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A trait-based approach for downscaling complexity in plankton ecosystem models

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Abstract

Although predator-prey cycles can be easily predicted with mathematical models it is only since recently that oscillations observed in a chemostat predator-prey (rotifer-algal) experiment offer an interesting workbench for testing model soundness. These new observations have highlighted the limitations of the conventional modelling approach in correctly reproducing some unexpected characteristics of the cycles. Simulations are improved when changes in algal community structure, resulting from natural selection operating on an assemblage of algal clones differing in competitive ability and defence against rotifer predation, is considered in multi-prey models. This approach, however, leads to extra complexity in terms of state variables and parameters. We show here that multi-prey models with one predator can be effectively approximated with a simpler (only a few differential equations) model derived in the context of adaptive dynamics and obtained with a moment-based approximation. The moment-based approximation has been already discussed in the literature but mostly in a theoretical context, therefore we focus on the strength of this approach in downscaling model complexity by relating it

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to the chemostat predator-prey experiment. Being based on mechanistic concepts, our modelling framework can be applied to any community of competing species for which a trade-off between competitive ability and resistance to predators can be appropriately defined. We suggest that this approach can be of great benefit for reducing complexity in biogeochemical modelling studies at the basin or global ocean scale.

Key words: Predator-prey cycles, Community ecology, Complexity reduction, Trait-based modelling, Trade-off, Moment-based approximation, Adaptation, ECEM 07

1 Introduction

Plankton ecosystem modelling is a fundamental tool for understanding the biogeochemical cycles of crucial elements like carbon or for investigating ecosystem functioning. In the last two decades, due to an increase in computer power along with the need of more realistic predictions, there has been a tendency of developing models of increased complexity (Baretta et al., 1995; Moore and et al., 2002; Le Quéré et al., 2005). The early and simple so-called NPZD (Nitrogen, Phytoplankton, Zooplankton and Detritus) models have "evolved" into more complex models representing many plankton functional types (PFTs) (Anderson, 2005). However, a higher degree of model complexity does not necessarily guarantee improved predictions (Fulton et al., 2003; Anderson, 2005; Hood et al., 2006).

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"Do we understand the ecology of PFTs well enough to build up model complexity?" was asking Anderson (2005) in his thought-provocative paper. In our opinion we still have a limited understanding of aquatic ecosystems and alternative approaches, ideally process-oriented, are highly desirable. For instance, a yet simple but fundamental predator-prey (rotifer-algal) system showed in a chemostat experiment some rather unexpected population cycles which were quantitatively impossible to predict with a classical NPZ kind of model (Fussmann et al., 2000), indicating that the model lacked of some important biological or ecological mechanism (Shertzer et al., 2002; Yoshida et al., 2003).

Inherently connected to the complexity issue is the problem of representing adaptive processes in ecological models. Being characterised by fixed parameters, current models can be regarded in a sense as "static representations of reality", although state variables do change with time. That is, the actual processes governing the interactions within plankton communities and between communities and the environment they live in are based on fixed characteristics (i.e. fixed algal food value, fixed algal competitive ability or fitness, etc.) thus excluding the possibility for communities to adapt to new situations and to change their properties to better fit the prevailing forcing at a certain time (Jørgensen, 1992). In other words, models using fixed parameters cannot account for changes in community structure or adaptation. In principle, there is no justification for setting fixed the competitive abilities (associated for instance to nutrient affinity, $1/K_N$, in a Michaelis-Menten type of growth) of algal communities. It is more likely that these competitive abilities change in response to varying environmental conditions. It is since long that attempts are being made to address these issues. The approach of considering zooplankton feeding preferences (Fasham et al., 1990) was probably one of the first to
introduce some sort of "flexibility" in the model systems. Other prominent strategies are represented by the structural dynamic modelling (Jørgensen, 1986, 1999; Zhang et al., 2003) or, more recently, by the optimality-based modelling for resource allocation (Klausmeier et al., 2004; Pahlow, 2005; Armstrong, 2006; Smith and Yamanaka, 2007). In order to account for adaptive processes, we shall describe an approach based on the derivation of trade-off functions and succession-driven changes of community-aggregated properties.

Species succession and species sorting processes in nature are determined by the characteristics (traits) of each individual and species in a community. Recently, there has been a renewed interest in trait-based approaches in ecology both in land (Lavorel and Garnier, 2002; McGill et al., 2006; Westoby and Wright, 2006; Ackerly and Cornwell, 2007) and marine (Litchman et al., 2007; Litchman and Klausmeier, 2008) ecology. For modelling the dynamics of traits and therefore for predicting the interactions between environmental fluctuations and ecosystem responses, trait-based models have been developed over the years, some in a theoretical framework and in contexts aiming at understanding species diversity (Tilman et al., 1997; Norberg et al., 2001; Loreau et al., 2003; Tilman, 2004; Savage et al., 2007) and some others as applications to real ecosystems (Wirtz and Eckhardt, 1996; Armstrong, 2003; Bruggeman and Kooijman, 2007; Pahlow et al., 2008). On a global scale, an approach based on stochastically-determined traits (Follows et al., 2007) generated an emergent community structure and biogeography consistent with observed global phytoplankton distributions.

