{J}_L = \mu_L \mathbf{J}_L \) are the powers that are associated with the photon fluxes, where \( \mu_L \) denotes the exergy of light, i.e. the exergy: energy that is extracted by the photosynthetic system from a mole of useful photons. The energy content of a photon with wavelength \( L_\lambda \) is \( h\dot{v}_L/L_\lambda \), where \( h = 6.625 \times 10^{-34} \) Js is Planck’s constant, and \( \dot{v}_L = 3 \times 10^8 \) m/s is the velocity of photons in vacuum. A photon of 720 nm (the maximum length that can be used for by photo pigments) has an enthalpy of 1239.5/720 = 1.72 eV (A 1239.5 nm photon has an energy of 1 eV). Photosystem II, using pigment \( P_{680} \), increases about 1.2 eV in potential upon absorbing of a photon, Photosystem I, using pigment \( P_{700} \), makes a jump of 1.7 eV [21]. (The pigments are named by the wavelength of the maximum absorption of the complex in which they are embedded.) Since both \( P_{680} \) and \( P_{700} \) have to be excited to trigger a reaction, the mean exergy of a photon in photosynthesis is either zero, for photons with wavelengths outside the interval between 550 and 720 nm, or 1.45 eV (which is also very close to the potential increase of bacterial photo pigments \( P_{870} \) and \( P_{840} \) upon capturing a useful photon), which amounts to 140 kJ per mole of useful photons (the number of Avogadro is \( 6.02 \times 10^{23} \), while 1 eV = \( 1.610^{-19} \) J). The quantity \( y_{L,E,A} = \mathbf{J}_{L,A,A}/\mathbf{J}_{E,A,A,A} \) stands for the quantum requirement of reserve \( i \) (in moles of photons per C-mole of reserve \( i \)).

The dissipating heat that is associated with the various transformations is

\[
\dot{p}_T = \dot{p}_L - \mathbf{J}^T \mu
\]

where \( \mu \) denotes the enthalpies of the various compounds. The balance equation excludes the heat flux that results from absorbed light that is not involved in photosynthesis, as
well as the energy of used photons that exceeds the amount that is extracted. The balance equation just states that the heat that dissipates in association with a transformation equals the difference between the energy in the light that is used for photosynthesis and the energy that is locked in the compounds. Endothermic reactions in terms of overall transformations cannot occur here because the entropy of biomass is zero, which implies that all elements of $\dot{p}_T$ should be non-negative, while the second law of thermodynamics implies that all are positive.

We can use the method of indirect calorimetry as follows. From (15) we know that

$$\mu^T J = \mu^T_O n_O + \mu^T_M n_M = (\mu^T_O - \mu^T_M n_M^{-1} n_O) \dot{J}_O,$$

where the vector of enthalpies is partitioned into contributions from the minerals and from the organic compounds, i.e.

$$\mu^T = \left( \mu^T_M : \mu^T_O \right).$$

Using $\dot{p}_T = \dot{J}_M \mu_T$ and (21) gives

$$\dot{p}_L = \left( \mu^T_O - (\mu^T_M + \mu^T_T) n_M^{-1} n_O \right) \dot{J}_O$$

(22)

In dark situations, where $\dot{p}_L = 0$, it follows that $\mu^T_O = (\mu^T_M + \mu^T_T) n_M^{-1} n_O$. In a combustion frame of reference we have, by definition that $\mu_M = 0$, and the chemical potentials of the organic compounds reduces to $\mu^T_O = \mu^T_T n_M^{-1} n_O$. In our numerical example this amounts in kJ mol$^{-1}$ to

<table>
<thead>
<tr>
<th>Element</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_{PA}$</td>
<td>395</td>
</tr>
<tr>
<td>$\mu_{PB}$</td>
<td>395</td>
</tr>
<tr>
<td>$\mu_{PV}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{PE}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{VD}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{ED}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{VA}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{E_1A}$</td>
<td>410</td>
</tr>
<tr>
<td>$\mu_{E_2A}$</td>
<td>139</td>
</tr>
<tr>
<td>$\mu_{VB}$</td>
<td>310</td>
</tr>
<tr>
<td>$\mu_{EB}$</td>
<td>139</td>
</tr>
</tbody>
</table>

For comparison, Heijen and van Dijken report the Gibbs energy of formation of (microbial) biomass $\text{CH}_{1.8}\text{O}_{0.5}\text{N}_{0.2}$ to be 474.6 kJ/ C-mol in a combustion frame of reference [27, 26], while these element frequencies would lead to 310 kJ C-mol on the basis of calorimetric coefficients (obtained from animals). Wacasey and Atkinson report combustion values scattering around 580 kJ/ C-mol for a wide variety of invertebrates [86].

