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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

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

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## 1 Introduction

2 Plankton ecosystem modelling is a fundamental tool for understanding the bio-  
3 geochemical cycles of crucial elements like carbon or for investigating ecosys-  
4 tem functioning. In the last two decades, due to an increase in computer power  
5 along with the need of more realistic predictions, there has been a tendency  
6 of developing models of increased complexity (Baretta et al., 1995; Moore and  
7 et al., 2002; Le Quéré et al., 2005). The early and simple so-called NPZD (Ni-  
8 trogen, Phytoplankton, Zooplankton and Detritus) models have "evolved" into  
9 more complex models representing many plankton functional types (PFTs)  
10 (Anderson, 2005). However, a higher degree of model complexity does not  
11 necessarily guarantee improved predictions (Fulton et al., 2003; Anderson,  
12 2005; Hood et al., 2006).

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

22 Inherently connected to the complexity issue is the problem of representing  
23 adaptive processes in ecological models. Being characterised by fixed param-  
24 eters, current models can be regarded in a sense as "static representations of  
25 reality", although state variables do change with time. That is, the actual pro-  
26 cesses governing the interactions within plankton communities and between  
27 communities and the environment they live in are based on fixed characteris-  
28 tics (i.e. fixed algal food value, fixed algal competitive ability or fitness, etc.)  
29 thus excluding the possibility for communities to adapt to new situations and  
30 to change their properties to better fit the prevailing forcing at a certain time  
31 (Jørgensen, 1992). In other words, models using fixed parameters cannot ac-  
32 count for changes in community structure or adaptation. In principle, there  
33 is no justification for setting fixed the competitive abilities (associated for in-  
34 stance to nutrient affinity,  $1/K_N$ , in a Michaelis-Menten type of growth) of  
35 algal communities. It is more likely that these competitive abilities change in  
36 response to varying environmental conditions. It is since long that attempts  
37 are being made to address these issues. The approach of considering zooplank-  
38 ton feeding preferences (Fasham et al., 1990) was probably one of the first to

39 introduce some sort of "flexibility" in the model systems. Other prominent  
40 strategies are represented by the structural dynamic modelling (Jørgensen,  
41 1986, 1999; Zhang et al., 2003) or, more recently, by the optimality-based  
42 modelling for resource allocation (Klausmeier et al., 2004; Pahlow, 2005; Arm-  
43 strong, 2006; Smith and Yamanaka, 2007). In order to account for adaptive  
44 processes, we shall describe an approach based on the derivation of trade-off  
45 functions and succession-driven changes of community-aggregated properties.

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

62 The temporal evolution of a community consisting of  $n$  plankton functional  
63 groups or species may of course be simulated by accounting for the dynamics  
64 of each separately. A trait-based approach can then help to constrain the char-

65 acteristics (parameters) of each species. With trade-offs governing interspecific  
66 differences, a realistic representation of community behavior is obtained by let-  
67 ting natural selection operate on an assemblage of species with different trait  
68 values (Bruggeman and Kooijman, 2007). However, although this approach  
69 requires little detail in terms of physiological parameters, it introduces a great  
70 number of state variables in its discretization of the trait distribution. As a  
71 result, this approach is computationally expensive and not suitable for prob-  
72 lems that are limited by computation resources (for example high-resolution  
73 spatially explicit models).

74 Drawing from the Dynamic Energy Budget (DEB) theory (Kooijman, 2000;  
75 Nisbet et al., 2000) and from the adaptive dynamics approach (Abrams et al.,  
76 1993; Dieckmann and Law, 1996; Leibold and Norberg, 2004; Norberg, 2004),  
77 we will present a self-consistent methodological framework for deriving trait-  
78 based models of aggregate group behaviour.

79 The new methodological framework consists of three steps:

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

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

88 Our model will describe a chemostat system comprising a nutrient resource,

89 a community of genetically different algal clones and a planktonic rotifer  
90 (Yoshida et al., 2003), in which it was observed 1) that evolutionary processes  
91 can take place at ecological time scales, and 2) the existence of an evolution-  
92 ary trade-off between algal food value and competitive ability. We built on the  
93 work of Yoshida et al. (2003) because their experiments are conceptually sim-  
94 ple, represent a controlled system and can give the readers an immediate sense  
95 of the plausibility of our model. Nevertheless, the structure of our aggregate  
96 model is general and can be applied to any community of competing species  
97 for which a trade-off between competitive ability for resource harvesting and  
98 resistance to predators can be appropriately defined.

## 99 **2 Algal competitive ability and resistance to predation**

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

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

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

122 Shertzer et al. (2002) and Yoshida et al. (2003) observed that only when rapid  
123 prey evolution in response to predation was considered could their model pre-  
124 dict also the quantitative features of the observations. The evolution hypoth-  
125 esis was directly tested in a chemostat experiment by Yoshida et al. (2003).  
126 They found that algae cultivated under constant and intense rotifer grazing  
127 pressure became lower in food value and were heritably smaller and competi-  
128 tively inferior relative to algae grown in the absence of rotifers. Yoshida et al.  
129 (2003) introduced clonal selection by specifying a set of competing clones in  
130 terms of their food value and related competitive ability and by postulating  
131 that the defensive "low food value" trait comes at the cost of reduced nutrient  
132 affinity (i.e. increased nutrient half-saturation). This relationship was speci-  
133 fied by a trade-off curve, which was based on two free parameters: a shape  
134 parameter and a scale or "cost" parameter (Yoshida et al., 2003).

