



Light-induced Mass Turnover in a Mono-species Community of Mixotrophs

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We formulate a simple model for growth of a facultative photoautotroph with chemoheterotrophic capabilities. The organism is described by zero, one or three reserve components, and one structural component, all taken to be generalized compounds. The rules of synthesizing units are used for interactions among the uptake processes of the various nutrients and light (parallel processing), and for the merging of autotrophic and heterotrophic activities (sequential processing). For simplicity, we focus on the assimilation of inorganic carbon, inorganic nitrogen and light, and of two organic compounds (dead reserves and dead structure) that originate from aging. The process of resource recycling in a closed environment, as driven by light, and its links with community's structure (amount of biomass) is analysed in this simplest of all communities. Explicit analytical expressions for the steady states show how structure and function depend on the system parameters light, total carbon and total nitrogen. The behaviour resembles the Monod model for the Canonical Community, a three-species ecosystem consisting of producers, consumers and decomposers. If trophic preferences of a mixotroph are allowed to follow a random walk across generations, a trophic structure evolves where mixotrophs coexist with auto- and heterotrophs. Depth profiles are presented for the implied steady-state concentrations of dissolved inorganic carbon and nitrogen.

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Introduction

Most photoautotrophic protists, usually called “algae”, have heterotrophic capabilities to supplement their energy and nutrient requirements (Droop, 1974; Neilson & Lewin, 1974; Rothhaupt, 1997). Algal species without chloroplasts are known in diatoms, chrysophytes, prymnesiophyceans, cryptophytes, and rhodophytes, while only half of the species of dinoflagellates have chloroplasts (Lee, 1999). These algal species thus became fully specialized in heterotrophic assimilation. The incorporation of

a single gene coding for a glucose transporter in the diatom *Phaeodactylum tricornutum* was enough to induce heterotrophic activity in this obligate phototroph (Zaslavskaya *et al.*, 2001). Heterotrophic activity also occurs in photoautolithotrophic cyanobacteria (Schneegurt *et al.*, 1997; Stal, 1991) and in chemoautolithotrophic cyanobacteria (Schneegurt *et al.*, 1997; Stal, 1991) and in chemoautolithotrophic bacteria (Karl, 1995). Such a metabolism classifies them as mixotrophs. Some of them take up dissolved organic carbon (pinocytosis), others can take up food particles (phagocytosis). Some need inputs from light as well as organic compounds, or can use organic compounds only if light is

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available [cometabolism, in e.g. the freshwater chrysophyte *Dinobryon* (Jones & Rees, 1994)], others can live on a single organic energy source [facultative mixotrophs such as the dinoflagellate *Fragilidium subglobosum* (Skovgaard, 1996)]. A wide range of metabolic modes exists (Jones, 1994). Some heterotrophs [especially ciliates such as *Strombidium* and *Laboea* (Stoecker *et al.*, 1988; Stoecker & Silver, 1990)] feed on photoautotrophs, and use them, or their chloroplasts, for autotrophic activities (Bouvier *et al.*, 1998; Laval-Peuto *et al.*, 1986; Stoecker *et al.*, 1987). Other forms classify as symbioses, such as corals, giant clams or vent mussels (Dover, 2000). Transitions from prey-predator to symbiotic relationships exist between photo- and heterotrophs, with a full integration into mixotrophic organisms (Raven, 1997). Model studies suggest that mixotrophic flagellates play an important role in organic matter transfer among microbial consortia (Thingstad *et al.*, 1996).

In northern temperate waters, different protists dominate in a particular sequence during the year, starting with diatoms in early spring, followed by prymnesiophyceans and dinoflagellates. Since the organic carbon content of the water continues to build up, heterotrophic activity of these groups also tends to increase.

The biosphere, and in particular the biota in the world's oceans, plays a central role in global geochemical cycles. An example is the fixation of inorganic carbon into organic material that sinks and is degraded in the deep layers. This export of carbon from the upper layers increases that from the atmosphere to the ocean, and affects global warming. At the moment, many ocean models are extended to incorporate biota-mediated transport and transformations of nutrients. This is frequently done, however, in a way that is not very realistic. Hence, a need exists for simple, but realistic, characterizations of biota's role in geochemical cycles. The motivation for this paper to model the processes of substrate uptake and use by mixotrophs is an attempt at such a simple characterization.

Here, we analyse a situation where the organic compounds originate from the organism itself, which allows us to study a non-trivial mono-species community. More specifically, we study

how light forces mass recycling in a system that is closed for mass and open for energy. We start with a spatially homogeneous system, and then consider a system with a one-dimensional spatial structure: the water column. Homeostasis of biomass implies strong stoichiometric constraints on nutrient turnover (Elser & Urabe, 1999; Loladze *et al.*, 2001). We implemented those constraints and mass and energy balances are satisfied exactly.

We do realize that, without the ocean context, such a system is mainly of theoretical interest, but we think that it represents the simplest ecosystem that is capable of full nutrient recycling. It is only through the understanding of such very simple artificial ecosystems, that we might hope to understand more realistic (and much more complex) ecosystems in full depth. Moreover, in simple models, the effect of parameter changes can be studied in sufficient detail. This system still allows explicit expressions for how structure (i.e. mass distribution) and function (i.e. recycling rates) depend on system parameters (light, total carbon and nitrogen) at steady state. Our future aim is to compare the one-species community with the Canonical Community (Kooijman & Nisbet, 2000; Kooijman, 2000), which is defined to be a three-taxon system, consisting of producers, consumers and decomposers. Nutrient recycling has obviously more degrees of freedom in Canonical Communities, which can be further increased by replacing the consumer population by a food web of species with different body sizes and, therefore, time-scales in their life histories. Although the one-species ecosystem is deliberately theoretical, the modelled quantitative ecophysiological behaviour of mixotrophs is meant to be realistic. Models' realism has been tested to experimental data on the ecophysiological performance of autotrophs and heterotrophs separately (Hanegraaf *et al.*, 2000a, b; Kooijman, 2000; Kooijman & Kooi, 1996; Kooijman *et al.*, 1991; Ratsak *et al.*, 1994, 1995).

Modelling Framework

The dynamic energy budget (DEB) theory is used to quantify metabolic processes. It explicitly respects the principles of energy and mass conservation, and stoichiometric constraints on the

synthesis of (one or more type of) reserves and structure, which together can be called biomass. The organism is, therefore, characterized by two state variables: mass of reserves M_E and structural mass M_V . The chemical composition of these components are taken to be constant. Changes in the reserve/structure ratio allow for particular changes in the chemical composition of biomass. The label “dynamic” relates to the changes of the balances during organisms’ full-life cycle. This is the cell cycle for unicellulars, and from fertilization to death in most multicellulars (which frequently involves an enormous increase in biomass).

Main modelling features are that nutrients and substrates are converted into reserves, and reserves are used for maintenance and growth (and development and reproduction, but these processes have less relevance for this paper). Only structure requires explicit maintenance.

Anabolic processes are modelled on the basis of Synthesizing Units (SUs) (Kooijman, 1998, 2000). SUs are (generalized) enzymes that translate (multi-type) arrival fluxes of substrates into a production flux of products (here reserves), on the assumption that the dissociation rate of the substrate–SU complex is negligibly small (Kooijman, 1998). This (theoretical) construct allows a simple and realistic modelling of simultaneous nutrient limitation of assimilation. Light is treated as a nutrient, with stoichiometric coupling with inorganic carbon to form carbohydrates.

The DEB theory takes uptake to be proportional to surface area of the structure, and maintenance to be proportional to structural mass. Here, we assume that surface area is proportional to mass, which defines the organism to be a V1-morph. This property eliminates the distinction between the individual and the population in the expressions for the fluxes. (The standard assumption is that shape is conserved during growth, which makes surface area proportional to volume^{2/3}, and necessitates the application of individual-based methods to analyse population dynamics.)

Popular models, such as those of Droop (no maintenance), Marr-Pirt (no reserves) and Monod (no reserve and no maintenance) are special cases of the DEB model. A conceptual

introduction to the DEB theory is given in Kooijman (2001) and Nisbet *et al.* (2000), a full presentation in Kooijman (2000), and an application to stoichiometric problems in Muller *et al.* (2001).

Appendix A summarizes the model equations; the next section gives some background to these equations. They have been coded in package DEBtool. § Masses are indicated with symbol M , and mass densities in the environment with X . For a fixed volume V of the environment, the relationship $X_* = M_*/V$ holds for all compounds $*$.

The Individual Organism

A diagram of the metabolism of the mixotroph is presented in Fig. 1.

We focus on the chemical elements C, H, O, and N, and lump the different chemical forms of dissolved inorganic carbon (DIC) and nitrogen (DIN) in single pools. When an organism with a reserve and a structure dies, two types of detritus are formed (dead structure and dead reserves), which can differ in their digestion efficiencies by the mixotroph. For simplicity, we assume complete mineralization to prevent the accumulation of matter that cannot be digested (which would require a continuous input into the system to ensure long-term existence).

We compare the results with a simpler alternative, where we have no reserve (and so a constant chemical composition), and a more complex alternative, where we have three reserves, a single generalized one, and two specialized ones, which allow for the accumulation of carbon (as carbohydrates or lipids) and nitrogen. The chemical composition has more freedom, and we no longer have a direct link between photosynthesis (or carbohydrates) and growth.

Water H and dioxygen O are always taken to be available *ad libitum*. This leaves light (L), DIC (C), and DIN (N) as possibly limiting compounds for autotrophic assimilation, and organic

§Information about the DEB research program and its results can be found at <http://www.bio.vu.nl/thb/deb>. You can freely download software package “DEBtool” from the electronic DEB laboratory, which allows numerical evaluations of the models described in this paper, including graphical presentations of evolutions in time, and of steady-state behaviour.

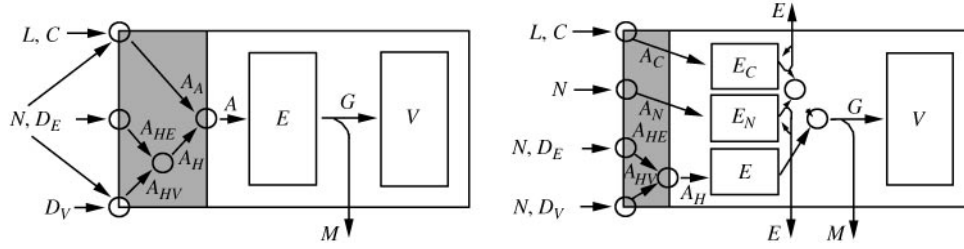


FIG. 1. Diagram of the metabolism of a mixotroph with one (left) or three (right) reserves. Resources (light L , inorganic carbon C , inorganic nitrogen N , detritus D_E and D_V), reserves, E , and structural mass, V , and the basic transformations (assimilation A , growth G , and maintenance M) are indicated. Excretion of reserves (E) is essential in the case of more than one reserve to implement stoichiometric constraints on growth. The excretion of inorganic nitrogen and carbon in association with the basic transformations is not indicated. The death process H converts reserves E into detritus D_E , and structural mass V into detritus D_V , while the C - and N -reserves transform into C and N . This is also not indicated. The grey area indicates the assimilation apparatus of the cell, a subset of the structural mass where no compounds accumulate.

substrates (D_V and D_E) and DIN as possibly limiting compounds for heterotrophic assimilation.