The total dissipating heat amounts to $\dot{p}_T = \dot{p}_L^T \mathbf{1}$, while at steady state we must have that the total dissipating heat must balance assimilated light, so $\dot{p}_T = -\dot{p}_L^T \mathbf{1}$, since $\mu^T J \mathbf{1} = 0$, because $\dot{J} \mathbf{1} = 0$ at steady state.

## 8 Top-down vs bottom-up control

A popular issue in the analysis of foodweb dynamics is the question of top-down or bottom-up control [8, 13, 31, 34, 56, 57, 68, 75]: are predators in control of prey densities or vica versa?. Simple models of linear food chains predict that if competition among consumer species is mediated only through the effects of the consumers on their resources, then increases in primary productivity lead to increases in steady state population and biomass at the top trophic level and at even-numbered trophic levels below it, whereas the steady states at odd-numbered levels below the top level are unaffected by enrichment [70, 71, 66, 1, 2, 39, 40]. These simple results become invalid for more complex food webs; in particular omnivory complicates the predictions significantly. Thus even in the “Monod” DAB model, the steady state density of algae is not “controlled” by the Daphnia, since they also eat bacteria.

The situation is yet more complicated if the consumers are represented by the full DEB model. The effect of an increase in prey density is not on growth, but on assimilation. Figure 6 illustrates how Daphnia assimilation reacts on an incremental increase in algae
and bacteria. Since *Daphnia* nutrition mainly depends on the reserves of algae and bacteria, the incremental increase in algae and bacteria is not only in their structural mass, but also in the reserves; we add an extremely small amount of algal and bacterial cells, with the same composition as the ones already present in the bottle. The sensitivity coefficients show that an increase of total nitrogen leads to an increase in the effect of food additions on consumers assimilation, till nitrogen ceases to be limiting. This holds for both the scaled and the unscaled sensitivities. An increase of total carbon, however, leads to a decrease in the assimilation sensitivity for food additions, till a plateau level, but and increase in the scaled sensitivity. An increase in light leads to a peak for the assimilation sensitivity.

A potentially useful piece of theory to address the control question quantitatively is Metabolic Control Analysis (MCA) [37, 28, 29], which aims to evaluate the amount of control each enzyme exercises on the flux of metabolites in a metabolic pathway. One source of interest in this evaluation is to identify the most limiting enzymes for the overall flux through the pathway, in order to increase the amount of that enzyme, or set of enzymes, in one way or another, and so increase the overall flux. MCA is built on two sets of control coefficients: flux control coefficients, which give the fractional change in flux resulting from a fractional change in concentrations of enzyme, and metabolite control coefficients, which give the fractional change in concentrations of substrate (metabolites), resulting from a fractional change in concentrations of enzyme. MCA is particularly useful, because of two relationships hold under certain conditions: the sum of all flux control coefficients amounts to unity, and the sum of all metabolite control coefficients amounts to zero. These relationships, known as ‘summation theorems’, only hold under rather restrictive conditions, including the assumption that enzyme concentrations are considered as model parameters, rather than part of the dynamic system; they are independent from the reactions that they catalize [3]. This hampers the application of MCA in ecological contexts. Allison et al [3] showed that the flux control coefficients for substrate on the dilution rate and the maximum specific growth rate in a chemostat with a micro-organism that follows the Monod model, does obey the summation relationships. The feedbacks and the existence of structural mass and reserves in our bottle seem too complex for an easy application of MCA, pointing to the need for further work in this area.

9 From canonical to natural communities

Although the numerical values that we used in this contribution are biologically realistic, the selected parameter values are only meant to illustrate the reasoning practically, and are not based on carefully executed estimation procedures with real empirical data. Indeed, there are many difficult issues involved in parameter estimation and model testing for DEB models [64]. Rather, our aim has been to describe principles of the systematic formulation of models that describe the mass and energy balances in the canonical community, as these principles carry over to systems with additional features. Furthermore, we have only touched on the dynamical analysis. This work obviously needs expansion, and we think that this can only be done in a meaningful way by comparing each model aspect in a family of related simplified models. We now describe some possible extensions to the theory, but we re-emphasize that every additional feature in a model carries with it new parameters whose values have to be estimated.