135 This approach, however, has some problems. 1) Population dynamics are  
136 highly sensitive to the shape and scale parameters of the trade-off function,  
137 but this functional relationship is completely empirical (i.e. based on a spe-  
138 cific experiment) and constrained only by two individual observations. 2) If  $n$

139 clones have to be specified in order to take into account evolutionary trade-  
140 offs, then the number of model equations would raise to  $n+2$  ( $n$  algal clones,  
141 1 nutrient and 1 rotifer), thus leading to a higher degree of complexity.

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

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

### 157 **3 A mechanistic approach to derive trade-off functions**

158 The term "mechanistic" relates to the idea that a natural process can be  
159 explained in purely physical or deterministic terms. The derivation of our  
160 trade-off function is inspired by DEB theory, which mechanistically describes  
161 how individual organisms acquire and utilize energy, and can serve as a link

162 between different levels of biological organization (Kooijman, 2000; Nisbet  
163 et al., 2000). Figure 1 illustrates, in purely physical terms, the allocation of a  
164 resource to different algal activities or pools in our model.

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

174 Therefore, by construction, the relation between nutrient harvesting and de-  
175 fence is

$$1 - \kappa = \alpha + \delta \tag{1}$$

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

$$\varphi_i = \frac{1}{(1 - \kappa - \alpha_i)}, \tag{2}$$

181 which will be the single trait varying between algal clones. The investments in  
 182 nutrient harvesting biomass can now be written as  $\alpha = 1 - \kappa - \varphi^{-1}$ . In a similar  
 183 fashion, the effective nutrient affinity of an algal clone  $i$  is assumed to be pro-  
 184 portional to the relative amount of nutrient harvesting biomass of that clone.  
 185 Then, the effective half-saturation constant for Michaelis-Menten nutrient up-  
 186 take will be

$$K_{Ni} = \frac{\tilde{K}_N}{\alpha(\varphi_i)} = \frac{\tilde{K}_N}{(1 - \kappa - \varphi_i^{-1})}, \quad (3)$$

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

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

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

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

200 To illustrate how our trade-off works, we present an example in which a com-  
 201 munity of 40 clones compete for nitrogen while they 'defend' against predation  
 202 by the rotifer. Figure 3 shows the distribution of these clones with respect to

203 their assigned edibility trait, chosen as an index varying between 1 (for clone 1)  
204 and 40 (for clone 40), at different time steps. In this particular run, all clones  
205 are given the same, relatively low, initial concentrations (model parameters  
206 are reported in Table 1). In the first period (days 0-5), nutrient concentration  
207 is high and grazing pressure is relatively low, clones are free to mainly com-  
208 pete for nutrient, therefore clones with relatively high edibility are favoured  
209 (days 5-10). As time progresses (days 10-15), the nutrient resource starts to  
210 be depleted and grazing pressure increases making less edible clones at this  
211 stage more successful. Towards the end of the run (day 120), a few clones  
212 (the fittest) with edibility trait value around 12 outcompete all the others.  
213 To maintain generality, we ascribe more importance to the relative value of  
214 edibility rather than to its absolute value. Therefore, an edibility index vary-  
215 ing from 0 to 40 implies that a clone with edibility trait 40 is 100% edible,  
216 whereas a clone with edibility 0 is a totally inedible clone. The fittest clone in  
217 our example is a 30% edible clone, being characterised by a value of 12.

218 This test shows how the combination of bottom-up and top-down processes,  
219 here mechanistically simulated with a function that trades off competitive  
220 ability against resistance to predation, can drive changes in algal commu-  
221 nity structure. Consistently with the competitive exclusion principle (Hardin,  
222 1960), only the few fittest clones survive by the end of the run (Figure 3).

223 In Figure 4 we present the time evolution of all variables represented in the  
224 model (nitrogen, rotifer and 40 algal clones) for two particular simulations:  
225 one producing an equilibrium (panels a-c) and the other producing limit cy-  
226 cles (panels d-f). The parameter configuration producing the equilibrium is  
227 the same as for run in Figure 3 and is reported in Table 1. The limit cycle  
228 behaviour is obtained by changing only the half-saturation for rotifer growth

229 ( $K_C = 200 \mu\text{mol N l}^{-1}$ ). We note here that low  $K_C$  values make predator feed-  
230 ing less sensitive to  $\varphi$  (because the term  $\tilde{C}$  in the denominator of equation A.5  
231 will always be larger), while higher values of  $K_C$  make predator feeding scaling  
232 linearly with  $\varphi$ . Consequently,  $K_C$  plays an important role in determining the  
233 model sensitivity to  $\varphi$ .

## 234 4 Approximating complex models

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

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

253 The rate of change of the total clonal generic biomass is written as

$$\frac{dC_T}{dt} \approx C_T \left[ r(\bar{\varphi}) + \frac{1}{2}v \frac{d^2r(\bar{\varphi})}{d\varphi^2} \right], \quad (4)$$

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

$$\frac{d\bar{\varphi}}{dt} \approx v \frac{dr(\bar{\varphi})}{d\varphi}. \quad (5)$$

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

$$\frac{dv}{dt} \approx v^2 \frac{d^2r(\bar{\varphi})}{d\varphi^2}. \quad (6)$$

258 We tested the accuracy of the approximation by running the multi-clone model  
259 with 40 clones (equations A.6-A.10) and calculating  $C_T$ ,  $\bar{\varphi}$  and  $v$  over time  
260 from the resulting species distribution. These variables were then compared  
261 to those obtained by running the approximated model (equations A.23-A.27).  
262 Both models were parameterised using the same parameter set (Table 1).