Nutrients (L , C , H , N) are converted into reserve precursors (E_A) in a transformation called auxiliary assimilation A_A (or autotrophic assimilation). These nutrients are considered to be complementary. Organic substrates (structure-detritus D_V and reserve-detritus D_E) and inorganic nitrogen N are converted into reserve precursors (E_H) in a transformation called auxiliary assimilation A_H (or heterotrophic assimilation). Inorganic nitrogen is considered to be complementary to both organic substrates. The reserve precursors E_A and E_H are converted into reserves E in a transformation called assimilation A . Precursors that are synthesized via the autotrophic route and both heterotrophic ones are taken to be substitutable. Reserves are used in a transformation called catabolism C , and spend on maintenance M and on the conversion into structural mass V in a transformation called growth G .

We use the SU-rules for the merging of fluxes of substitutable compounds, and for the production process from complementary compounds. The flux $\dot{J}_A$ of compound A merges with flux $\dot{J}_B$ of compound B into a product flux according to

$$(\dot{J}_m^{-1} + (\rho_A \dot{J}_A + \rho_B \dot{J}_B)^{-1})^{-1}$$

with $\dot{J}_m = \alpha \dot{J}_{Am} + (1 - \alpha) \dot{J}_{Bm}$ and $\alpha = (1 + \rho_B \dot{J}_B / \rho_A \dot{J}_A)^{-1}$ where the binding probabilities ρ_A , ρ_B and the maximum fluxes $\dot{J}_{Am}$, $\dot{J}_{Bm}$ are parameters. The merged flux reaches the maximum $\dot{J}_{Am}$ for $\dot{J}_A \rightarrow \infty$, which implies that part of both

compounds A and B is not processed. The merging represents a simple addition for large capacities ($\dot{J}_{Am} \gg \rho_A \dot{J}_A$ and $\dot{J}_{Bm} \gg \rho_B \dot{J}_B$). The binding probabilities set organisms' preference for the substitutable substrates.

The production flux from the fluxes $\dot{J}_A$ and $\dot{J}_B$ of complementary compounds A and B amounts to

$$(\dot{J}_m^{-1} + (\rho_A \dot{J}_A)^{-1} + (\rho_B \dot{J}_B)^{-1} - (\rho_A \dot{J}_A + \rho_B \dot{J}_B)^{-1})^{-1},$$

where ρ_A and ρ_B accommodate both the binding probabilities and the stoichiometric requirements. The maximum production flux $\dot{J}_m$ (a parameter) is reached if $\dot{J}_A \rightarrow \infty$ as well as $\dot{J}_B \rightarrow \infty$. The numerical behavior (for small production rates) is very similar to the popular minimum rule, but this formulation avoids sharp switches, and specifies the fate of the non-limiting substrate.

AUTOTROPHIC ASSIMILATION

The uptake of light, DIC and DIN is quantified via their contribution in the reserves that are assimilated via the autotrophic route. These nutrients are processed in parallel, which means that an increase in the abundance of one nutrient can increase the assimilation of the other. The affinity for the nutrients is quantified by the saturation constants K_C and K_N and that for photons by the flux $\dot{J}_{L,FK}$; the parameters z_C , z_{C_H} and z_N weigh the relative contributions of DIC, carbohydrates and DIN in the autotrophic assimilation process, and $\dot{J}_{E_A,Am}$ quantifies the maximum autotrophic assimilation rate (see Appendix A).

The photosynthetic system of protoctists consists of two photosystems (PSs). When a photon is captured by an unexcited PSII, it switches to the excited state, transfers an electron from water to PSI, and switches back to the unexcited state. PSI can likewise capture a photon, and also accepts an electron from PSII, which allows it to pass an electron via NADPH to the carbon-fixation cycle (Calvin–Benson cycle). This cycle also accepts a carbon dioxide molecule, reduces it to carbohydrate and delivers its products to the synthesis machinery. The latter machinery also accepts DIN to synthesize reserve precursors. We assume that all units behave as SUs (Kooijman, 1998): PSII, the C-carrier and the N-carrier represent 1-SUs, and PSI, the Calvin–Benson cycle and the synthesizing machinery represent 1,1-SUs. We simplify the expressions by assuming a very high capacity for the electron input system into the carbon-fixation cycle, which makes it (approximately) linear in the light intensity. This does not imply the absence of a saturation of the use of light for increasing light intensities, however, because the electrons experience an increased resistance in their use in the metabolism, due to limitations by DIC and DIN (see Fig. 2).

The output from the carbon-fixation cycle can be derived according to a similar reasoning. Although photorespiration can easily be incorporated via a competitive binding of dioxygen and carbon dioxide (Kooijman, 2000), we refrain from this detail, because it requires dioxygen as an explicit state variable in the system.

The assimilation of reserves E is via a reserve-precursor E_A . The reserve precursors via the autotrophic route are merged with the reserve precursors of the heterotrophic route to yield reserves.

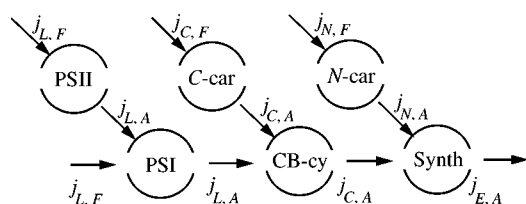


FIG. 2. Diagram of the autotrophic assimilation, where light L , DIC C and DIN N are converted into reserve precursors E_A by pigment-systems I & II, the Calvin–Benson cycle, and a synthesis machinery, using carriers for the uptake of C and N .

HETEROTROPHIC ASSIMILATION

Detritus is primarily used as a carbon and energy source by heterotrophic microorganisms. DIN that is required to transform detritus into reserves does not appear as explicit flux. It combines with the DIN that is (possibly) released during the degradation of detritus in a DIN flux that follows from the conservation law for elements. The DIN that is required for the transformation only appears in the expression for the transformation rate, via the saturation constants K_{N_E} and K_{N_V} (see Appendix A). If detritus contains enough nitrogen, these saturation constants for DIN should be taken to be infinitesimally small. This eliminates the potentially limiting effect of DIN in the processing of organic substrate. Similarly, the production of DIC in association with heterotrophic assimilation directly follows from the conservation law for elements.

The uptake of organic substrates is quantified via their contribution in the reserves that are assimilated via the heterotrophic route. The affinity for structure-detritus and reserve-detritus is quantified by the saturation constants K_{D_V} and K_{D_E} . The parameters $j_{E_V, A_{HVM}}$ and $j_{E_E, A_{HEM}}$ quantify the maximum heterotrophic assimilation rates on both substrates (see Appendix A).

The assimilation of reserves E is via a reserve-precursor E_H . The reserve precursors via the autotrophic route are merged with the reserve precursors of the heterotrophic route to yield reserves. No accumulation of heterotrophic reserve precursors or other assimilates occurs. If the organic substrates are rich enough in nitrogen, DIN is not required, and can even be produced in association with the organo-assimilation. The organic substrates are processed sequentially, which means that an increase in the abundance of one substrate reduces the assimilation of the other. This is modelled via assimilates E_E and E_V . So substrate D_E and DIN N are assimilated into assimilates E_E , and substrate D_V and DIN into assimilates E_V , while assimilates E_E and E_V are assimilated into reserve heterotrophic reserve-precursors E_H .

FROM DETRITUS AND DIN TO ASSIMILATE

The assimilation of substrate D_V and D_E are structurally similar, but the parameters that are

involved can be different. Reserves-detritus D_E (dead reserves) will be much easier to process than structure-detritus D_V (dead structure), because the latter can be rich in compounds such as cellulose. Assuming a fixed stoichiometric coupling between detritus and DIN, the assimilation fluxes follow the rules of a 1,1-SU. The binding probabilities ρ_{E_V} and ρ_{E_E} weigh the preference for structure-detritus relative to reserve-detritus, while the parameters $\dot{k}_{E_V}$ and $\dot{k}_{E_E}$ quantify their assimilation capacities.

MERGING OF ASSIMILATES AND RESERVE PRECURSORS

The specific heterotrophic reserve precursor flux is synthesized from the specific fluxes of assimilates according to the rules for sequentially processed substitutable compounds. Since the handling times can differ, the capacity of the heterotrophic reserve-precursor synthesis is not constant, but depends on the ratio of the accepted fluxes of assimilates. This construction satisfies the requirement that the case of two identical assimilates cannot be distinguished from a single assimilate in a concentration equal to the sum of the two identical assimilates. The construct implies that an increase in the abundance of one type reduces the assimilation of the other.

The merging of the two types of reserve precursors is structurally similar to the merging of assimilates, with the property that an increase of the autotrophic reserve-precursor flux (generally) reduces the processing of heterotrophic reserve precursors, and vice versa, as is characteristic for facultative mixotrophs. The binding probabilities ρ_{E_A} and ρ_{E_H} weigh the preference for the autotrophic and heterotrophic assimilation routes, while the parameters $\dot{k}_{E_A}$ and $\dot{k}_{E_H}$ quantify their capacities. This accommodates the necessary flexibility that is required to capture the whole spectrum of mixotrophs, as discussed in Stoecker (1998). The auto- and heterotrophic activities almost add in the chlorococcoid green alga *Senedesmus obliquus* (Combres *et al.*, 1994), while other species suppress heterotrophy under light-saturating conditions (Fingerhut *et al.*, 1990) (on acetate). Part of this variation might be linked to acetate being a carbon and/or energy source,

which involves the enzyme isocitrate lyase (Combres *et al.*, 1994).

The actual uptake of photons, nutrients and organic substrates is quantified from the synthesis of reserves via the different uptake routes by fixed stoichiometric coupling. The yield parameters $y_{D_V E}$ and $y_{D_E E}$ quantify the requirements for structure-detritus and reserve-detritus to form reserves, and the chemical coefficient n_{NE} specifies the nitrogen requirement for reserves (relative to carbon).

We do not account for the accumulation of assimilates or reserve precursors, which implies that any resistance in the metabolic processing, instantaneously translates into a reduction of the uptake.

RESERVE DYNAMICS, GROWTH, MAINTENANCE AND AGING

The use of reserves follows a first-order kinetics on the basis of densities. This follows from the assumptions that (1) a cell does not change in chemical composition during the cell cycle at steady state (weak homeostasis assumption) and (2) it must be possible to partition the reserves into several fractions, where each fraction follows identical kinetics, without affecting the reserve kinetics. These assumptions quantify the catabolic flux. The specific reserve turnover rate is called $\dot{k}_E$.