The temporal evolution of a community consisting of n plankton functional groups or species may of course be simulated by accounting for the dynamics of each separately. A trait-based approach can then help to constrain the char-
acteristics (parameters) of each species. With trade-offs governing interspecific
differences, a realistic representation of community behavior is obtained by let-
ting natural selection operate on an assemblage of species with different trait
values (Bruggeman and Kooijman, 2007). However, although this approach
requires little detail in terms of physiological parameters, it introduces a great
number of state variables in its discretization of the trait distribution. As a
result, this approach is computationally expensive and not suitable for prob-
lems that are limited by computation resources (for example high-resolution
spatially explicit models).

Drawing from the Dynamic Energy Budget (DEB) theory (Kooijman, 2000;
Nisbet et al., 2000) and from the adaptive dynamics approach (Abrams et al.,
1993; Dieckmann and Law, 1996; Leibold and Norberg, 2004; Norberg, 2004),
we will present a self-consistent methodological framework for deriving trait-
based models of aggregate group behaviour.

The new methodological framework consists of three steps:

(1) derive a mechanistic trade-off from resource-allocation principles;
(2) consider a full model for a community of $n$ components subject to the
derived trade-off;
(3) approximate the full model with an aggregate model for macroscopic
quantities like total clone biomass, mean trait value and variance.

We will illustrate the adaptive behaviour of the community (in the tempo-
ral evolution of mean trait and trait variance) under changing environmental
conditions.

Our model will describe a chemostat system comprising a nutrient resource,
a community of genetically different algal clones and a planktonic rotifer (Yoshida et al., 2003), in which it was observed 1) that evolutionary processes can take place at ecological time scales, and 2) the existence of an evolutionary trade-off between algal food value and competitive ability. We built on the work of Yoshida et al. (2003) because their experiments are conceptually simple, represent a controlled system and can give the readers an immediate sense of the plausibility of our model. Nevertheless, the structure of our aggregate model is general and can be applied to any community of competing species for which a trade-off between competitive ability for resource harvesting and resistance to predators can be appropriately defined.

2 Algal competitive ability and resistance to predation

The concept that organisms face trade-offs in their ability to allocate limited energy and resources to growth, reproduction and defence is central to most theories explaining the diversity of life on Earth (Tilman, 2000). The trade-off between competitive ability and resistance to predators is particularly common and well-studied (Leibold, 1989, 1996; Grover, 1994, 1995; Tilman, 2000; Jessup and Bohannan, 2008), and has been suggested to underlie several characteristic patterns exhibited by some of the most elaborate predator-prey experiments (Fussmann et al., 2000; Yoshida et al., 2003).

Fussmann et al. (2000) set up a food chain experiment in a chemostat (a continuous flow-through system) consisting of a planktonic rotifer, *Brachionus calyciflorus*, feeding on unicellular green algae, *Chlorella vulgaris*, and used nitrogen as the limiting resource for algal growth. The system was controlled by two parameters, the nitrogen concentration of the inflow medium (\(N_i\)) and

\[ N_i \]
the dilution rate (d), that is the fraction of the volume of the system replaced daily. Different experimental conditions resulted in different population dynamics comprising coexistence at equilibria, coexistence on limit cycles, or extinction of the predator or both predator and prey. Fussmann et al. (2000) also proposed a simple model consisting of four differential equations with which they were able to qualitatively reproduce each of these behaviours. However, the model failed to predict important quantitative features such as the periods and relative phases of the observed rotifer-algal cycles (see Fig. 1 in Shertzer et al., 2002).

Shertzer et al. (2002) and Yoshida et al. (2003) observed that only when rapid prey evolution in response to predation was considered could their model predict also the quantitative features of the observations. The evolution hypothesis was directly tested in a chemostat experiment by Yoshida et al. (2003). They found that algae cultivated under constant and intense rotifer grazing pressure became lower in food value and were heritably smaller and competitively inferior relative to algae grown in the absence of rotifers. Yoshida et al. (2003) introduced clonal selection by specifying a set of competing clones in terms of their food value and related competitive ability and by postulating that the defensive “low food value” trait comes at the cost of reduced nutrient affinity (i.e. increased nutrient half-saturation). This relationship was specified by a trade-off curve, which was based on two free parameters: a shape parameter and a scale or ”cost” parameter (Yoshida et al., 2003).

This approach, however, has some problems. 1) Population dynamics are highly sensitive to the shape and scale parameters of the trade-off function, but this functional relationship is completely empirical (i.e. based on a specific experiment) and constrained only by two individual observations. 2) If
clones have to be specified in order to take into account evolutionary trade-offs, then the number of model equations would raise to $n+2$ ($n$ algal clones, 1 nutrient and 1 rotifer), thus leading to a higher degree of complexity.