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

267 The quality of a moment-based approximation theoretically decreases with in-  
268 creasing moment order: the mathematical approximation for the total biomass

269 is better than that of the mean, and the approximation for the mean is better  
270 than that of the variance (see Appendix A.2). In this respect, the present ag-  
271 gregate approximation for the variance performs remarkably well (Figure 5).  
272 The mean absolute error in the standard deviation is 1.3% of its relevant  
273 range, which is close to the 1.1% error in the total biomass and better than  
274 the 2.6% error in the mean. This may appear somewhat surprising, but does  
275 not indicate a problem in the formulation of the aggregate model. Detailed  
276 investigation of the aggregate model shows that the initial dynamics of the  
277 mean are controlled by the 2<sup>nd</sup> and 3<sup>rd</sup> order terms, which are omitted in  
278 the aggregate model. This dominance of higher-order terms lasts only 4 days.  
279 However, this period is sufficient to create a deviation in the mean that in  
280 turn makes the approximation of the total biomass less precise, while it hap-  
281 pens to improve the approximation of the variance. This feature is specific to  
282 the present system and initial conditions. The performance of the aggregation  
283 method is on the whole very satisfactory and comparable to results obtained  
284 when more complicated moment closures are included (Norberg et al., 2001).

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

288 Most of our model solutions tended to a steady-state characterised by the  
289 survival of only a very few clones (competitive exclusion, Hardin, 1960) -  
290 an aspect represented by the trait variance approaching to zero for a wide  
291 range of parameter sets (Figure 5 shows only two examples). This implies  
292 that the adaptive capacity of the system is mainly caused by a change in  
293 its components (clones) by species sorting processes (succession driven by  
294 interactions - resource competition in our case). One aspect that can 'solve'

295 the tendency to a steady-state characterised by a zero variance would be to  
296 consider exogenous processes tending to sustain high functional diversity such  
297 as immigration or hatching from resting stages (Norberg, 2004; Leibold and  
298 Norberg, 2004). While these processes are plausible in real ecosystems, they  
299 are certainly not applicable to a closed system like the chemostat.

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

## 311 5 Conclusions

312 Trait-based modelling approaches require assumptions on trade-offs. Changes  
313 in traits have to be based on an appropriate balance between benefits and  
314 costs in order to avoid that the system 'adapts' toward unrealistic trait values.  
315 With the exception of a few resource allocation-based studies (Armstrong,  
316 2006; Klausmeier et al., 2004; Bruggeman and Kooijman, 2007), trade-offs are  
317 generally formulated without a mechanistic justification.

318 We presented a theoretical framework that combines a mechanistic approach  
319 to derive trade-off functions with a moment-closure technique (Wirtz and Eck-  
320 hardt, 1996; Norberg et al., 2001) to approximate models and applied it to a  
321 resource, one predator and multi-prey system in order to describe the macro-  
322 scopic characteristics of the algal community. The approximated model pro-  
323 vides a remarkably good estimates of the average clone type and total biomass.  
324 Being able to capture the macroscopic characteristics of an entire community  
325 (such as total aggregate biomass, average trait distribution and trait variance,  
326 the latter representing a measure of group or species diversity), aggregate or  
327 community-ecology models can have great advantages in terms of downscaling  
328 the complexity of PFT models or multi-species models.

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

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

339 In agreement with the view expressed by Norberg et al. (2001), we argue that  
340 the approach of aggregating the behaviour of group of species represents a use-  
341 ful and effective alternative for downscaling complexity in plankton ecosystem  
342 models. We suggest that aggregate plankton models can be of great advantage

343 in particular for basin and global ocean modelling studies, as these can benefit  
344 from the reduction in computational cost enabled by species aggregation.

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351 *A.1 Multi-clone model*

352 As explained in the main text (section 3), we specify a set of  $n$  competing  
 353 clones in terms of their "edibility" (equation 2), that is the affinity of ro-  
 354 tifers for the  $i^{\text{th}}$  clone. Therefore, the investment of the  $i^{\text{th}}$  clone in nutrient  
 355 harvesting biomass can be written as

$$\alpha(\varphi_i) = 1 - \kappa - \varphi_i^{-1}, \quad (\text{A.1})$$

356 with  $i = 1, \dots, n$ .

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

$$f_i(N) = \mu_c \left[ \frac{N}{N + K_{Ni}(\varphi_i)} \right], \quad (\text{A.2})$$

361 with  $K_{Ni}$  representing the effective nutrient half-saturation (equation 3).

362 The mortality rate is denoted by  $m_C$ . All biomass lost through mortality is  
 363 assumed to re-enter the nutrient pool.

364 The effective prey availability as experienced by the rotifer is the sum of the  
 365 populations of all algal clones, weighed according to their edibility,

$$\tilde{C} = \sum_{i=0}^n \varphi_i C_i. \quad (\text{A.3})$$

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

$$g = \frac{\mu_B}{\varepsilon} \left( \frac{\tilde{C}}{\tilde{C} + K_C} \right) B, \quad (\text{A.4})$$

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

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

$$g_i = \frac{\mu_B}{\varepsilon} \left( \frac{\varphi_i C_i}{\tilde{C} + K_C} \right) B. \quad (\text{A.5})$$

376 The full set of  $n+2$  differential equations is then written as follows:

$$\frac{dN}{dt} = - \sum_{i=0}^n \left[ \frac{C_i}{\kappa} (f_i - m_C) \right] + \delta (N_0 - N), \quad (\text{A.6})$$

$$\frac{dC_1}{dt} = (f_1 - m_C - g_1 - \delta)C_1, \quad (\text{A.7})$$

$$\vdots \quad (\text{A.8})$$

$$\frac{dC_n}{dt} = (f_n - m_C - g_n - \delta)C_n, \quad (\text{A.9})$$

$$\frac{dB}{dt} = \left[ \frac{\mu_B}{\kappa} \left( \frac{\tilde{C}}{\tilde{C} + K_C} \right) - m_B - \delta \right] B. \quad (\text{A.10})$$

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

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

386 In the last equation, representing the change in rotifer biomass,  $m_B$  denotes  
 387 rotifer mortality. This lost is assumed to end up as refractory particulate  
 388 biomass, which is not modeled further.