The maintenance flux is assumed to be proportional to structural mass; the maintenance rate coefficient $\dot{k}_M$ has the interpretation of the ratio of the specific reserve flux required for maintenance and that for the synthesis of structure. The reserves allocated to maintenance appear as excreted nutrients (DIC, water, DIN), while using dioxygen. This process is fully quantified by the conservation of elements.

The growth flux is proportional to the difference between the catabolic and maintenance fluxes, using a fixed conservation efficiency $y_{VE} = y_{EV}^{-1}$. Nutrient excretion is also associated with growth, and the quantities directly follow from the conversion efficiency from reserves to structure, and conservation of chemical elements. The chemical coefficient n_{NV} quantifies the nitrogen per carbon in the structure and determines the DIN production that is associated with growth.

The hazard rate for the aging process is taken to be proportional to the use of dioxygen in association with catabolism. Other causes of death can exist (such as predation), but this is not modelled here because we study a single-species community; these causes can be mimicked by increasing the aging rate artificially.

The hazard rate, so the instantaneous death rate, amounts to

$$\dot{h} = -\frac{j_{O,M} + j_{O,G}}{m_{Oh}} = \dot{h}_\dagger \frac{m_E}{y_{EV} + m_E}, \quad m_E = \frac{X_E}{X_V},$$

where m_{Oh} scales the dioxygen fluxes to their effect on the hazard rate and $\dot{h}_\dagger$ is the hazard rate at infinite reserve density (which can never be reached). The mechanism is via effects of free radicals.

Aging converts reserves and structural mass into two types of detritus: dead reserves D_E , and dead structural mass D_V . No change in chemical composition is involved, and no nutrient flux is associated with the aging process.

SIMPLIFICATIONS AND EXTENSIONS

The model can be simplified by omitting the reserve. This can be done in an elegant way by reducing the reserve capacity down to zero by increasing the turnover rate of the reserve (see Appendix A). This results in the SU-extended Marr-Pirt model. As a consequence, maintenance is directly paid from assimilation, but we have written out the more popular equivalent formulation, where maintenance is paid from structure and we avoid the problem of specifying what happens if assimilation is not enough to pay maintenance costs. The no-reserve model has just a single type of biomass (structure), and consequently a single type of detritus.

Its qualitative steady-state behaviour turns out to be very similar to that of the DEB model. Reserves are particularly important in transients, where they allow changes in the composition of biomass, and a more natural accommodation of maintenance costs.

The one-reserve model for mixotrophs can be extended to include nitrogen and carbon reserves, in addition to generalized reserves (Kooijman, 2000). Such an extension is essential to

capture growth during wind-induced migrations in a gradient of high light at the surface and high nutrient at the thermocline. A mixotroph with a single reserve can hardly grow in such situations, because it is either light- or nutrient-limited. Appendix A shows that this model variant does not have more parameters, only two extra state variables.

These reserves make excretion of nitrogen and carbon reserve unavoidable, because of stoichiometric constraints on the structure. The constraints require a fixed C/N-ratio, so usually one of the reserve drains limits growth, the other is in excess. A fixed fraction of this excess reserve flux is fed back to the reserve, the rest is excreted. This fraction cannot be equal to one (no excretion), because the upper bound for that reserve is then lost (in situations where the other reserve is limiting growth). For simplicity, we assume that the mineralization of excreted carbon and nitrogen reserves is instantaneous, and that the turnover rates of all three reserves are equal. Experimental evidence for the latter assumption can be found in Kooijman (2000).

Cometabolism of auto- and heterotrophic assimilates has been observed in e.g. the green alga *Chlamydomonas reinhardtii* (Thacker & Syrett, 1972). This extension would be natural in the framework of SU, where the binding probabilities of substrates depend on the binding of complementary substrates.

Many other extensions are possible. Many cyanobacteria are able to convert elemental nitrogen into DIN. The sedimentation of carbonates via coccoliths from prymnesio-phyceans represent a substantial carbon sink of great geological significance (Westbroek, 1991). The incorporation of phosphorus and iron can be done in a rather straightforward way.

Dioxygen is assumed to be non-limiting. Depending on parameter values, oxygen depletion can occur, and the organism switches to fermentative metabolism. This especially occurs when sediments of detritus build up. Sulphur plays an important role in these processes, and the carbon and sulphur cycles become coupled. A continuous build-up of sediment (detritus) can only occur if the system has an influx of nitrogen and carbon from outside (atmosphere, rivers), else it will become extinct.

The Organism in its Environment

Suppose that the population is living in an environment that is fully closed for mass and fully open for energy (light, thermal exchange). The thermodynamic system comprises both the organisms and the environment. The volume changes are taken to be negligibly small, and pressure and temperature are constant. No spatial structure exists, and all compounds are distributed homogeneously, including the two types of detritus.

Let $\mathbf{J}$ denote the matrix of fluxes of compounds; element $J_{i,j}$ stands for the flux of compound i that is associated with transformation j . Let $\mathbf{J}_C$ denote the vector of C-fluxes. (Note that Table 1 shows $\mathbf{J}^T$, rather than $\mathbf{J}$, if the signs are replaced by quantitative expressions.) Index $\mathcal{M}$ collects the five minerals (including light), $\mathcal{O}$ the four organic compounds; so $\mathbf{J}^T = (\mathbf{J}_{\mathcal{M}}; \mathbf{J}_{\mathcal{O}})^T$. Vector $\mathbf{J}_{\mathcal{M},G}$ denotes the five mineral fluxes that are associated with growth, $\mathbf{J}_{\mathcal{O},G}$ does the same for the four organic fluxes. The matrix $\mathbf{n}_{\mathcal{M}}$ collects the 4×5 chemical indices for minerals, $\mathbf{n}_{\mathcal{O}}$ is the 4×4 matrix of chemical indices for the organic compounds; $\mathbf{n} = (\mathbf{n}_{\mathcal{M}}; \mathbf{n}_{\mathcal{O}})$.

The conservation of elements in each transformation implies $\mathbf{nJ} = \mathbf{0}$. This matrix equation gives four conservation equations for each

transformation, which determine the five mineral fluxes involved in each transformation. An implication is that some of the information in the initial conditions never gets lost (namely the total amounts of the four elements).

The change of the densities of all compounds $\mathbf{X}$ in this closed system is $d/dt \mathbf{X} = \mathbf{J}\mathbf{1} = X_V \mathbf{j}\mathbf{1}$. This defines all trajectories for all concentrations, given the initial conditions $\mathbf{X}(0)$. In steady state, we must have $\mathbf{j}\mathbf{1} = \mathbf{0}$.

Figure 3 shows the distribution of carbon and nitrogen at steady state. An increase of carbon, at constant total nitrogen, leads to DIN depletion in the environment upto a very low threshold level; a further increase of total carbon only affects DIC, but not the distribution of nitrogen. The same holds for an increase of nitrogen, at constant total carbon. A decrease of light has hardly an effect upto some threshold value, below which the community cannot exist. Given the rather complex and nonlinear interaction of light, DIC, DIN and detritus in the limitation of growth, the steady-state behaviour of the system is surprisingly simple, and can be obtained analytically in the case that DIN does not colimit the digestion of detritus (see Appendix A).

TABLE 1

*The chemical compounds of the mono-species community and their transformations and indices**

Transformations		Compounds								
		Minerals					Detritus		Living matter	
		Light	DIC	Water	Dioxygen	DIN	Dead structure	Dead reserve	Structure	Reserves
		<i>L</i>	<i>C</i>	<i>H</i>	<i>O</i>	<i>N</i>	<i>D_V</i>	<i>D_E</i>	<i>V</i>	<i>E</i>
Autotrophic-assimilation	<i>A_A</i>	—	—	—	+	—				+
Heterotrophic-assimilation V	<i>A_{HV}</i>		+	+	—	+ / —	—			+
Heterotrophic-assimilation E	<i>A_{HE}</i>		+	+	—	+ / —		—		+
Growth	<i>G</i>		+	+	—	+			+	—
Maintenance	<i>M</i>		+	+	—	+				—
Death	<i>H</i>						+	+	—	—
Carbon	C		1				1	1	1	1
Hydrogen	H			2		3	1.6	1.8	1.6	1.8
Oxygen	O		2	1	2		0.4	0.5	0.4	0.5
Nitrogen	N					1	0.1	0.2	0.1	0.2

*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 compounds.

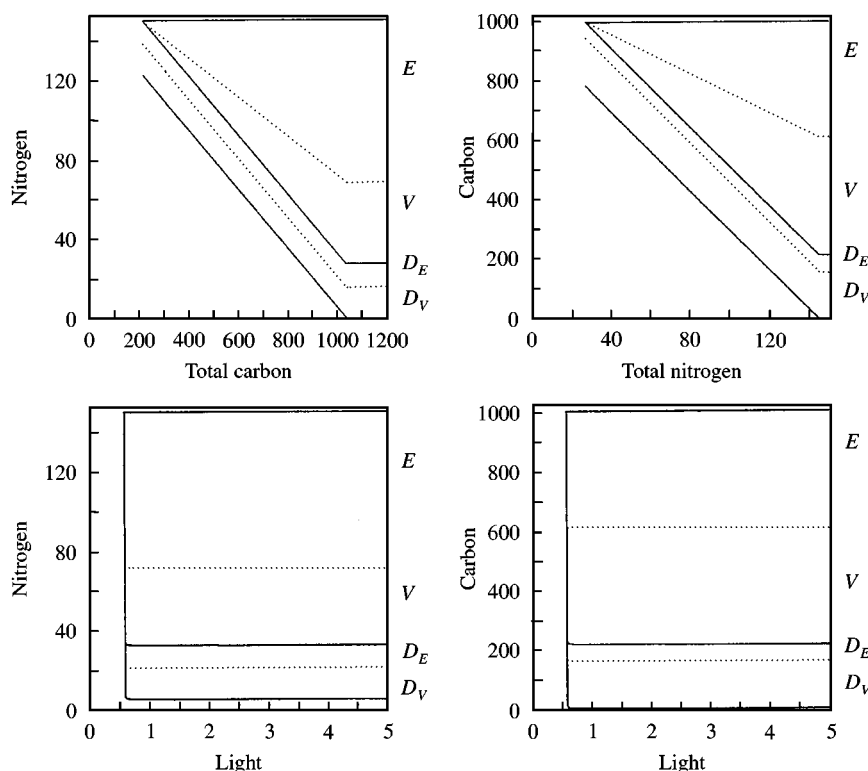


FIG. 3. The steady-state distribution of carbon and nitrogen in the mixotroph community while increasing the total amount of carbon (upper left), nitrogen (upper right) or light (lower panels). The non-changed amounts are $1000 \mu\text{M}$ for carbon, $150 \mu\text{M}$ for nitrogen, and 5 mol d^{-1} for light. The amount of carbon and nitrogen are plotted cumulatively, from bottom to top, for minerals (DIC C, or DIN N), detritus (structural D_V , reserve D_E) and biomass (structural V , and reserve E).