In order to design a more general model framework we will derive in the following a mechanistic, single-parameter trade-off function from resource-allocation principles (Bruggeman and Kooijman, 2007). The derivation is based on general energy-partitioning arguments and can lead to the formulation of trade-off functions for a wide variety of traits, including basal respiration, the maximum growth rate, and light-, nutrient- and prey affinity. The trade-off is subsequently combined with an aggregation method to produce a community model that is based only on a few parameters and state variables. As we shall see, this model closely reproduces the behaviour of a multi-species system thus proving effective in downscaling complexity.

It is not our intention here to revisit the works of Fussmann et al. (2000) and Yoshida et al. (2003) by providing a detailed quantitative description of the observed predator-prey dynamics. Our ultimate aim is rather to provide a general method for deriving trade-off functions and to approximate multi-species models with aggregate variables in order to downscale model complexity.

3 A mechanistic approach to derive trade-off functions

The term ”mechanistic” relates to the idea that a natural process can be explained in purely physical or deterministic terms. The derivation of our trade-off function is inspired by DEB theory, which mechanistically describes how individual organisms acquire and utilize energy, and can serve as a link
between different levels of biological organization (Kooijman, 2000; Nisbet et al., 2000). Figure 1 illustrates, in purely physical terms, the allocation of a resource to different algal activities or pools in our model.

We assume that each algal clone partitions assimilated energy and mass over three pools: 1) generic biomass, 2) nutrient harvesting biomass (with dimensionless allocation coefficient $\alpha$), and 3) defence biomass (with dimensionless allocation coefficient $\delta$). The fraction allocated to generic biomass, which relates to energy invested in all activities other than nutrient harvesting and defence, is denoted by $\kappa$, and assumed equal for all clones. The partition of the remaining fraction ($1-\kappa$) between nutrient harvesting and defence pools is assumed to be clone-specific. The generic biomass of a clone $i$ is a measure of population size and is denoted by $C_i$.

Therefore, by construction, the relation between nutrient harvesting and defence is

$$1 - \kappa = \alpha + \delta$$  \hspace{1cm} (1)

Similar to Yoshida et al. (2003), we will define each algal clone by its "edibility" ($\varphi_i$) with respect to rotifers (i.e.: the affinity of the rotifer for clone $i$). The affinity of the rotifer for clone $i$ is assumed to be inversely proportional to the relative amount of defence biomass of that clone, i.e., its defence biomass per unit of total biomass,

$$\varphi_i = \frac{1}{(1 - \kappa - \alpha_i)}.$$  \hspace{1cm} (2)
which will be the single trait varying between algal clones. The investments in nutrient harvesting biomass can now be written as $\alpha = 1 - \kappa - \varphi^{-1}$. In a similar fashion, the effective nutrient affinity of an algal clone $i$ is assumed to be proportional to the relative amount of nutrient harvesting biomass of that clone. Then, the effective half-saturation constant for Michaelis-Menten nutrient uptake will be

$$K_{N_i} = \frac{\tilde{K}_N}{\alpha(\varphi_i)} = \frac{\tilde{K}_N}{(1 - \kappa - \varphi_i^{-1})},$$

where $\tilde{K}_N$ is a constant parameter. We note here that there is a lower boundary for $\varphi$. In fact, if $\alpha = 0$ (the extreme case in which all investments go into defensive mechanisms) then the minimum that $\varphi$ can reach is $(1 - \kappa)^{-1}$. Therefore $\varphi \geq (1 - \kappa)^{-1}$ (or else $\delta \leq 1 - \kappa$).

In Figure 2 we show various trade-off functions obtained at different values of $\kappa$. Note that $\kappa$ is only a scale parameter and does not have an effect on the shape of the trade-off function.

With respect to the trade-off function of Yoshida et al. (2003), Equation 3 is simpler (it depends only on one scaling parameter) and more general in the sense that it is derived based on a typical resource-predator-prey system.

In summary, $n$ competing clones are specified in terms of their defensive traits, (or edibility, $\varphi$), this leads to a multi-clone model comprising $n+2$ differential equations (see Appendix A.1 for more details).

To illustrate how our trade-off works, we present an example in which a community of 40 clones compete for nitrogen while they ’defend’ against predation by the rotifer. Figure 3 shows the distribution of these clones with respect to
their assigned edibility trait, chosen as an index varying between 1 (for clone 1) and 40 (for clone 40), at different time steps. In this particular run, all clones are given the same, relatively low, initial concentrations (model parameters are reported in Table 1). In the first period (days 0-5), nutrient concentration is high and grazing pressure is relatively low, clones are free to mainly compete for nutrient, therefore clones with relatively high edibility are favoured (days 5-10). As time progresses (days 10-15), the nutrient resource starts to be depleted and grazing pressure increases making less edible clones at this stage more successful. Towards the end of the run (day 120), a few clones (the fittest) with edibility trait value around 12 outcompete all the others. To maintain generality, we ascribe more importance to the relative value of edibility rather than to its absolute value. Therefore, an edibility index varying from 0 to 40 implies that a clone with edibility trait 40 is 100% edible, whereas a clone with edibility 0 is a totally inedible clone. The fittest clone in our example is a 30% edible clone, being characterised by a value of 12.