390 Modeling the complete set of clones is straightforward, but becomes rapidly  
 391 computationally expensive as the number of clones increases. This makes  
 392 multi-clone models unsuitable for many applications. Therefore, we approxi-  
 393 mate the behavior of the complete set of clones instead, using an aggregate  
 394 model that contains only the total clonal generic biomass ( $C_T$ ), the mean  
 395 edibility and the variance of the edibility, i.e.:

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

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

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

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

400 The time derivate of the total biomass equals

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

401 which may be rewritten as

$$\frac{dC_T}{dt} = \sum_{i=0}^n C_i r(\varphi_i), \quad (\text{A.15})$$

402 with  $r(\varphi_i)$  denoting the generic biomass-specific growth rate of an algal clone  
 403 (equation A.7), i.e.:

$$r(\varphi_i) = f_i - m_C - g_i - \delta. \quad (\text{A.16})$$

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

$$r(\varphi_i) = \sum_{j=0}^{\infty} \frac{1}{j!} (\varphi_i - \bar{\varphi})^j \left. \frac{\partial^j}{\partial \varphi^j} r(\varphi) \right|_{\varphi=\bar{\varphi}}, \quad (\text{A.17})$$

405 and insert this in A.15,

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

406 After rearranging, we obtain

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

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

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

409 noting that  $M_0 = 1$ ,  $M_1 = 0$  and  $M_2 = v$ . Inserting A.19 in A.18 and writing  
 410 out only the first three terms, we obtain

$$\frac{dC_T}{dt} = C_T \left[ r(\varphi)|_{\varphi=\bar{\varphi}} + \frac{1}{2}v \frac{\partial^2}{\partial \varphi^2} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \frac{1}{6}M_3 \frac{\partial^3}{\partial \varphi^3} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \dots \right]. \quad (\text{A.20})$$

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

$$\frac{d\bar{\varphi}}{dt} = v \frac{\partial}{\partial \varphi} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \frac{1}{2}M_3 \frac{\partial^2}{\partial \varphi^2} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \dots, \quad (\text{A.21})$$

$$\frac{d\bar{\varphi}}{dt} = M_3 \frac{\partial}{\partial \varphi} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \frac{1}{2} (M_4 - v^2) \frac{\partial^2}{\partial \varphi^2} r(\varphi) \Big|_{\varphi=\bar{\varphi}} + \dots, \quad (\text{A.22})$$

412 see for instance Norberg et al. (2001).

413 In the above equations, higher-order central moments such as the skewness  $M_3$   
 414 and kurtosis  $M_4$  appear. In theory one could derive expressions for the evo-  
 415 lution of these higher moments as well. However, in the resulting equations  
 416 moments of even higher order appear. This is the well-known moment closure  
 417 problem: to derive self-contained expressions for the behavior of the system,  
 418 the infinite series of moments must be closed by expressing higher-order mo-  
 419 ments in terms of lower order moments.

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

427 In theory, the method of Norberg et al. (2001) is more accurate than a simple

428 closure based on an assumed distribution shape, such as the one employed by  
429 Wirtz and Eckhardt (1996). However, a closure based on results of multi-clone  
430 simulations is not always feasible; in some cases (e.g., detailed spatially explicit  
431 setups) computationally expensive multi-clone simulations are not possible.  
432 Also, parameterisations obtained with one or more reference simulations are  
433 not guaranteed to work well when the model is embedded in different environ-  
434 ments. As we intend to demonstrate the validity of the aggregation method for  
435 a variety of problems and in very different environments, we choose to employ  
436 and validate the simple normal moment closure in the present study.

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

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

$$\frac{d\bar{\varphi}}{dt} \approx v \frac{\partial}{\partial \varphi} r(\varphi) \Big|_{\varphi=\bar{\varphi}}, \quad (\text{A.24})$$

$$\frac{dv}{dt} \approx v^2 \frac{\partial^2}{\partial \varphi^2} r(\varphi) \Big|_{\varphi=\bar{\varphi}}. \quad (\text{A.25})$$

439 Equations for nutrient and rotifer complete the new model:

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

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

440 noting that the effective prey availability (equation A.3) is now written as the  
441 product of the mean edibility and total biomass (see also equation A.12): the

442 density-dependent predation term  $g$  has been rewritten in terms of community-  
443 aggregated variables. The same is done for  $g_i$ , resulting in a specific growth  
444 rate  $r$  that is independent of the abundance of the individual species  $C_i$ . This  
445 elimination of direct density dependence greatly facilitates the application of  
446 the moment-based aggregation method (Savage et al., 2007).

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

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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:  $K_C=200 \mu\text{mol N l}^{-1}$ .