The transient behaviour can be really complex, depending on parameter values and initial conditions. If we inoculate a (closed) batch culture with a very small amount of mixotrophs, the culture can evolve through a sequence of limitations: it can initially be nitrogen-limited, then carbon-limited, and then nitrogen-limited again.

The response of the mixotroph community to changes in total carbon, nitrogen and light is similar to that of the SU-extended Monod model for a Canonical Community (Kooijman & Nisbet, 2000; Kooijman, 2000), i.e. a three-species community that consists of producers, consumers and decomposers: steady-state total biomass decreases for decreasing total carbon and nitrogen, till threshold levels are met at zero biomass. A positive minimum amount of carbon exists for the mixotroph community because detritus (that contains carbon) cannot be degraded completely; Appendix A shows how its amount at steady state depends on parameter values. This minimum amount of carbon for a Canonical

Community is zero because the decomposer population can decrease independent of the consumer population.

Spatial Structure

Suppose that we have a large number of stacked spatially homogeneous units, that represent a water column. The thickness of a unit is infinitesimally small, and we write $\mathbf{X}(t, L_z)$ for the concentrations of the compounds at time t and depth $L_z \in (-L_m, 0)$. Mass exchange between the units is possible, but otherwise the water column as a whole is closed for mass. Since light comes from above, and water absorbs light, light intensity decreases for increasing depth. This affects the ratio of the autotrophic route for assimilation, and the heterotrophic one. Concentration gradients build up as a consequence, and induce diffusive and/or convective transport through the column, which is modelled as a down-gradient mixing process.

The light intensity decreases with depth as

$$J_{L,F}(L_z) = J_{L,F}(0) \exp \{ \alpha L_z / L_m \}, \quad (1)$$

where self-shading is ignored for simplicity. The light-induced reaction-diffusion equation for the change in concentration amounts to

$$\frac{\partial}{\partial t} \mathbf{X} = \mathbf{J}\mathbf{1} + \mathbf{diag}(\dot{\mathbf{K}}_V) \frac{\partial^2}{\partial L_z^2} \mathbf{X}, \quad (2)$$

where $\mathbf{diag}(\dot{\mathbf{K}}_V)$ denotes the diagonal matrix of constant vertical mixing coefficients. At the boundaries, there is no flux of either compound and hence

$$\frac{\partial \mathbf{X}}{\partial L_z} = \mathbf{0} \quad \text{for } L_z = -L_m, 0. \quad (3)$$

With given initial condition $\mathbf{X}(0, L_z)$, the evolution of the system is well-defined.

The equations are solved with the method of lines in which the spatial derivatives are discretized using central differences on a regular grid $L_{z_0} = -L_m, \dots, L_{z_N} = 0$, with $L_m = 70$ m. The resulting system of $6N$ ordinary differential equations is solved with a standard NAG-library routine. It turns out that in the results below, a value $N = 40$ gives sufficiently accurate results. The values of parameters used are the same as used in the previous section. The value of the constant mixing coefficient $\dot{\mathbf{K}}_V$ for all components is based on the choice that the characteristic length scale of vertical diffusive transport ($\approx \sqrt{\pi \dot{\mathbf{K}}_V t}$) is about 1 m (over one day) which gives $\dot{\mathbf{K}}_V = 0.5 \text{ m}^2 \text{ d}^{-1}$. Initial conditions are in μM : $X_C = 2400$, $X_N = 40$, $X_{D_v} = 10^{-6}$, $X_{D_e} = 10^{-6}$, $X_V = 10^{-2}$, $X_E = 10^{-2}$ and the parameter which controls the vertical penetration of light is chosen as $\alpha = 5$. With the later choice, the light intensity is reduced to about 6% at 40 m depth.

In the first set of results, the light forcing is fixed in time with $J_{L,A}(0) = -5$. In the second set, the light forcing is modulated by a day-night function $F(t)$ [$J_{L,A}(0) = -5 \times F(t)$] which is plotted in Fig. 4. The amplitude of this function is chosen, such that the amount of light received over 1 day equals that of the constant light forcing case.

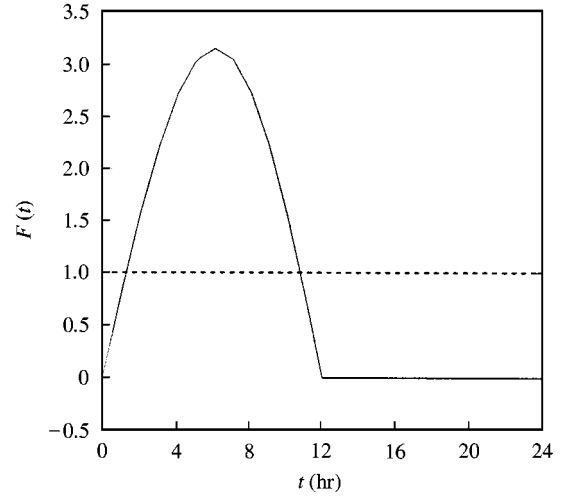


FIG. 4. Prescribed day-night amplitude $F(t)$ of the light intensity. On the horizontal axis, the time is in hours. This function is a sinus during daytime, and zero at night.

The steady-state profiles of the different components, which result after time integration of the equations under constant forcing starting at the initial condition, are shown in Fig. 5. The surface layers are depleted of nitrogen and also the carbon content is minimal because of high biological activity in the surface layers. Most of the reserves are made through the autotrophic route as can be seen from a plot of α_{E_A} vs. depth (note that the depth is now on the vertical axis) in Fig. 6.

In deeper layers, light intensity decreases rapidly but down to about 30 m, the threshold for production is not yet crossed. Below this threshold, heterotrophic activity takes over as can be seen through the decreasing value of α_{E_A} . Near this threshold, heterotrophic activity is still low, which causes the maxima of detritus levels and in α_{E_A} . In still deeper layers, there is almost only heterotrophic activity which causes the concentrations of the detritus components to decrease. Below about 55 m, the concentration of biomass becomes negligibly small. Our mass balance approach allows the evaluation of dissolved dioxygen profiles, after the specification of the oxygen content of the compounds. Such profiles indirectly quantify the balance between autotrophic and heterotrophic activity.

Figure 7 shows that the effects of diurnal cyclic external forcing is confined to the upper layer (not surprisingly). Each profile differs by

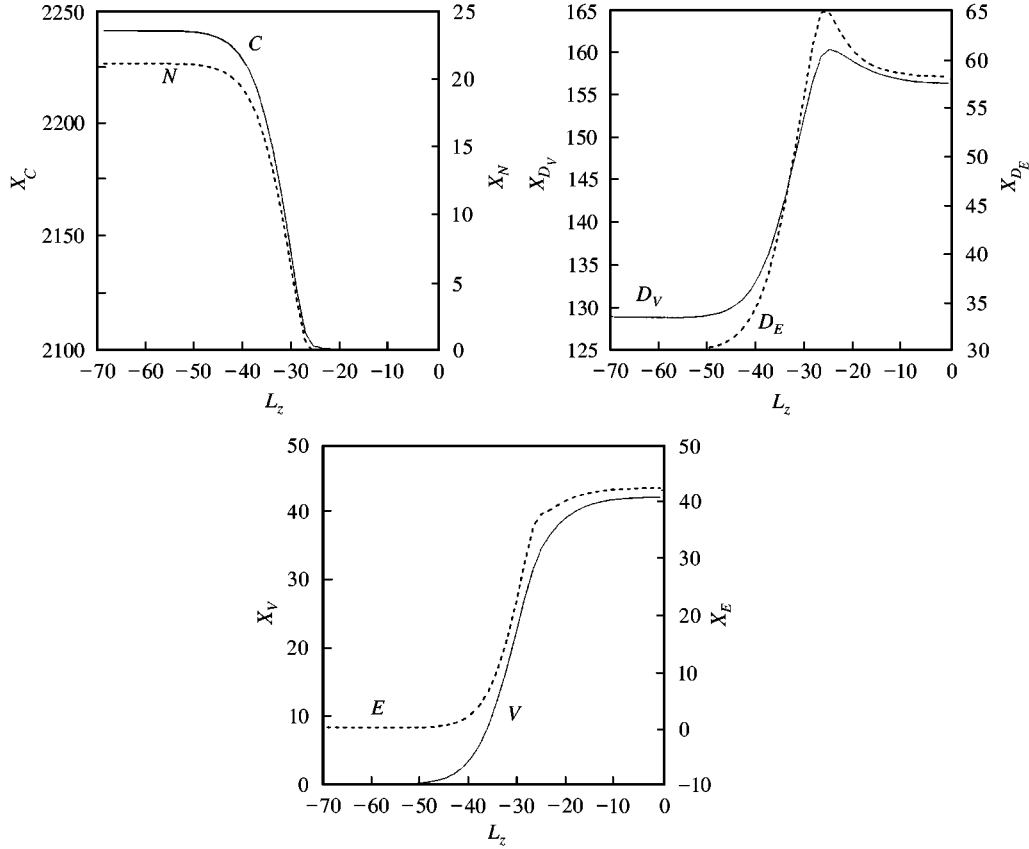


FIG. 5. Steady-state profiles under constant light forcing ($\dot{J}_{L,A}(0) = -5$). The drawn (dashed) variable is plotted on the left (right) axis.

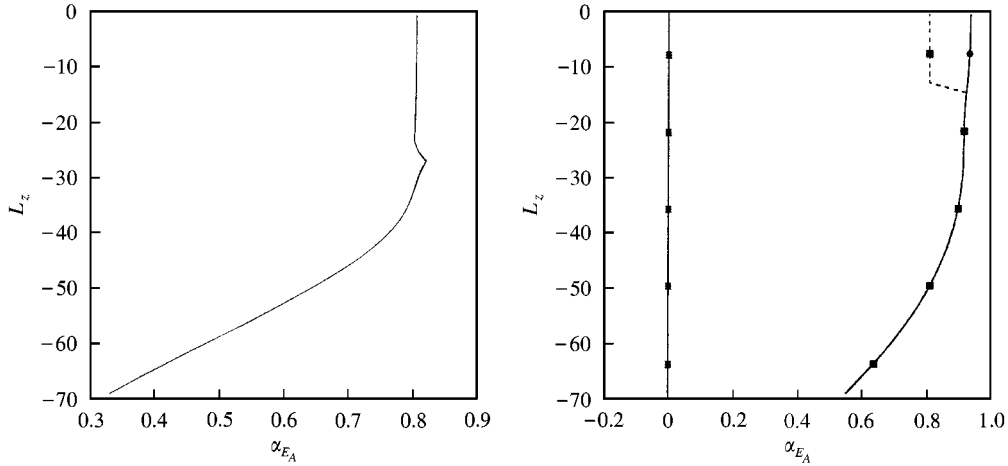


FIG. 6. Steady-state profile of the coefficient $\alpha_{E,A}$, i.e. the fraction of reserves that are synthesized along the autotrophic pathway; the importance of the heterotrophic pathway increases with depth. The left panel shows the fraction $\alpha_{E,A}$ at constant light, the right one during the diurnal cycle: (—●—) 4 hr; (---■---) 8 hr; (—●—) 12 hr; (---▲---) 16 hr; (—●—) 20 hr; (---▲---) 24 hr.