The canonical community has properties that are relevant to most aquatic and ter-
Figure 6: The steady state control of consumer assimilation by producer (—) and decomposer (···) densities in the DAB-community while increasing the total amount of light (left), carbon (middle), or nitrogen (right). The upper panels give the unscaled values, lower panels the scaled ones. The non-changed amounts are 1000 units for carbon, 500 units for nitrogen, and 1000 for light. The reserve densities of producers and decomposers are kept fixed, e.g. 
\[
\lim_{dM_{VA} \to 0} J^d_{VD, AD} = \lim_{dM_{VA} \to 0} J^d_{VD, AD} (M_{VA} + dM_{VA} M_{E1A} + dM_{VA} m_{E1A} M_{E2A} + dM_{VA} M_{E2A}) - J^{d}_{VD, AD} (M_{VA} + M_{E1A} + M_{E2A}) \quad \text{def} \quad \frac{d}{dM_{VA}} J^{d}_{VD, AD}.
\]
restrial ecosystems, but it requires considerable system-specific extensions to acquire a minimum degree of realism in any given context. As an example, for planktonic communities, these extensions might include

- **Nutrients** Since ammonia is rare relative to nitrate, the inclusion of nitrate is obvious, but such an extension comes with ammonia-nitrate interactions in terms of uptake by algae [22] and conversion by oxidation, which involves bacteria. The generation of nitrate from (atmospheric) nitrogen by blue-green bacteria also seems essential. The next step is to include phosphate and iron, because they are frequently found to be limiting. Phosphate is present as ion, but also as polyphosphate. Iron occurs in several chemical species, and $\text{Fe}^{2+}$-$\text{Fe}^{3+}$ interactions need to be considered.

- **Species diversity** The inclusion of one species of producer and one species of consumer is close to a caricature of the real situation.

  The quantitative effects of the replacement of the consumer population by a food web of consumer populations is hard to evaluate. Body size scaling relations for feeding, reproduction, characteristic times and spatial scales become important in this extension. The DEB theory offers valuable entries into this complex matter [41].

  The realistic inclusion of competing algae has to account for differences in their properties. Diatoms are the first group to appear in the season, probably because of their large surface area relative to the maintenance-requiring mass (they have huge vacuoles that probably require little maintenance). The occurrence of diatoms cannot be understood without the inclusion of silica, which they use to build their cell walls. Diatom blooms are followed by various other groups, such as haptophyceans, and in summer, dinophyceans. The increase of concentrations of organic compounds during the season, comes with a general tendency among ‘algal’ groups to changes from rather pure autotrophy to mixotrophy, by using organic compounds and prey on bacteria and micro zooplankton. Of particular importance are changes in the size structure of the algal community, since size is a major determinant of edibility by zooplankton, and inedible algal species may constitute “refuges” for substantial quantities of elemental matter [46].

  The quantitative importance of (viral) diseases in plankton dynamics is still an open question [79]. Blooming makes plankton susceptible, because of the short times required to travel from one host to the other.

- **Products and export** Three elements of plankton dynamics are of major importance to the oceans ecosystem:

  The export of organic material to layers below the euphotic zone. Marine snow serves as elevator, or conveyer belt if you wish, and represents food for communities below the euphotic zone. Feecal pellets play a role, but also microbial floc formation and appendicularian feeding houses. This export implies an uptake of carbon dioxide from the atmosphere (and from the layers below the euphotic zone). The production of organic compounds by algae, its decomposition by bacteria and the consumption by zooplankton and mixotrophs might be of importance, as indicated in the introduction.

  The export of carbonate to deeper layers, a process where coccolithophores play an important role [88, 89]. This transport enhances uptake from the atmosphere and might affect global climate. The residence time of carbonate in deep layers is really long, and burial in sediments might extend the time characteristic time to geological
The export of dimethyl sulfide (DMS) to the atmosphere is of importance due to its oxidation to sulphuric acid, which serves as condensation kernel for water (cloud formation), affecting the albedo, and, therefore, the global heat balance [12, 48]. The discussion about its importance is far from completed, and its inclusion into modelling requires extensions involving the dynamics of excretion of DMS precursors and their microbe-mediated transformation.