This test shows how the combination of bottom-up and top-down processes, here mechanistically simulated with a function that trades off competitive ability against resistance to predation, can drive changes in algal community structure. Consistently with the competitive exclusion principle (Hardin, 1960), only the few fittest clones survive by the end of the run (Figure 3).

In Figure 4 we present the time evolution of all variables represented in the model (nitrogen, rotifer and 40 algal clones) for two particular simulations: one producing an equilibrium (panels a-c) and the other producing limit cycles (panels d-f). The parameter configuration producing the equilibrium is the same as for run in Figure 3 and is reported in Table 1. The limit cycle behaviour is obtained by changing only the half-saturation for rotifer growth
We note here that low $K_C$ values make predator feeding less sensitive to $\varphi$ (because the term $\tilde{C}$ in the denominator of equation A.5 will always be larger), while higher values of $K_C$ make predator feeding scaling linearly with $\varphi$. Consequently, $K_C$ plays an important role in determining the model sensitivity to $\varphi$.

4 Approximating complex models

As we have seen so far, the need to include adaptive processes in a predator-prey model has lead to a rather complex multi-clone model. Although the multi-clone model presented here is more general (and the assumed trade-off between algal competitive ability for nutrient harvesting and defence against grazing is based on less parameters) with respect to the model proposed by Yoshida et al. (2003), it is nevertheless desirable to downscale the inherent complexity of these models in a way that changes in the multi-clone community structure are appropriately reproduced by simpler models.

Here we present a method to approximate the multi-clone model introduced in the previous section. This method is based on the adaptive dynamics approach (Abrams et al., 1993; Dieckmann and Law, 1996; Leibold and Norberg, 2004; Norberg, 2004). Using so-called moment approximation techniques (Wirtz and Eckhardt, 1996; Norberg et al., 2001), a multi-clone model of $n+2$ differential equations can be reduced (see Appendix A.2 for a detailed derivation) to only five differential equations that are able to capture the dynamics of the macroscopic characteristics of the group such as total algal biomass ($C_T$), the average edibility trait ($\bar{\varphi}$) and the edibility trait variance ($v$), which is a measure of clone diversity.
The rate of change of the total clonal generic biomass is written as

$$\frac{dC_T}{dt} \approx C_T \left[ r(\bar{\varphi}) + \frac{1}{2} v \frac{d^2 r(\bar{\varphi})}{d\varphi^2} \right],$$

(4)

with $r(\bar{\varphi})$ denoting the generic biomass-specific growth rate of an algal clone (equation A.7). The rate of changes of the average edibility trait is written as

$$\frac{d\bar{\varphi}}{dt} \approx v \frac{dr(\bar{\varphi})}{d\varphi}.$$  

(5)

An analogous equation for the rate of change of the trait variance can be derived,

$$\frac{dv}{dt} \approx v^2 \frac{d^2 r(\bar{\varphi})}{d\varphi^2}.$$  

(6)

We tested the accuracy of the approximation by running the multi-clone model with 40 clones (equations A.6-A.10) and calculating $C_T$, $\bar{\varphi}$ and $v$ over time from the resulting species distribution. These variables were then compared to those obtained by running the approximated model (equations A.23-A.27).

Both models were parameterised using the same parameter set (Table 1).

The comparison between the results obtained with the two models are shown in Figure 5 both for equilibrium (panels a-c) and limit cycle (panels d-f) behaviours. The result is quite clear: the reduced model can approximate the dynamic behaviour of the full model with high accuracy.

The quality of a moment-based approximation theoretically decreases with increasing moment order: the mathematical approximation for the total biomass
is better than that of the mean, and the approximation for the mean is better than that of the variance (see Appendix A.2). In this respect, the present aggregate approximation for the variance performs remarkably well (Figure 5). The mean absolute error in the standard deviation is 1.3% of its relevant range, which is close to the 1.1% error in the total biomass and better than the 2.6% error in the mean. This may appear somewhat surprising, but does not indicate a problem in the formulation of the aggregate model. Detailed investigation of the aggregate model shows that the initial dynamics of the mean are controlled by the $2^{nd}$ and $3^{rd}$ order terms, which are omitted in the aggregate model. This dominance of higher-order terms lasts only 4 days. However, this period is sufficient to create a deviation in the mean that in turn makes the approximation of the total biomass less precise, while it happens to improve the approximation of the variance. This feature is specific to the present system and initial conditions. The performance of the aggregation method is on the whole very satisfactory and comparable to results obtained when more complicated moment closures are included (Norberg et al., 2001).

In agreement with Shertzer et al. (2002), our models show that relatively high predation pressure during rotifer peaks select for better-defended algae (see Figure 6).