4 hr as indicated in the legend. The mean profiles show similar features as the steady-state profiles under constant forcing; slight discrepancies in the values at the bottom are due to finite integration

time; it takes longer for the periodic orbit to equilibrate than under steady force. The buffering effect of the reserves is clearly visible; the structure hardly cycles.

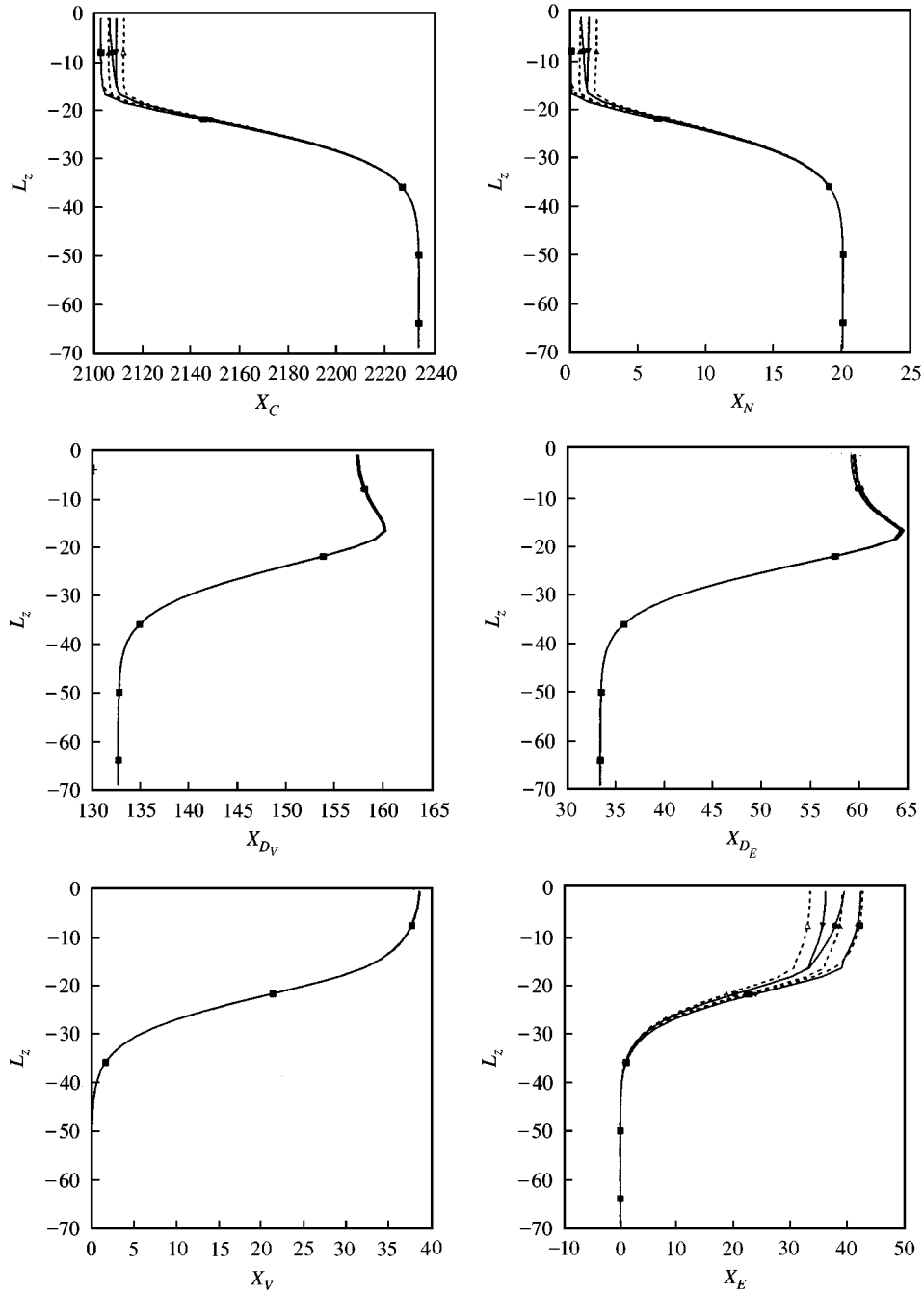


FIG. 7. Spatial profiles of the different components over one day-night cycle: (—●—) 4 hr; (---■---) 8 hr; (—◆—) 12 hr; (---▲---) 16 hr; (—▼—) 20 hr; (---+---) 24 hr.

Also, these profiles have the realistic property that nitrogen is rare at the surface, and abundant at depth, while the opposite holds for biomass. The mixing rate in real-world oceans is fast enough to destroy the gradient, as observed in our profiles; the mixing layer depends on wind, and is maintained by a temperature-dependent

density difference with the underlying ocean. Comparison of the diurnally forced profiles for reserves and structural mass clearly reveals the function of reserves by buffering cellular metabolism in a varying environment. The profiles of α_{E_A} show that indeed autotrophic activity is zero at night and that at daytime, autotrophic activity

is maximal. The transition between day and night can be seen in these plots as a strong decrease of α_{E_A} near the surface.

Self-organization of Trophic Structure

The DEB theory deals with individuals in the first place. If surface area is proportional to volume, the individual structure collapses and the fate of a population can be followed through the reserve density dynamics of a typical individual and the sum of the structural masses of all individuals. Any initial difference between reserve densities among individuals will decay exponentially at a rate equal to the reserve turnover rate. This holds if the parameters of all individuals are equal.

Suppose now that the trophic parameters ρ_{E_A} , ρ_{E_V} and ρ_{E_E} make a random walk on the interval (0, 1). That is, for each individual they are constant, but when the individual divides after doubling its structural mass, one of the two daughters inherits the value of the mother, but the value of the other daughter remains the same with probability $\frac{1}{2}$, or is 0.05 higher or lower with probability $\frac{1}{4}$. The boundaries 0 and 1 are taken to be reflecting, and the three parameters walk independently.

The assimilation capacity and the growth costs are associated with these trophic parameters on the basis of the idea that the assimilatory capacity has to be synthesized at a cost. So we take $y_{EV} = y_{EV}^0 + \rho_{E_A} y_{EV}^A + \rho_{E_V} y_{EV}^V + \rho_{E_E} y_{EV}^E$; $j_{E_A,Am} = \rho_{E_A} j_{E_A,Am}^A$; $j_{E_V,Am} = \rho_{E_V} j_{E_V,Am}^V$; $j_{E_E,Am} = \rho_{E_E} j_{E_E,Am}^E$.

Starting with a single individual without detritus, the growth rate will initially be maximal (for autotrophs), but the growing population will eventually hit a C or N limitation, depending on the ratio for total C and N in the system. The aging process kills all long-term memory of the system, so a stable (or cyclic changing) frequency distribution of the trophic parameters will evolve that tells us whether or not function segregation will occur from mixotrophs to auto- and heterotrophs, and, within the heterotrophs, whether or not specialization on a single substrate will occur. The result might depend on the system conditions: total C and total N; we used light-saturating conditions in our computer simulation study.

The parameter values are supposed to reflect a genotype that has some variability across generations. The theory on adaptive dynamics (Dieckmann & Law, 1996; Geritz *et al.*, 1997; Metz *et al.*, 1996) deals with the process of breaking up of an initial unimodal frequency distribution of parameter values in bi- and multimodal distributions, reflecting speciation. The present system is self-organizing, since the development of a trophic niche for little used resources will result in a (relatively) rapid growth, and more copies of that parameter value (gene); a pure implementation of Darwinian self-selection in a homogeneous system that is closed for mass. No fitness measures are required in this holistic case.

Computer simulation studies so far suggest that mixotrophs can coexist (for a very long time) with heterotrophs and autotrophs that developed from mixotrophs by ceasing one of the pathways with a very small probability (mutation). Heterotrophs and autotrophs can together potentially out-compete mixotrophs, but none of them in isolation because lack of either nutrients or organic matter will cease their existence. Although one would expect that the scatter in preference parameter values builds up gradually, as a result of the random walk, this does not seem to happen; the scatter remains rather small. This also holds for the (nearly pure) hetero- and autotrophs. This is probably due to low growth at the margins. These results call for a more systematic analysis of this process of self-organization.

Discussion

We presented, and evaluated, a relatively simple model for the uptake of nutrients and organic compounds by mixotrophs, that incorporates the most essential features of ecosystem functioning. The model observes stoichiometric constraints, as well as mass and energy balances. Although the implementation of these principles might seem natural and elementary, it necessitates the specification of a considerable number of fluxes. Yet, the steady-state behaviour of systems' components can still be obtained analytically. A new feature is, we believe, that the rules of uptake and use of resources by organisms implicitly specify depth profiles for nutrients and

organic matter, which have realistic features. We evaluated diurnal cycles in light intensity and showed how they affect gradients. Typical mixing rates are large enough to eliminate most gradients, and require greater thermal detail on mixing in a stratified water column to restore the gradients.

We did not evaluate these and other thermal aspects, which directly follow from light input, metabolic heat and radiation. Temperature affects all transformation and transport rates and modifies how light induces mass turnover and transport. The Arrhenius relationship

$$\dot{k}(T) = \dot{k}(T_1) \exp \{T_A/T_1 - T_A/T\}$$

is a useful first approximation for how any rate $\dot{k}$ depends on absolute temperature T , given its value at a reference temperature T_1 and an Arrhenius temperature of $T_A = 12\,500$ K. This relationship holds within a certain temperature range only, with death at the upper bound, and torpor at the lower one. Such extensions are feasible and could be considered for implementation in ocean circulation models.

Algae are important to the physical chemistry of oceans o.a. through the organic carbon pump: detritus leaves the photozone by sedimentation. This export increases the transport of carbon dioxide from the atmosphere to the ocean and greatly enhances the buffer capacity of oceans for carbon dioxide. The pumping can only be quantified satisfactorily with a physical model for mixing in the photozone. The zero- and one-reserve models for mixotrophs will hardly show growth, because of light or nutrient limitation; we need a three-reserve model for this application.