**Spatial structure** The above-mentioned export processes cannot be understand fully without a vertical spatial structure, that acknowledges that light comes from above, while nutrients are more abundant in the layers below the photic zone. Wind induced turbulence is essential to quantify the availability of light and nutrients. The role of intracellular reserves become even more pronounced in this context. It is not yet obvious to what extend horizontal structure can be avoided for a basic quantitative understanding of the plankton system. The description of ocean currents, requires, apart from effects of wind, details of basin morphology to evaluate effects of earth (and moon) rotation.

This list can easily be extended; we only mention the effects of UV radiation on the physiological performance of plankton and the production and effects of toxicants by certain algal group, which recently became of interest, in connection with reductions of ozon in the upper atmosphere and eutrophication problems in coastal areas, respectively.

Although the complexity of real-world plankton systems is well known by people working in plankton dynamics, it can easily become of depressive complexity in the eyes of modellers and quantitative analysts. A lot have been done already, but it is still little with respect to what is necessary for a quantitative understanding. We think that a few elements in the art of modeling are essential: to make explicit use of mass and energy conservation, in order to exclude weird unrealistic behaviour and reduce degrees of freedom; to model organisms using Dynamic Energy Budgets, in order to include some sound biology; to simplify considerably in order to avoid frightening amounts of variables and parameters. Although modern computational methods solved many problems in the numerical evaluation, complex models usually contribute little to our basic understanding because each parameter value and each relationship comes with considerable uncertainty. Work with simplified models implies a modular setup of model structure and comparisons of models with simplified versions to tell details apart from main relationships. We are still far away from a quantitative understanding of real-world ecosystem dynamics and still have a long way to go and develop theoretical explorations before more detailed descriptions and predictions are feasible, if ever.

10 Discussion

We showed how dynamical mass and energy balances can be used to constrain the dynamics of a simplified community, leading to a dynamics that differs substantially from models that leave part of the compounds that are involved in the ‘black box’. An example is the popular class of logistic models, where the carrying capacity relates to the ratio of intrinsic food production by the environment and the maintenance costs by individuals, while the amount of food is not modelled explicitly. The use of balances is still rare in population
dynamics models, while the more successful models for weather and climate are all based on energy balances [54]. We expect to see a parallel development for population dynamical models in the future.

We made extensive use of the linear nature of mass and energy fluxes, by deriving them by addition of fluxes to and from individuals. Although we pushed simplicity to the extreme, many more realistic features complicate the dynamics, not the incorporation of dynamic balances for mass and energy. If individuals would show complex forms of interaction for instance, this would primarily and directly affect feeding, but most of the other formulations can be left unchanged. Opening of the bottle does not give additional problems, and the application of balances should by no means be confined to closed systems.

The DEB model treats several mass fluxes different from many other models and physiological texts. Energy in nitrogen waste, for instance, is frequently subtracted from food intake to evaluate production fluxes. This procedure originates from evaluations of static energy budgets, which are frequent in physiological and ecological texts. In the DEB model, both assimilation, maintenance and growth can contribute to nitrogen waste, which is included into overhead costs for these processes. The same holds for respiration (i.e. oxygen consumption or carbon dioxide production), which is frequently converted conceptually into energy using fixed conversion coefficients, and interpreted as maintenance costs; so energy use, as reflected by respiration, is subtracted from assimilation to evaluate production. In the DEB model all three basic energy fluxes contribute to respiration (which is treated as two different mass fluxes), while the ratio between oxygen consumption and carbon dioxide production need not be constant (and is in fact found to be varying, especially among micro-organisms). The basic difference is that the DEB model makes a sharp distinction between energy allocated to growth, and energy fixed into new tissue. (The same holds for reproduction.) This distinction can only be made in dynamic models, because the overhead costs for growth can only be evaluated from the relationship between changes in food intake and growth. A full discussion of similarities and differences between the DEB and other models is beyond the scope of this text.

A remarkable observation is the existence of stable steady states at low carbon and nitrogen levels, and unstable ones for high levels. Maximum assimilation, in the latter case, is achieved at low nitrogen levels, which requires further investigation.

Acknowledgments

We thank Bob Kooi, Martin Boer, Fleur Kelpin Erik Muller and James Kay for their very constructive suggestions. This study has been supported by grant 013/1204.10 to SALMK from the Dutch Government, National Research Programme on global air pollution and climate change. It has also been supported by the National Center for Ecological Analysis and Synthesis (NCEAS), through a sabattical fellowship to RMN, and by the US Environmental Protection Agency (Grant # R82-3588-01-2 to RMN).

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