Parameter description	Symbol	Unit	Value
Dilution rate	$d$	$\text{d}^{-1}$	0.69
Constant nitrogen inflow	$N_0$	$\mu\text{mol N l}^{-1}$	80
Algal maximum growth rate	$\mu_C$	$\text{d}^{-1}$	3.3
Rotifer maximum growth rate	$\mu_B$	$\text{d}^{-1}$	2.25
Algal mortality	$m_C$	$\text{d}^{-1}$	0.05
Rotifer mortality	$m_B$	$\text{d}^{-1}$	0.1
Rotifer assimilation efficiency	$\varepsilon$	-	0.25
Fraction of energy invested in generic biomass	$\kappa$	-	0.8
Half-saturation for algal growth (at $\alpha = 1$ )	$\tilde{K}_N$	$\mu\text{mol N l}^{-1}$	0.4
Half-saturation for rotifer growth (at $\varphi = 1$ )	$K_C$	$\mu\text{mol N l}^{-1}$	1,000

583 1 Schematisation of our mechanistic approach to derive a  
584 trade-off function for the nutrient-algae-rotifer system. The  
585 nutrient resource (N) is partitioned among generic biomass  
586 and two other cellular activities: defence ( $\delta$ ) and nutrient  
587 harvesting ( $\alpha$ ). The rotifer biomass (B) and mortality terms,  
588 both for the predator ( $m_B$ ) and the prey ( $m_C$ ), are also  
589 indicated. 35

590 2 Tradeoff functions (equation 3) drawn at different values of  $\kappa$ .  
591 The strategy to invest in defence against predation (that is  
592 to become less edible, i.e. low  $\varphi$ ) comes at the cost of nutrient  
593 affinity (that is to grow slowly, i.e. high  $K_N$ ). Note that  $\kappa$  is  
594 only a scale parameter and does not have an effect on the  
595 shape of the trade-off function. Note also the lower limits of  
596  $\varphi$  at different  $\kappa$ . For  $\kappa=0.8$  (the value used in our model run)  
597 then  $\varphi > 5$ . 36

- 598 3 Time evolution of clone concentrations. Each bar in the main  
599 plot represents the concentration of a clone (y-axis) with its  
600 assigned edibility trait value (x-axis, uniformly distributed  
601 from 5 to 40). As time progresses, clones with intermediate  
602 trait values (between 10-25) appear to be more successful than  
603 the others, until the end of the run (day 120) when clones with  
604 edibility trait value around 12 outcompete all the others. The  
605 two side bars show temporal changes in nitrogen and rotifer  
606 concentrations. 37
- 607 4 Results obtained with the multi-clone model showing  
608 concentrations of nitrogen, rotifer, and all 40 clones as  
609 functions of time. Two different simulations are presented  
610 here: one (panels a-c) resulting in an equilibrium and the other  
611 (panels d-f) resulting in limit cycles. 38
- 612 5 Comparison of total clone concentration, mean trait value and  
613 variance of trait obtained with the multi-clone model and the  
614 aggregate model for two different simulations: one (panels a-c)  
615 resulting in an equilibrium and the other (panels d-f) resulting  
616 in limit cycles. 39
- 617 6 Dynamic behaviour of the mean edibility trait compared with  
618 the rotifer concentration both obtained with the aggregate  
619 model in the case of limit cycles (replotted from Figures 4e  
620 and 5e, respectively). 40

621 7 Adaptive value of the edibility trait at different nutrient  
622 concentrations and grazing pressures. The edibility trait values  
623 are obtained by running the models to steady-state with  
624 (panel a) fixed rotifer maximum growth rate ( $\mu_B=2.25 \text{ d}^{-1}$ )  
625 and variable nitrogen inflow, and with (panel b) fixed nutrient  
626 inflow ( $N_0=80 \mu\text{mol l}^{-1}$ ) and variable grazing pressure (see  
627 equation A.5). Remarkably, the two models produce almost  
628 indistinguishable results.

41

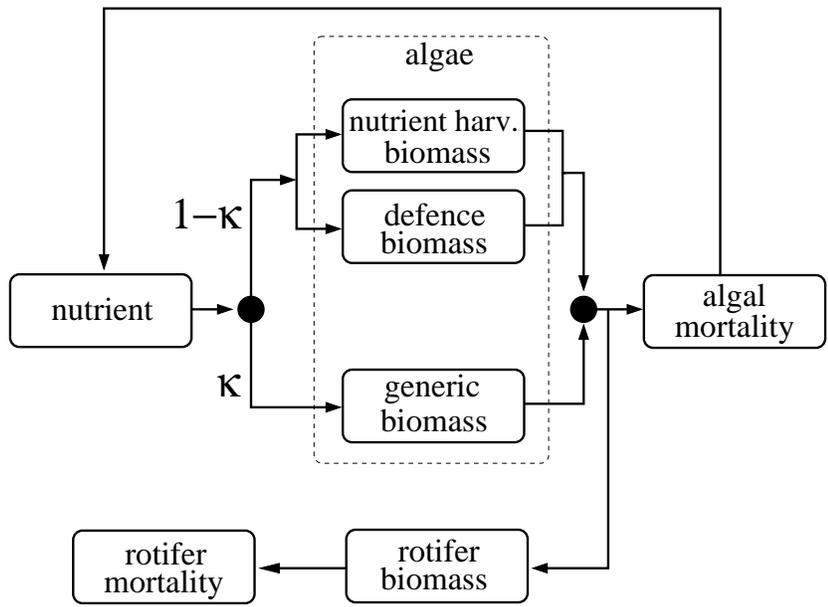


Fig. 1.