The sedimentation rate of detritus is greatly enhanced by the process of predation, via faecal pellets. The sinking rates of faecal pellets is several orders of magnitude higher than that of individual cells. Appendicularians produce feeding houses at relatively high speed, which also contribute substantially to "marine snow", because these polysaccharides function as condensation kernel for smaller particles. A natural incorporation of this process is via the concept of the Canonical Community (Kooijman & Nisbet, 2000): a three-species community consisting of producers (obligate photoautotrophs),

decomposers and consumers, which feed on producers and decomposers. The various functions of the mixotrophs studied here are then segregated among several functional groups.

The mixotroph community behaves in a manner very similar to the Canonical Community when we use a Monod model. The response to a reduction of total nitrogen for both communities can be very different though, when we use a DEB model (Kooijman & Nisbet, 2000). At low nitrogen, just above the existence threshold, the Canonical Community stores, or can store, almost all carbon in producers, and hardly any in consumers and decomposers. The mixotroph community lacks this flexibility. At this moment, it is not yet clear if the DEB model for Canonical Communities has multiple steady states; this has motivated the analysis of the more simple single-species community of mixotrophs.

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APPENDIX A

Summary of Model Equations and Steady States

The notation is introduced in Table A.1. We neglect self-shading. Light influx $\dot{J}_{L,F}$ (negative, because photons disappear) is scaled with parameter $\dot{J}_{L,FK}$ (positive; all parameters are positive). A multiplication of these two rates with an arbitrary number (different from zero) has no effect. The light influx can be taken as proportional to the solar irradiance (photon flux per

TABLE A.1
Frequently used symbols for variables*

Index	Transformation	Index	Compound	Index	Element
F_i	Feeding (uptake)	W	Total biomass	C	Carbon
A	Assimilation	V	Structural biomass	H	Hydrogen
A_A	Autotrophic assimilation	E	General reserve	O	Oxygen
A_{HE}	Heterotrophic assimilation of D_E	E_C	C-reserve	N	Nitrogen
A_{HV}	Heterotrophic assimilation of D_V	E_N	N-reserve		
C	Catabolism	E_i	Reserve precursor		
M	Maintenance	D_i	Detritus		
G	Growth	C	DIN		
E	Excretion	H	Water		
H	Aging	O	Dioxygen (O_2)		
D	Diffusion	N	DIN		
Symbol	Dim	Interpretation			
t	t	Time			
L	l	Depth below water surface			
X_i	$\text{mol } l^{-3}$	Concentration of compound i			
K_i	$\text{mol } l^{-3}$	Saturation constant for compound i			
x_i	—	Scaled concentration of compound i : X_i/K_i			
M_i	(C-)mol	Mass of compound i			
m_i	$\text{mol } i \text{ mol}^{-1} V^{-1}$	Structure-specific mass of compound i : M_i/M_V			
$y_{i,j}$	$\text{mol } i \text{ mol}^{-1} j^{-1}$	Mol compound i required per mol compound j			
$\dot{J}_{i,j}$	$\text{mol } i \text{ t}^{-1}$	Flux of compound i associated with transformation j			
$j_{i,j}$	$\text{mol } i \text{ mol}^{-1} V^{-1} t^{-1}$	Structure-specific flux of compound i : $\dot{J}_{i,j}/M_V$			
$j_{i,Am}, j_{i,AK}$	$\text{mol } i \text{ mol}^{-1} V^{-1} t^{-1}$	Structure-specific max assimilation & saturation flux, of compound i			
$n_{i,j}$	—	Chemical coefficient for element i in compound j			
$\dot{h}$	t^{-1}	Dilution rate			
$\dot{k}_E, \dot{k}_M$	t^{-1}	Reserve turnover rate, maintenance rate			
ρ_i	—	Binding probability of compound i to SU			
α_i	—	Weight coefficient for compound i			
z_i	—	Flux ratio $j_{i,Am}/j_{i,AK}$ for compound i			
f_i	—	Scaled functional response for transformation i			
κ_i	—	Fraction of rejected reserves i that is returned to reserve i			

*Dots refer to rates (dimension: time^{-1}), not to derivatives with respect to time, which are indicated by d/dt. Index m refers to the maximum value. In the dimension column, l means length, t time.

unit of surface area of water/air boundary layer). Although $\dot{J}_{L,F}$ is listed as a parameter, it is in fact an external forcing on the system, like the total amounts of carbon and nitrogen.

We present three models, by delineating no, one and three reserves. They have been coded in the downloadable package DEBtool (see footnote on page no. 235). The models conserve carbon and nitrogen strictly, so the dimension of the systems equals the number of state variables minus 2.

NO-RESERVE MODEL

Specification of Changes in State Variables

This system has four state variables: DIC C , DIN N , detritus D , biomass V . The state variables partake in five transformations: autotrophic assimilation A_A , heterotrophic assimilation A_H , growth G , maintenance M , hazard H . The changes are given by

$$\frac{d}{dt} X_C = X_V(j_{C,A_A} + j_{C,A_H} + j_{C,M}),$$

$$\frac{d}{dt} X_N = X_V(j_{N,A_A} + j_{N,A_H} + j_{N,M}),$$

$$\frac{d}{dt} X_D = X_V(j_{D,A_H} + j_{D,H}),$$

$$\frac{d}{dt} X_V = X_V(j_{V,G} + j_{V,H}).$$

Specification of Fluxes

Organic fluxes

$$j_{V,A_A} = \alpha_A j_{V,A},$$

$$j_{V,A_H} = (1 - \alpha_A) j_{V,A},$$

$$j_{D,A_H} = -y_{DV} j_{V,A_H},$$

$$j_{V,G} = j_{V,A} + j_{V,M},$$

$$j_{V,M} = -\dot{k}_M,$$

$$j_{V,H} = -\dot{h}_\dagger,$$

$$j_{D,H} = -j_{V,H}.$$

Mineral fluxes

$$\dot{j}_{C,A_A} = -\dot{j}_{V,A_A},$$

$$\dot{j}_{C,A_H} = -\dot{j}_{D,A_H} - \dot{j}_{V,A_H},$$

$$\dot{j}_{C,M} = -\dot{j}_{V,M},$$

$$\dot{j}_{N,A_A} = -n_{NV} \dot{j}_{V,A_A},$$

$$\dot{j}_{N,A_H} = -n_{NV} \dot{j}_{D,A_H} - n_{NV} \dot{j}_{V,A_H},$$

$$\dot{j}_{N,M} = -n_{NV} \dot{j}_{V,M},$$

with functional responses

$$f_N = \frac{1}{1 + x_N^{-1}} \quad \text{with } x_N = \frac{X_N}{K_N}, \quad (\text{A.1})$$

$$f_C = \frac{1}{1 + x_C^{-1}} \quad \text{with } x_C = \frac{X_C}{K_C}, \quad (\text{A.2})$$

$$f_{C_H} = \frac{(1 + z_C^{-1})}{1 + z_C^{-1} f_C^{-1} + x_L^{-1} - (z_C f_C + x_L)^{-1}}$$

$$\text{with } x_L = \frac{-\dot{j}_{L,F}}{\dot{j}_{L,FK}}. \quad (\text{A.3})$$

and auxiliary fluxes

$$j_{V_A,A_A} = \frac{j_{V_Am}(1 + z_N^{-1} + z_{C_H}^{-1} - (z_N + z_{C_H})^{-1})}{1 + z_N^{-1} f_N^{-1} + z_{C_H}^{-1} f_{C_H}^{-1} - (z_N f_N + z_{C_H} f_{C_H})^{-1}},$$

$$j_{V_H,A_H} = j_{V_Am}(1 + x_{N_V}^{-1} + x_D^{-1} - (x_{N_V} + x_D)^{-1})^{-1}$$

$$\text{with } x_{N_V} = X_N/K_{N_V}; \quad x_D = X_D/K_D,$$

$$j_{V,A} = (\dot{k}^{-1} + \alpha_A(\rho_A j_{V_A,A_A})^{-1})^{-1}$$

$$\text{with } \dot{k} = \alpha_A \dot{k}_A + (1 - \alpha_A) \dot{k}_H;$$

$$\alpha_A = \left(1 + \frac{\rho_H j_{V_H,A_H}}{\rho_A j_{V_A,A_A}}\right)^{-1}.$$

System Parameters

$$\dot{j}_{L,F},$$

$$X_{C+} = X_C + X_D + X_V,$$

$$X_{N+} = X_N + n_{NV}(X_D + X_V).$$

Steady States

$$j_{V,A}^* = \dot{k}_M + \dot{h}_\dagger;$$

$$\alpha_A^* = 1 - \frac{\dot{h}_\dagger j_{V,A}^{*-1}}{y_{DV}};$$

$$j_{V,A,A}^* = \frac{\alpha_A^*/\rho_A}{j_{V,A}^{*-1} - \dot{k}^{*-1}};$$

$$j_{V,H,A_H}^* = \frac{(1 - \alpha_A^*)/\rho_H}{j_{V,A}^{*-1} - \dot{k}^{*-1}};$$

$$\dot{k}^* = \alpha_A^* \dot{k}_A + (1 - \alpha_A^*) \dot{k}_H;$$

$$f_C^* = (f_{C_H}^{*-1} (z_C + 1) - z_C)^{-1};$$

$$f_{C_H}^* = \frac{\sqrt{1 + 4/(\alpha^* z_N - z_N - 1)} - 1}{2z_{C_H}/z_N};$$

$$f_N^* = \frac{\sqrt{1 + 4/(\alpha^* z_{C_H} - z_{C_H} - 1)} - 1}{2z_N/z_{C_H}};$$

$$\alpha^* = \frac{1 + z_N^{-1} + z_{C_H}^{-1} - (z_N + z_{C_H})^{-1}}{j_{V,A,A}^*/j_{V,Am}}.$$

If light intensity allows existence:

C-limited

$$X_C^* = K_C (f_C^{*-1} - 1)^{-1}$$

$$X_N^* = X_{N+} - n_{NV} (X_D^* + X_V^*)$$

$$X_D^* = K_D \left(\frac{j_{V,Am}}{j_{V,H,A_H}^*} - 1 \right)^{-1}$$

$$X_V^* = X_{C+} - X_C^* - X_D^*$$

Parameters Compared with 1 Reserve Model

Extra: $j_{V,Am}$, y_{DV} , ρ_A , ρ_H , $\dot{k}_A$, $\dot{k}_H$.

Redundant: $j_{E_V,A_{HV}m}$, $j_{E_E,A_{HE}m}$, $j_{E_A,Am}$, $y_{D_V E}$, $y_{D_E E}$, y_{E_V} , $\dot{k}_E$, n_E , ρ_{E_A} , ρ_{E_H} , ρ_{E_V} , ρ_{E_E} , $\dot{k}_{E_A}$, $\dot{k}_{E_H}$, $\dot{k}_{E_V}$, $\dot{k}_{E_E}$.