Most of our model solutions tended to a steady-state characterised by the survival of only a very few clones (competitive exclusion, Hardin, 1960) - an aspect represented by the trait variance approaching to zero for a wide range of parameter sets (Figure 5 shows only two examples). This implies that the adaptive capacity of the system is mainly caused by a change in its components (clones) by species sorting processes (succession driven by interactions - resource competition in our case). One aspect that can ‘solve’
the tendency to a steady-state characterised by a zero variance would be to consider exogenous processes tending to sustain high functional diversity such as immigration or hatching from resting stages (Norberg, 2004; Leibold and Norberg, 2004). While these processes are plausible in real ecosystems, they are certainly not applicable to a closed system like the chemostat.

Finally, with Figure 7 we show the adaptive value of edibility when the models are run to steady-state under different nutrient concentrations and grazing pressures. Increasing nutrient concentration selects for clones characterised by lower edibility traits. At the highest nitrogen inflows, clones with high nutrient affinity (see equation 2) are rapidly outcompeted and only those clones very low in food value survive in the chemostat. An analogous effect is produced by increasing the rotifer maximum growth rate, confirming that also increasing grazing pressure (see equation A.5) selects for better defended-clones. At steady-state, the aggregate model reproduces with remarkable high accuracy the predictions of the full model over a wide range of nutrient concentrations (Figure 7a) and grazing pressures (Figure 7b).

5 Conclusions

Trait-based modelling approaches require assumptions on trade-offs. Changes in traits have to be based on an appropriate balance between benefits and costs in order to avoid that the system 'adapts' toward unrealistic trait values. With the exception of a few resource allocation-based studies (Armstrong, 2006; Klausmeier et al., 2004; Bruggeman and Kooijman, 2007), trade-offs are generally formulated without a mechanistic justification.
We presented a theoretical framework that combines a mechanistic approach to derive trade-off functions with a moment-closure technique (Wirtz and Eckhardt, 1996; Norberg et al., 2001) to approximate models and applied it to a resource, one predator and multi-prey system in order to describe the macroscopic characteristics of the algal community. The approximated model provides a remarkably good estimates of the average clone type and total biomass. Being able to capture the macroscopic characteristics of an entire community (such as total aggregate biomass, average trait distribution and trait variance, the latter representing a measure of group or species diversity), aggregate or community-ecology models can have great advantages in terms of downscaling the complexity of PFT models or multi-species models.

The approach also led to a description of combined top-down and bottom-up controls. In other words, the trade-off function allowed us to describe the adaptive behaviour of many species (with the full model) or of community-aggregate properties (with the aggregate model) to changing environmental conditions, represented in the particular example described here by nutrient availability and grazing pressure.

Although presented in relation to a particular chemostat experiment, our modelling framework is based on general concepts and can therefore be applied to any community of competing species for which a trade-off between competitive ability and resistance to predators can be appropriately defined.

In agreement with the view expressed by Norberg et al. (2001), we argue that the approach of aggregating the behaviour of group of species represents a useful and effective alternative for downscaling complexity in plankton ecosystem models. We suggest that aggregate plankton models can be of great advantage
in particular for basin and global ocean modelling studies, as these can benefit from the reduction in computational cost enabled by species aggregation.

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A Appendix

A.1 Multi-clone model

As explained in the main text (section 3), we specify a set of \( n \) competing clones in terms of their "edibility" (equation 2), that is the affinity of rotifers for the \( i \)th clone. Therefore, the investment of the \( i \)th clone in nutrient harvesting biomass can be written as

\[
\alpha(\varphi_i) = 1 - \kappa - \varphi_i^{-1},
\]

(A.1)

with \( i = 1, \ldots, n \).

As in Bruggeman and Kooijman (2007), the internal nutrient availability of a clone is assumed to be proportional to its nutrient harvesting biomass. Algal growth is modeled with a Michaelis-Menten functional response, with the relative increase in the generic biomass of clone \( i \) given by

\[
f_i(N) = \mu_c \left[ \frac{N}{N + K_{N_i}(\varphi_i)} \right],
\]

(A.2)

with \( K_{N_i} \) representing the effective nutrient half-saturation (equation 3).

The mortality rate is denoted by \( m_C \). All biomass lost through mortality is assumed to re-enter the nutrient pool.

The effective prey availability as experienced by the rotifer is the sum of the populations of all algal clones, weighed according to their edibility,
\[ \hat{C} = \sum_{i=0}^{n} \varphi_i C_i. \]  \hspace{1cm} (A.3)

The total rate of algae consumption by rotifers is modelled with a Michaelis-Menten functional response, dependent on the effective prey availability,

\[ g = \frac{\mu_B}{\varepsilon} \left( \frac{\hat{C}}{C + K_C} \right) B, \]  \hspace{1cm} (A.4)

with \( B \) denoting rotifer biomass, \( \mu_B \) denoting the maximum rotifer growth rate, and \( \varepsilon \) the assimilation efficiency. This assimilation efficiency equals the fraction of assimilated algal biomass that ends up in newly produced rotifer biomass. The remaining fraction (1-\( \varepsilon \)) of assimilated algal biomass is assumed to end up as external particulate organic matter (Fussmann et al., 2000), which is assumed to be refractory and leave the chemostat through dilution.