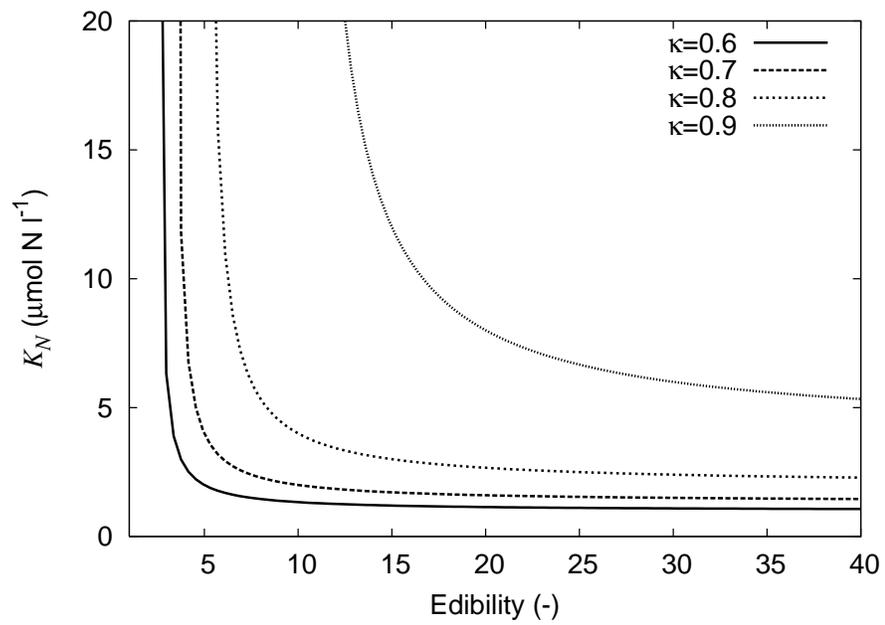
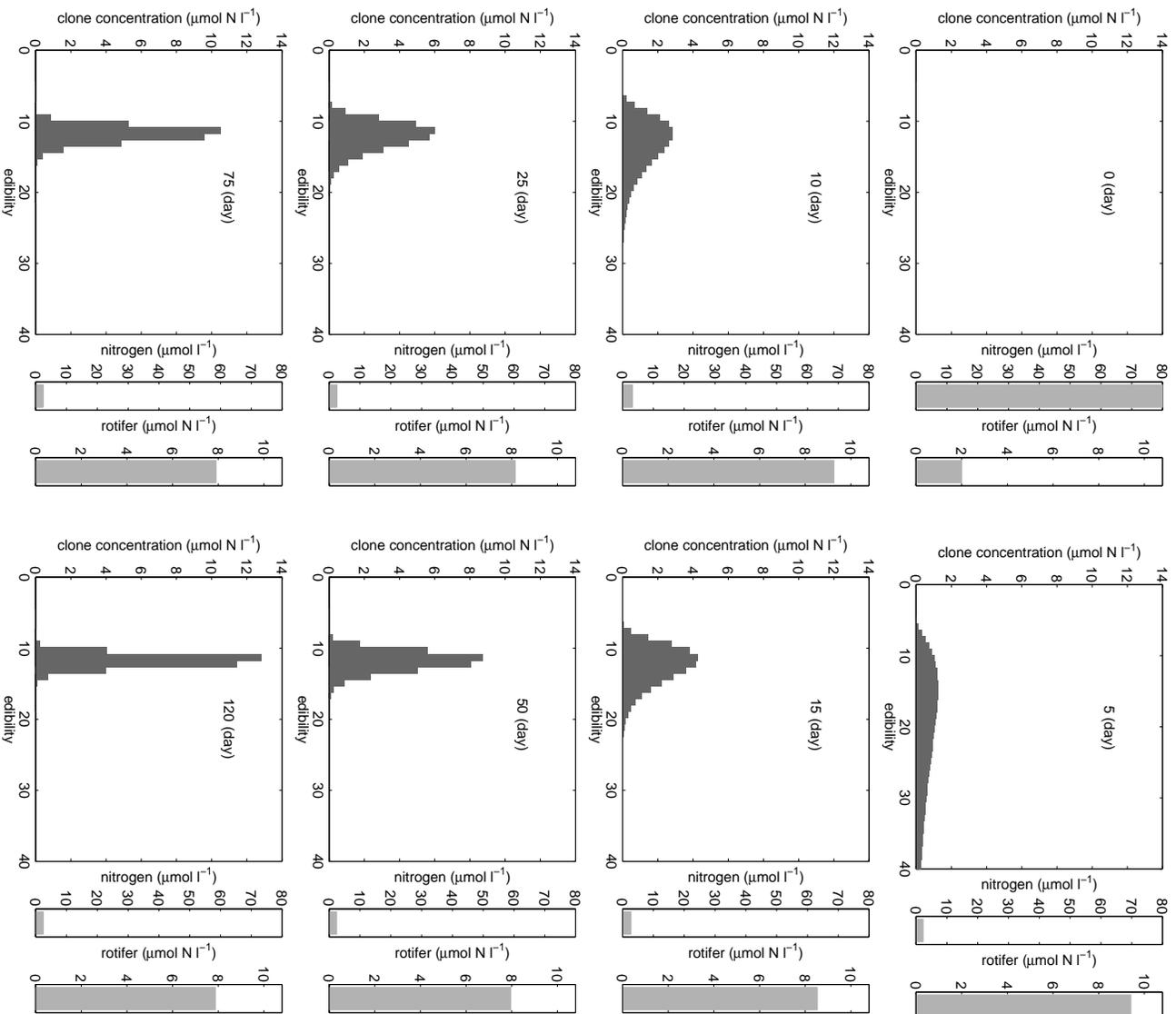


Fig. 2.