ONE-RESERVE MODEL

Specification of Changes in State Variables

The system has six state variables: DIC C , DIN N , structure-detritus D_V , reserve-detritus D_E , structure V , reserve E . They partake in five transformations: autotrophic assimilation A_A , heterotrophic assimilation A_H (of structure-detritus A_{HV} , and of reserve-detritus A_{HE}), growth G , maintenance M , hazard H . The changes are given by

$$\frac{d}{dt} X_C = X_V (j_{C,A_A} + j_{C,A_{HV}} + j_{C,A_{HE}} + j_{C,G} + j_{C,M}),$$

$$\frac{d}{dt} X_N = X_V (j_{N,A_A} + j_{N,A_{HV}} + j_{N,A_{HE}} + j_{N,G} + j_{N,M}),$$

N-limited

$$\text{or } X_{C+} - X_D^* - X_V^*,$$

$$\text{or } K_N (f_N^{*-1} - 1)^{-1},$$

$$\text{or } K_D \left(\frac{j_{V,Am}}{j_{V,H,A_H}^*} - 1 \right)^{-1} \text{ for small } K_{N_V},$$

$$\text{or } (X_{N+} - X_N^*)/n_{NV} - X_D^*.$$

At C/N limitation switch: $z_{C_H} f_{C_H}^* = z_N f_N^*$,

At L/C limitation switch: $\dot{J}_{L,F} = -\dot{J}_{L,FK} z_C f_C^*$,

At L/N limitation switch:

$$\dot{J}_{L,F} = -\dot{J}_{L,FK} z_C (\sqrt{1 + 4/z_C \beta^*} - 1)/2,$$

$$\beta^* = z_{C_H} z_N^{-1} f_N^{*-1} - 1.$$

$$\frac{d}{dt} X_{D_V} = X_V (j_{D_V,A_{HV}} + j_{D_V,H}),$$

$$\frac{d}{dt} X_{D_E} = X_V (j_{D_E,A_{HE}} + j_{D_E,H}),$$

$$\frac{d}{dt} X_V = X_V (j_{V,G} + j_{V,H}),$$

$$\frac{d}{dt} X_E = X_V(j_{E,A_A} + j_{E,A_{HV}} + j_{E,A_{HE}})$$

$$+ j_{E,G} + j_{E,M} + j_{E,H}).$$

Specification of Fluxes

Organic fluxes

$$j_{E,A_A} = \alpha_{E_A} j_{E,A},$$

$$j_{E,A_{HE}} = \alpha_{E_E}(1 - \alpha_{E_A})j_{E,A},$$

$$j_{E,A_{HV}} = (1 - \alpha_{E_E})(1 - \alpha_{E_A})j_{E,A},$$

$$j_{D_E,A_{HE}} = -y_{D_E E} j_{E,A_{HE}},$$

$$j_{D_V,A_{HV}} = -y_{D_V E} j_{E,A_{HV}},$$

$$j_{V,G} = \frac{m_E \dot{k}_E - y_{EV} \dot{k}_M}{m_E + y_{EV}}$$

$$j_{E,G} = -y_{EV} j_{V,G},$$

$$j_{E,M} = -y_{EV} \dot{k}_M,$$

$$j_{V,H} = -h_{\dagger} \frac{m_E}{y_{EV} + m_E},$$

$$j_{D_V,H} = -j_{V,H},$$

$$j_{E,H} = m_E j_{V,H},$$

$$j_{D_E,H} = -j_{E,H}.$$

$$\text{with } m_E = X_E/X_V$$

Mineral fluxes

$$j_{C,A_A} = -j_{E,A_A},$$

$$j_{C,A_{HV}} = -j_{D_V,A_{HV}} - j_{E,A_{HV}},$$

$$j_{C,A_{HE}} = -j_{D_E,A_{HE}} - j_{E,A_{HE}},$$

$$j_{C,G} = -j_{V,G} - j_{E,G},$$

$$j_{C,M} = -j_{E,M},$$

$$j_{N,A_A} = -n_{NE} j_{E,A_A},$$

$$j_{N,A_{HV}} = -n_{NV} j_{D_V,A_{HV}} - n_{NE} j_{E,A_{HV}},$$

$$j_{N,A_{HE}} = -n_{NE} j_{D_E,A_{HE}} - n_{NE} j_{E,A_{HE}},$$

$$j_{N,G} = -n_{NV} j_{V,G} - n_{NE} j_{E,G},$$

$$j_{N,M} = -n_{NE} j_{E,M},$$

with functional responses f_N in (A.1), f_C in (A.2) and f_{C_H} in (A.3), and with the auxiliary fluxes

$$j_{E_E,A_{HE}} = j_{E_E,A_{HE}m} (1 + x_{N_E}^{-1} + x_{D_E}^{-1} - (x_{N_E} + x_{D_E})^{-1})^{-1}, \quad (\text{A.4})$$

$$\text{with } x_{N_E} = X_{N_E}/K_{N_E}; \quad x_{D_E} = X_{D_E}/K_{D_E},$$

$$j_{E_V,A_{HV}} = j_{E_V,A_{HV}m} (1 + x_{N_V}^{-1} + x_{D_V}^{-1} - (x_{N_V} + x_{D_V})^{-1})^{-1} \quad (\text{A.5})$$

$$\text{with } x_{N_V} = X_{N_V}/K_{N_V}; \quad x_{D_V} = X_{D_V}/K_{D_V},$$

$$j_{E_H,A_H} = (\dot{k}_{E_H}^{-1} + \alpha_{E_E} (\rho_{E_E} j_{E_E,A_{HE}})^{-1})^{-1}$$

$$\text{with } \dot{k}_{E_H} = \alpha_{E_E} \dot{k}_{E_E} + (1 - \alpha_{E_E}) \dot{k}_{E_V};$$

$$\text{and } \alpha_{E_E} = \left(1 + \frac{\rho_{E_V} j_{E_V,A_{HV}}}{\rho_{E_E} j_{E_E,A_{HE}}}\right)^{-1},$$

$$j_{E_A,A_A} = \frac{j_{E_A,A}m(1 + z_N^{-1} + z_{C_H}^{-1} - (z_N + z_{C_H})^{-1})}{1 + z_N^{-1} f_N^{-1} + z_{C_H}^{-1} f_{C_H}^{-1} - (z_N f_N + z_{C_H} f_{C_H})^{-1}},$$

$$j_{E,A} = (\dot{k}_{EM}^{-1} + \alpha_{E_A} (\rho_{E_A} j_{E_A,A_A})^{-1})^{-1}$$

$$\text{with } \dot{k}_{EM} = \alpha_{E_A} \dot{k}_{E_A} + (1 - \alpha_{E_A}) \dot{k}_{E_H};$$

$$\text{and } \alpha_{E_A} = \left(1 + \frac{\rho_{E_H} j_{E_H,A_H}}{\rho_{E_A} j_{E_A,A_A}}\right)^{-1}.$$

Parameters and Provisional Values

$j_{L,F}$	— 5	mol d^{-1}	X_{C+}	1000	μM	X_{N+}	150	μM
$j_{E_V, A_{HV}m}$	1.5	$\text{mol mol}^{-1} \text{d}^{-1}$	$j_{E_E, A_{HE}m}$	2	$\text{mol mol}^{-1} \text{d}^{-1}$	$j_{E_A, Am}$	2.5	$\text{mol mol}^{-1} \text{d}^{-1}$
$j_{L, FK}$	25	mol d^{-1}	K_C	500	μM	K_N	0.1	μM
K_{N_V}	0.001	μM	K_{N_E}	0.001	μM	K_{D_V}	2500	μM
K_{D_E}	1000	μM	ρ_{E_H}	0.8	—	ρ_{E_A}	0.9	—
ρ_{E_V}	0.7	—	ρ_{E_E}	0.9	—	k_{E_A}	10	$\text{mol mol}^{-1} \text{d}^{-1}$
k_{E_H}	10	$\text{mol mol}^{-1} \text{d}^{-1}$	k_{E_V}	5	$\text{mol mol}^{-1} \text{d}^{-1}$	k_{E_E}	5	$\text{mol mol}^{-1} \text{d}^{-1}$
z_C	10	—	z_N	10	—	z_{C_H}	10	—
$y_{D_V E}$	4	mol mol^{-1}	$y_{D_E E}$	2.5	mol mol^{-1}	y_{EV}	1.5	mol mol^{-1}
$\dot{k}_E$	0.6	d^{-1}	$\dot{k}_M$	0.1	d^{-1}	$\dot{h}_\dagger$	0.45	d^{-1}
n_{NV}	0.1	—	n_{NE}	0.2	—	L_m	70	m

System Parameters

$$j_{L,F},$$

$$X_{C+} = X_C + X_{D_V} + X_{D_E} + X_V + X_E,$$

$$X_{N+} = X_N + n_{NV}(X_{D_V} + X_V) + n_{NE}(X_{D_E} + X_E).$$

Steady States

$$\alpha_{E_E}^* = \left(1 + \frac{y_{D_E E}}{m_E^* y_{D_V E}}\right)^{-1};$$

$$\alpha_{E_A}^* = \left(1 + \frac{j_{E_A, A_{HE}}^*}{\alpha_{E_E}^* j_{E_A, A}^*}\right)^{-1};$$

$$m_E^* = \frac{y_{EV} k_M}{\dot{k}_E - \dot{h}_\dagger};$$

$$j_{V,G}^* = \frac{\dot{k}_M \dot{h}_\dagger}{\dot{k}_M + \dot{k}_E - \dot{h}_\dagger};$$

$$\dot{k}_{E_{HM}}^* = \alpha_{E_E}^* \dot{k}_{E_E} + (1 - \alpha_{E_E}^*) \dot{k}_{E_V};$$

$$\dot{k}_{EM}^* = \alpha_{E_A}^* \dot{k}_{E_A} + (1 - \alpha_{E_A}^*) \dot{k}_{E_H};$$

$$j_{E,A}^* = y_{EV}(\dot{k}_M + j_{V,G}^*) + \frac{\dot{h}_\dagger m_E^{*2}}{y_{EV} + m_E^*};$$

$$j_{E_A, A_{HV}}^* = \frac{\dot{h}_\dagger}{y_{D_V E}} \frac{m_E^*}{y_{EV} + m_E^*};$$

$$j_{E_A, A_{HE}}^* = \frac{\dot{h}_\dagger}{y_{D_E E}} \frac{m_E^{*2}}{y_{EV} + m_E^*};$$

$$j_{E_A, A_A}^* = \frac{\alpha_{E_A}^* / \rho_{E_A}}{j_{E,A}^{*-1} - \dot{k}_{EM}^{*-1}};$$

$$j_{E_H, A_H}^* = j_{E_A, A_A}^* (\alpha_{E_A}^{*-1} - 1) \rho_{E_A} / \rho_{E_H};$$

$$j_{E_E, A_{HE}}^* = \frac{\alpha_{E_E}^* / \rho_{E_E}}{j_{E_H, A_H}^{*-1} - \dot{k}_{E_{HM}}^{*-1}};$$

$$j_{E_V, A_{HV}}^* = j_{E_E, A_{HE}}^* (\alpha_{E_E}^{*-1} - 1) \rho_{E_E} / \rho_{E_V};$$

$$j_{E_A, A_A}^* = j_{E,A}^* - j_{E_A, A_{HE}}^* - j_{E_A, A_{HV}}^*;$$

$$j_{E_A, H}^* = (1 - \alpha_{E_A}^*) j_{E,A}^*;$$

$$f_{\tilde{C}}^* = (f_{C_H}^{*-1} (z_C + 1) - z_C)^{-1};$$

$$f_{C_H}^* = \frac{\sqrt{1 + 4/(\alpha^* z_N - z_N - 1)} - 1}{2z_{C_H}/z_N};$$

$$f_N^* = \frac{\sqrt{1 + 4/(\alpha^* z_{C_H} - z_{C_H} - 1)} - 1}{2z_N/z_{C_H}};$$

$$\alpha^* = \frac{1 + z_N^{-1} + z_{C_H}^{-1} - (z_N + z_{C_H})^{-1}}{j_{E_A, A_A}^* / j_{E_A, Am}^*}.$$