Given the total rate of algal generic biomass consumption, the relative loss rate of a single algal clone due to predation equals

\[ g_i = \frac{\mu_B}{\varepsilon} \left( \frac{\varphi_i C_i}{\hat{C} + K_C} \right) B. \]  \hspace{1cm} (A.5)

The full set of \( n+2 \) differential equations is then written as follows:
\[
\frac{dN}{dt} = - \sum_{i=0}^{n} \left[ \frac{C_i}{\kappa} (f_i - m_C) \right] + \delta (N_0 - N), \quad (A.6)
\]
\[
\frac{dC_1}{dt} = (f_1 - m_C - g_1 - \delta)C_1, \quad (A.7)
\]
\[
\vdots
\]
\[
\frac{dC_n}{dt} = (f_n - m_C - g_n - \delta)C_n, \quad (A.9)
\]
\[
\frac{dB}{dt} = \left[ \frac{\mu_B}{\kappa} \left( \frac{\tilde{C}}{\tilde{C} + K_C} \right) - m_B - \delta \right] B. \quad (A.10)
\]

The first equation represents the change in external nutrient with \( N_0 \) denoting the nutrient concentration entering the chemostat. Note that the division by \( \kappa \) in equations A.6 and A.10 accounts for the fact that \( f_i, m_C \) and \( g \) describe the relative change in generic algal biomass \( C \), whereas changes in nutrient and predator density reflect changes in total algal biomass \( C/\kappa \).

The net growth rate of the multi-clone population with edibility \( \varphi_i \), in units of generic biomass per time, combines contributions of assimilation, mortality, predation and chemostat dilution, with \( \delta \) denoting the dilution rate of the chemostat.

In the last equation, representing the change in rotifer biomass, \( m_B \) denotes rotifer mortality. This lost is assumed to end up as refractory particulate biomass, which is not modeled further.
Modeling the complete set of clones is straightforward, but becomes rapidly computationally expensive as the number of clones increases. This makes multi-clone models unsuitable for many applications. Therefore, we approximate the behavior of the complete set of clones instead, using an aggregate model that contains only the total clonal generic biomass \( C_T \), the mean edibility and the variance of the edibility, i.e.:

\[
C_T = \sum_{i=0}^{n} C_i, \quad (A.11)
\]

\[
\bar{\varphi} = \frac{1}{C_T} \sum_{i=0}^{n} \varphi_i C_i, \quad (A.12)
\]

\[
v = \frac{1}{C_T} \sum_{i=0}^{n} (\varphi_i - \bar{\varphi})^2 C_i. \quad (A.13)
\]

This technique for aggregation has been described in detail by Wirtz and Eckhardt (1996) and by Norberg et al. (2001). Here we briefly illustrate the aggregation method by deriving the equation for the dynamic behavior of the total biomass.

The time derivative of the total biomass equals

\[
\frac{dC_T}{dt} = \frac{d}{dt} \sum_{i=0}^{n} C_i = \sum_{i=0}^{n} \frac{dC_i}{dt}, \quad (A.14)
\]

which may be rewritten as

\[
\frac{dC_T}{dt} = \sum_{i=0}^{n} C_i r(\varphi_i), \quad (A.15)
\]
with $r(\varphi_i)$ denoting the generic biomass-specific growth rate of an algal clone (equation A.7), i.e.:

$$r(\varphi_i) = f_i - m_C - g_i - \delta.$$  \hspace{1cm} (A.16)

We now Taylor-expand the specific growth rate around the mean trait value,

$$r(\varphi_i) = \sum_{j=0}^{\infty} \frac{1}{j!} (\varphi_i - \bar{\varphi})^j \frac{\partial^j}{\partial \varphi^j} r(\varphi) \bigg|_{\varphi = \bar{\varphi}},$$  \hspace{1cm} (A.17)

and insert this in A.15,

$$\frac{dC_T}{dt} = \sum_{i=0}^{n} C_i \sum_{j=0}^{\infty} \frac{1}{j!} (\varphi_i - \bar{\varphi})^j \frac{\partial^j}{\partial \varphi^j} r(\varphi) \bigg|_{\varphi = \bar{\varphi}}.$$  

After rearranging, we obtain

$$\frac{dC_T}{dt} = \sum_{j=0}^{\infty} \frac{1}{j!} \frac{\partial^j}{\partial \varphi^j} r(\varphi) \bigg|_{\varphi = \bar{\varphi}} \sum_{i=0}^{n} C_i (\varphi_i - \bar{\varphi})^j.$$  \hspace{1cm} (A.18)