1

Fig. 3.

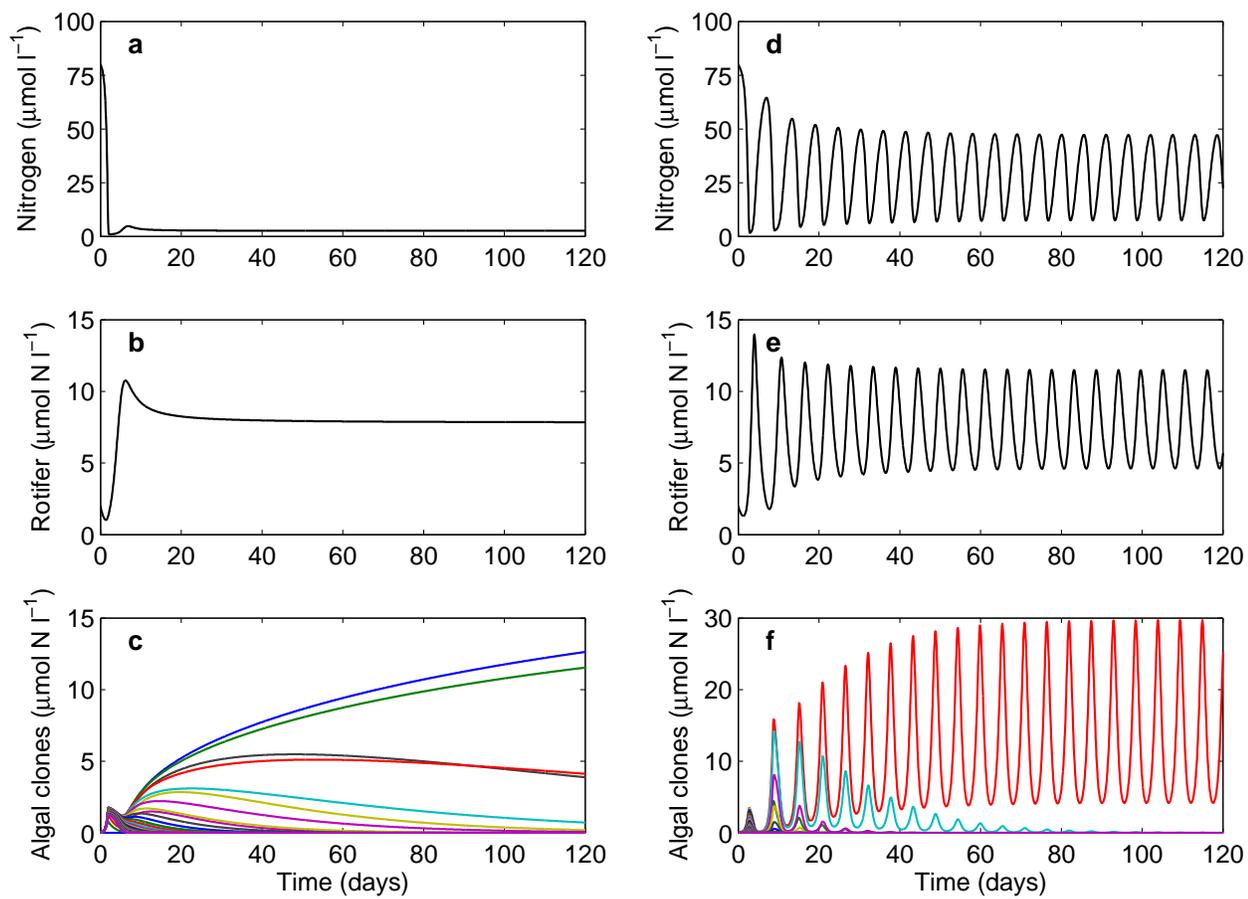


Fig. 4.