If light intensity allows existence:

C-limited	N-limited
$X_C^* = K_C (f_C^{*-1} - 1)^{-1}$	or $X_{C+} - X_{D_E}^* - X_E^* - X_{D_V}^* - X_V^*$,
$X_N^* = X_{N+} - n_{NE}(X_{D_E}^* + X_E^*) - n_{NV}(X_{D_V}^* + X_V^*)$	or $K_N (f_N^{*-1} - 1)^{-1}$,
$X_{D_V}^* = K_{D_V} \left(\frac{j_{E_V, A_{HV}}}{j_{E_V, A_{HV}}^*} - 1 \right)^{-1}$	or $K_{D_V} \left(\frac{j_{E_V, A_{HV}}}{j_{E_V, A_{HV}}^*} - 1 \right)^{-1}$ for small K_{N_V} ,
$X_{D_E}^* = K_{D_E} \left(\frac{j_{E_E, A_{HE}}}{j_{E_E, A_{HE}}^*} - 1 \right)^{-1}$	or $K_{D_E} \left(\frac{j_{E_E, A_{HE}}}{j_{E_E, A_{HE}}^*} - 1 \right)^{-1}$ for small K_{N_E} ,
$X_V^* = \frac{X_{C+} - X_C^* - X_{D_V}^* - X_{D_E}^*}{1 + m_E^*}$	or $\frac{X_{N+} - X_N^* - n_{NV}X_{D_V}^* - n_{NE}X_{D_E}^*}{n_{NV} + n_{NE}m_E^*}$,
$X_E^* = X_V^* m_E^*$	or $X_V^* m_E^*$.

The properties of the no-reserve model at the limitation switches also apply to the one-reserve model.

THREE-RESERVE MODEL

Specification of Changes in State Variables

The system has eight state variables: DIC C , DIN N , structure-detritus D_V , reserve-detritus D_E , structure V , (heterotrophic) reserve E , carbon-reserve E_C , nitrogen-reserve E_N . They partake in six transformations: autotrophic assimilation A_A , heterotrophic assimilation A_H , excretion E , growth G , maintenance M , hazard H . The changes are given by

$$\begin{aligned} \frac{d}{dt} X_C &= X_V(j_{C,A_A} + j_{C,A_{HV}} + j_{C,A_{HE}} + j_{C,E} \\ &\quad + j_{C,G} + j_{C,M} + j_{C,H}), \\ \frac{d}{dt} X_N &= X_V(j_{N,A_A} + j_{N,A_{HV}} + j_{N,A_{HE}} + j_{N,E} \\ &\quad + j_{N,G} + j_{N,M} + j_{N,H}), \\ \frac{d}{dt} X_{D_V} &= X_V(j_{D_V,A_{HV}} + j_{D_V,H}), \\ \frac{d}{dt} X_{D_E} &= X_V(j_{D_E,A_{HE}} + j_{D_E,H}), \\ \frac{d}{dt} X_V &= X_V(j_{V,G} + j_{V,H}), \end{aligned}$$

$$\frac{d}{dt} X_E = X_V(j_{E,A_{HV}} + j_{E,A_{HE}} + j_{E,G} + j_{E,M} + j_{E,H}),$$

$$\frac{d}{dt} X_{E_C} = X_V(j_{E_C,A_A} - j_{E_C,E} + j_{E_C,G} + j_{E_C,M} + j_{E_C,H}),$$

$$\frac{d}{dt} X_{E_N} = X_V(j_{E_N,A_A} - j_{E_N,E} + j_{E_N,G} + j_{E_N,M} + j_{E_N,H}),$$

Specification of Fluxes

Organic fluxes

$$j_{V,G} = \frac{k_E \alpha - k_M}{\alpha + 1} \quad \text{with } m_E = \frac{X_E}{X_V};$$

$$m_{E_C} = \frac{X_{E_C}}{X_V}; \quad m_{E_N} = \frac{X_{E_N}}{X_V}$$

$$\begin{aligned} \text{and } \alpha &= \frac{m_E}{y_{EV}} + \left(\left(\frac{m_{E_C}}{y_{E_C V}} \right)^{-1} \right. \\ &\quad \left. + \left(\frac{m_{E_N}}{y_{E_N V}} \right)^{-1} - \left(\frac{m_{E_C}}{y_{E_C V}} + \frac{m_{E_N}}{y_{E_N V}} \right)^{-1} \right)^{-1}, \end{aligned}$$

$$\begin{aligned} j_{E_C,E} &= (1 - \kappa_{E_C})(m_{E_C}(k_E - j_{V,G}) \\ &\quad - \alpha_A y_{E_C V}(j_{V,G} + k_M)) \quad \text{with } \alpha_A = 1 - \alpha_H, \end{aligned}$$

$$\begin{aligned} j_{E_N,E} &= (1 - \kappa_{E_N})(m_{E_N}(k_E - j_{V,G}) \\ &\quad - \alpha_A y_{E_N V}(j_{V,G} + k_M)) \quad \text{with } \alpha_H = m_E / \alpha y_{EV}. \end{aligned}$$

$$j_{E,AHE} = \alpha_{E_E} j_{E,A_H},$$

$$j_{E,AHV} = (1 - \alpha_{E_E}) j_{E,A_H},$$

$$j_{D_E,AHE} = -y_{D_E} j_{E,AHE},$$

$$j_{D_V,AHV} = -y_{D_V} j_{E,AHV},$$

$$j_{E,G} = -j_{V,G} \alpha_H y_{EV},$$

$$j_{E_C,G} = -j_{V,G} \alpha_A y_{E_C V},$$

$$j_{E_N,G} = -j_{V,G} \alpha_A y_{E_N V},$$

$$j_{E,M} = -\dot{k}_M \alpha_H y_{EV},$$

$$j_{E_C,M} = -\dot{k}_M \alpha_A y_{E_C V},$$

$$j_{E_N,M} = -\dot{k}_M \alpha_A y_{E_N V},$$

$$j_{V,H} = -\frac{\dot{h}_\dagger m_E}{y_{EV} + m_E} - \frac{\dot{h}_\dagger m_{E_C}}{y_{E_C V} + m_{E_C}} \\ - \frac{\dot{h}_\dagger m_{E_N}}{y_{E_N V} + m_{E_N}},$$

$$j_{D_V,H} = -j_{V,H},$$

$$j_{D_E,H} = -j_{E,H},$$

$$j_{E,H} = m_E j_{V,H},$$

$$j_{E_C,H} = m_{E_C} j_{V,H},$$

$$j_{E_N,H} = m_{E_N} j_{V,H},$$

Mineral fluxes

$$j_{C,A_A} = -j_{E_C,A_A},$$

$$j_{C,AHV} = -j_{D_V,AHV} - j_{E,AHV},$$

$$j_{C,AHE} = -j_{D_E,AHE} - j_{E,AHE},$$

$$j_{C,E} = j_{E_C,E},$$

$$j_{C,G} = -j_{V,G} - j_{E,G} - j_{E_C,G},$$

$$j_{C,M} = -j_{E,M} - j_{E_C,M},$$

$$j_{C,H} = -j_{E_C,H},$$

$$j_{N,A_A} = -j_{E_N,A_A},$$

$$j_{N,AHV} = -n_{NV} j_{D_V,AHV} - n_{NE} j_{E,AHV},$$

$$j_{N,AHE} = -n_{NE} j_{D_E,AHE} - n_{NE} j_{E,AHE},$$

$$j_{N,E} = j_{E_N,E},$$

$$j_{N,G} = -n_{NV} j_{V,G} - n_{NE} j_{E,G} - j_{E_N,G},$$

$$j_{N,M} = -n_{NE} j_{E,M} - j_{E_N,M},$$

$$j_{N,H} = -j_{E_N,H},$$

with functional responses f_N in eqn (A.1), f_C in eqn (A.2) and f_{C_H} in eqn (A.3), and with the auxiliary fluxes $j_{E_E,AHE}$ in eqn (A.4) and $j_{E_V,AHV}$ in eqn (A.5) and

$$j_{E_C,A_A} = j_{E_C,Am} f_{C_H},$$

$$j_{E_N,A_A} = j_{E_N,Am} f_N,$$

$$j_{E,A_H} = (\dot{k}_{E_H M}^{-1} + \alpha_{E_E} (\rho_{E_E} j_{E,AHE})^{-1})^{-1}$$

$$\text{with } \dot{k}_{E_H M} = \alpha_{E_E} \dot{k}_{E_E} + (1 - \alpha_{E_E}) \dot{k}_{E_V};$$

$$\alpha_{E_E} = (1 + (\rho_{E_V} j_{E_V,AHV} / \rho_{E_E} j_{E,AHE}))^{-1}$$

System Parameters

$$j_{L,F},$$

$$X_{C+} = X_C + X_{D_V} + X_{D_E} + X_V + X_E + X_{E_C},$$

$$X_{N+} = X_N + n_{NV} (X_{D_V} + X_V)$$

$$+ n_{NE} (X_{D_E} + X_E) + X_{E_N}.$$

Parameters Compared with One-reserve Model

$$\text{Extra: } \kappa_{E_C}, \kappa_{E_N}, y_{E_C V}, y_{E_N V}, j_{E_C,Am}, j_{E_N,Am}.$$

$$\text{Redundant: } \rho_{E_A}, \rho_{E_H}, j_{E_A Am}, z_{C_H}, \dot{k}_{E_A}, \dot{k}_{E_H}.$$