In the second summation we may recognize the $j^{th}$ central moment of the edibility in the algal community, i.e.:

$$M_j = \frac{1}{C_T} \sum_{i=0}^{n} C_i (\varphi_i - \bar{\varphi})^j,$$  \hspace{1cm} (A.19)

noting that $M_0 = 1$, $M_1 = 0$ and $M_2 = \nu$. Inserting A.19 in A.18 and writing out only the first three terms, we obtain
\[
\frac{dC_T}{dt} = C_T \left[ r(\varphi)|_{\varphi=\bar{\varphi}} + \frac{1}{2} v \frac{\partial^2}{\partial \varphi^2} r(\varphi) \right. \\
\left. + \frac{1}{6} M_3 \frac{\partial^3}{\partial \varphi^3} r(\varphi) \right|_{\varphi=\bar{\varphi}} + \ldots \right]. \quad (A.20)
\]

Likewise, equations for the dynamics of the mean and variance can be derived

\[
\frac{d\bar{\varphi}}{dt} = v \frac{\partial}{\partial \varphi} r(\varphi) \bigg|_{\varphi=\bar{\varphi}} + \frac{1}{2} M_3 \frac{\partial^2}{\partial \varphi^2} r(\varphi) \bigg|_{\varphi=\bar{\varphi}} + \ldots, \quad (A.21)
\]

\[
\frac{d\bar{\varphi}^2}{dt} = M_3 \frac{\partial}{\partial \varphi} r(\varphi) \bigg|_{\varphi=\bar{\varphi}} + \frac{1}{2} \left( M_4 - v^2 \right) \frac{\partial^2}{\partial \varphi^2} r(\varphi) \bigg|_{\varphi=\bar{\varphi}} + \ldots, \quad (A.22)
\]

see for instance Norberg et al. (2001).

In the above equations, higher-order central moments such as the skewness \( M_3 \) and kurtosis \( M_4 \) appear. In theory one could derive expressions for the evolution of these higher moments as well. However, in the resulting equations moments of even higher order appear. This is the well-known moment closure problem: to derive self-contained expressions for the behavior of the system, the infinite series of moments must be closed by expressing higher-order moments in terms of lower order moments.

Different moment closure techniques exist. For instance, Norberg et al. (2001) describe the skewness and kurtosis with simple functions of the mean, variance and optimum of the optimal trait value. Parameters of these simple functions were estimated from the result of multi-clone simulations. Alternatively, Wirtz and Eckhardt (1996) assume the trait distribution to be well-approximated by a normal distribution, and directly insert the relationships between higher- and lower moments for that distribution: \( M_3 = 0 \), and \( M_4 = 3v^2 \).

In theory, the method of Norberg et al. (2001) is more accurate than a simple
closure based on an assumed distribution shape, such as the one employed by
Wirtz and Eckhardt (1996). However, a closure based on results of multi-clone
simulations is not always feasible; in some cases (e.g., detailed spatially explicit
setups) computationally expensive multi-clone simulations are not possible.

Also, parameterisations obtained with one or more reference simulations are
not guaranteed to work well when the model is embedded in different environ-
ments. As we intend to demonstrate the validity of the aggregation method for
a variety of problems and in very different environments, we choose to employ
and validate the simple normal moment closure in the present study.

Given the normal moment closure, the dynamics of the total biomass, mean
and variance are finally approximated by

\[
\frac{dC_T}{dt} \approx C_T \left[ r(\varphi)\big|_{\varphi = \bar{\varphi}} + \frac{1}{2}v^2 \frac{\partial^2 r(\varphi)}{\partial \varphi^2} \big|_{\varphi = \bar{\varphi}} \right], \quad (A.23)
\]

\[
\frac{d\bar{\varphi}}{dt} \approx v \frac{\partial r(\varphi)}{\partial \varphi} \bigg|_{\varphi = \bar{\varphi}}, \quad (A.24)
\]

\[
\frac{dv}{dt} \approx v^2 \frac{\partial^2 r(\varphi)}{\partial \varphi^2} \bigg|_{\varphi = \bar{\varphi}}. \quad (A.25)
\]

Equations for nutrient and rotifer complete the new model:

\[
\frac{dN}{dt} = \frac{C_T}{\kappa} \left[ f(\varphi)\big|_{\varphi = \bar{\varphi}} + \frac{1}{2}v^2 \frac{\partial^2 f(\varphi)}{\partial \varphi^2} \big|_{\varphi = \bar{\varphi}} - m_C \right] + \delta (N_0 - N), \quad (A.26)
\]

\[
\frac{dB}{dt} = \left[ \frac{\mu_B}{\kappa} \left( \frac{\bar{\varphi}C_T}{\bar{\varphi}C_T + K_C} \right) - m_B - \delta \right] B, \quad (A.27)
\]

noting that the effective prey availability (equation A.3) is now written as the
product of the mean edibility and total biomass (see also equation A.12): the
density-dependent predation term $g$ has been rewritten in terms of community-aggregated variables. The same is done for $g_i$, resulting in a specific growth rate $r$ that is independent of the abundance of the individual species $C_i$. This elimination of direct density dependence greatly facilitates the application of the moment-based aggregation method (Savage et al., 2007).