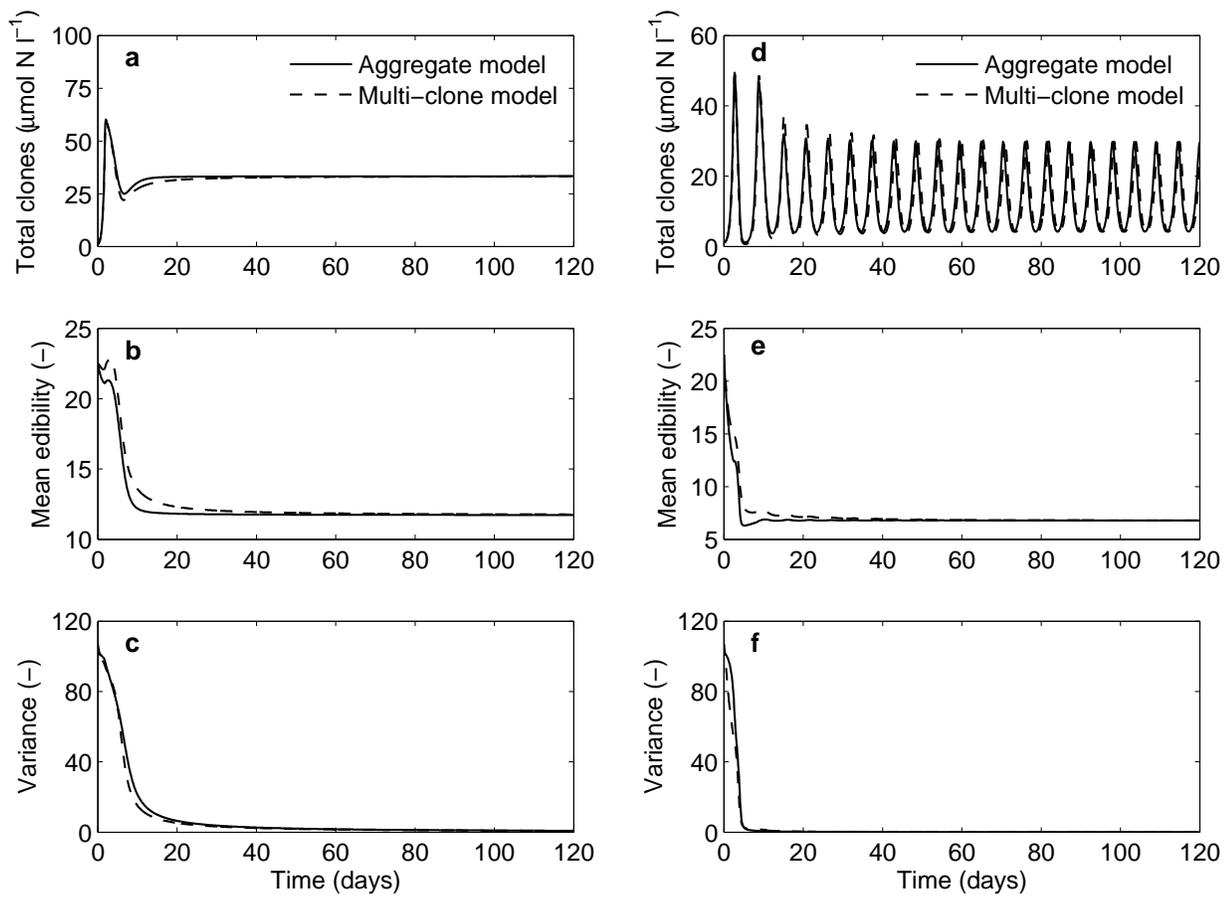


Fig. 5.

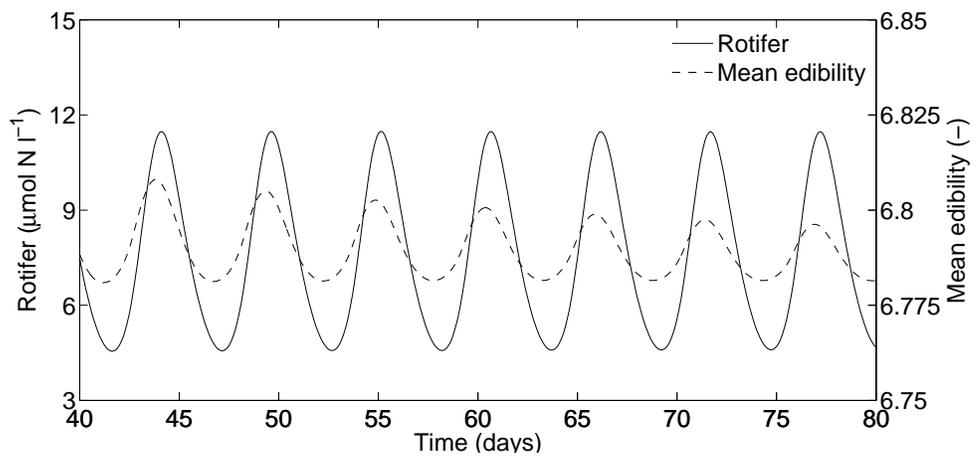


Fig. 6.

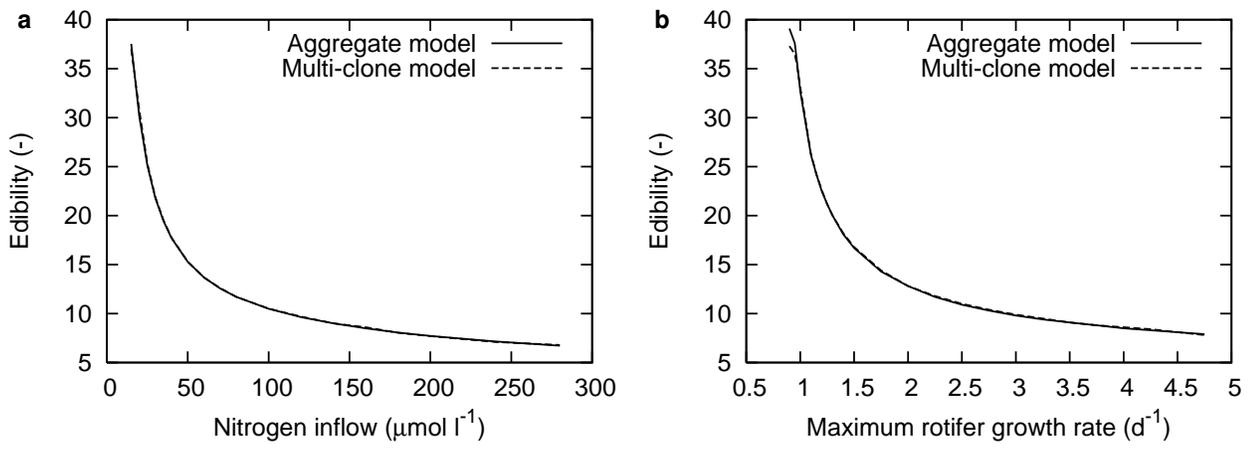


Fig. 7.