We note that for the dynamics of the total biomass the first three terms of the Taylor expansion are included and independent of the normal closure, for the dynamics of the mean the first two terms are included with only the first term being independent on the normal closure, and for the dynamics of the variance the first two terms are included with the first term being dependent on the normal closure.
References


Loreau, M., Mouquet, N., Gonzalez, A., 2003. Biodiversity as spatial insur-
ance in heterogeneous landscapes. Proceedings of the National Academy of Sciences 100 (22), 12765–12770.


Table 1

List of parameters used in the models (sources: Fussmann et al., 2000; Yoshida et al., 2003) for generating the equilibrium behaviour. Limit cycles are generated by changing only one parameter: $K_C = 200 \mu\text{mol N l}^{-1}$.

<table>
<thead>
<tr>
<th>Parameter description</th>
<th>Symbol</th>
<th>Unit</th>
<th>Value</th>
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<tbody>
<tr>
<td>Dilution rate</td>
<td>$d$</td>
<td>d$^{-1}$</td>
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<td>Constant nitrogen inflow</td>
<td>$N_0$</td>
<td>$\mu\text{mol N l}^{-1}$</td>
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<td>Algal maximum growth rate</td>
<td>$\mu_C$</td>
<td>d$^{-1}$</td>
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</tr>
<tr>
<td>Rotifer maximum growth rate</td>
<td>$\mu_B$</td>
<td>d$^{-1}$</td>
<td>2.25</td>
</tr>
<tr>
<td>Algal mortality</td>
<td>$m_C$</td>
<td>d$^{-1}$</td>
<td>0.05</td>
</tr>
<tr>
<td>Rotifer mortality</td>
<td>$m_B$</td>
<td>d$^{-1}$</td>
<td>0.1</td>
</tr>
<tr>
<td>Rotifer assimilation efficiency</td>
<td>$\varepsilon$</td>
<td>-</td>
<td>0.25</td>
</tr>
<tr>
<td>Fraction of energy invested in generic biomass</td>
<td>$\kappa$</td>
<td>-</td>
<td>0.8</td>
</tr>
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<td>Half-saturation for algal growth (at $\alpha = 1$)</td>
<td>$\tilde{K}_N$</td>
<td>$\mu\text{mol N l}^{-1}$</td>
<td>0.4</td>
</tr>
<tr>
<td>Half-saturation for rotifer growth (at $\varphi = 1$)</td>
<td>$K_C$</td>
<td>$\mu\text{mol N l}^{-1}$</td>
<td>1,000</td>
</tr>
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</table>
1 Schematisation of our mechanistic approach to derive a trade-off function for the nutrient-algae-rotifer system. The nutrient resource (N) is partitioned among generic biomass and two other cellular activities: defence (δ) and nutrient harvesting (α). The rotifer biomass (B) and mortality terms, both for the predator ($m_B$) and the prey ($m_C$), are also indicated.

2 Tradeoff functions (equation 3) drawn at different values of $\kappa$. The strategy to invest in defence against predation (that is to become less edible, i.e. low $\varphi$) comes a the cost of nutrient affinity (that is to grow slowly, i.e. high $K_N$). Note that $\kappa$ is only a scale parameter and does not have an effect on the shape of the trade-off function. Note also the lower limits of $\varphi$ at different $\kappa$. For $\kappa=0.8$ (the value used in our model run) then $\varphi > 5$. 
3 Time evolution of clone concentrations. Each bar in the main plot represents the concentration of a clone (y-axis) with its assigned edibility trait value (x-axis, uniformly distributed from 5 to 40). As time progresses, clones with intermediate trait values (between 10-25) appear to be more successful than the others, until the end of the run (day 120) when clones with edibility trait value around 12 outcompete all the others. The two side bars show temporal changes in nitrogen and rotifer concentrations.

4 Results obtained with the multi-clone model showing concentrations of nitrogen, rotifer, and all 40 clones as functions of time. Two different simulations are presented here: one (panels a-c) resulting in an equilibrium and the other (panels d-f) resulting in limit cycles.

5 Comparison of total clone concentration, mean trait value and variance of trait obtained with the multi-clone model and the aggregate model for two different simulations: one (panels a-c) resulting in an equilibrium and the other (panels d-f) resulting in limit cycles.

6 Dynamic behaviour of the mean edibility trait compared with the rotifer concentration both obtained with the aggregate model in the case of limit cycles (replotted from Figures 4e and 5e, respectively).
Adaptive value of the edibility trait at different nutrient concentrations and grazing pressures. The edibility trait values are obtained by running the models to steady-state with (panel a) fixed rotifer maximum growth rate ($\mu_B=2.25 \text{d}^{-1}$) and variable nitrogen inflow, and with (panel b) fixed nutrient inflow ($N_0=80 \mu\text{mol}\text{l}^{-1}$) and variable grazing pressure (see equation A.5). Remarkably, the two models produce almost indistinguishable results.
Fig. 1.
$K_N (\mu\text{mol N l}^{-1})$

Edibility (-)

$\kappa=0.6$  
$\kappa=0.7$  
$\kappa=0.8$  
$\kappa=0.9$

Fig. 2.
Fig. 3.
Fig. 4.
Fig. 5.
Fig. 6.
Fig. 7.