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Phytoplankton competition and coexistence: Intrinsic ecosystem dynamics and impact of vertical mixing

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Abstract:

This paper aims at studying analytically the functioning of a very simple ecosystem model with two phytoplankton species. First, using the dynamical system theory, we determine its nonlinear equilibria, their stability and characteristic timescales with a focus on phytoplankton competition. Particular attention is paid to the model sensitivity to parameter change. Then, the influence of vertical mixing and sinking of detritus on the vertically-distributed ecosystem model is investigated.

The analytical results reveal a high diversity of ecosystem structures with fixed points and limit cycles that are mainly sensitive to variations of light intensity and total amount of nitrogen matter. The sensitivity to other parameters such as re-mineralisation, growth and grazing rates is also specified. Besides, the equilibrium analysis shows a complete segregation of the two phytoplankton species in the whole parameter space.

The embedding of our ecosystem model into a one-dimensional numerical model with diffusion turns out to allow coexistence between phytoplankton species, providing a possible solution to the 'paradox of plankton' in the sense that it prevents the competitive exclusion of one phytoplankton species. These results improve our knowledge of the factors that control the structure and functioning of plankton communities.

Keywords: Modelling; Ecosystem; Competition; Phytoplankton; Dynamical system; Water mixing

1 Introduction

2 Plankton biodiversity has always intrigued biologists who wondered how it
3 was possible that numerous phytoplankton species can coexist on a very lim-
4 ited number of mineral resources (the "paradox of plankton" described by
5 Hutchinson (1961)). A few explanations have been given to this paradox (see
6 for a review, Roy and Chattopadhyay, 2007): predator control (Krivan, 1996,
7 1997), temporal forcing such as the seasonal cycle (Hutchinson, 1961), spatio-
8 temporal effects (ocean dynamics) which will interest us in the present study,
9 and self-organized ecosystem dynamics (Huisman and Weissing, 1999; Pas-
10 sarge and Huisman, 2002).

11 Numerous sea surveys have been conducted to answer this paradox and two
12 methods were successively used to extract data on phytoplankton diversity:
13 cell counts (Riley, 1957; Jeffrey and Hallegraeff, 1980; Fryxell et al., 1985) and
14 the measurement of photosynthetic pigments used as biomarkers (Claustre
15 et al., 1994; Vidussi et al., 2001; Vaillancourt et al., 2003; Sweeney et al.,
16 2003; Dandonneau et al., 2006). These studies revealed that the distribution
17 of phytoplankton species or size class was related to dynamical structures such
18 as cyclones, anticyclones, fronts. This showed a clear connection between the
19 dominating species and ocean dynamics, which constrains the distribution of
20 nutrients and light available for the plant. But these data are really difficult
21 to interpret because they result from many possible phenomena; furthermore,
22 they did not provide an adequate sampling to resolve the spatio-temporal
23 biological variability.

24 Modelling is a way to describe interactions inside an ecosystem, which can
25 then be embedded in a simulated ocean circulation to study its behaviour in

26 a pelagic environment. Bracco et al. (2000) showed a slowdown of the weak
27 species disappearance in a highly turbulent circulation. Rivière and Pondaven
28 (2006), Lima et al. (2002a), Martin et al. (2001) examined the biological re-
29 sponse to a fully-developped frontal dynamics using more or less complex
30 ecosystem model, respectively, NPPZD, NPPZZD, and an even more com-
31 plex model with bacteria and nitrate-ammonium differentiation. They all con-
32 cluded to a distribution of their two phytoplankton species strongly influenced
33 by mesoscale processes but they had no clear results about what dynamical
34 processes drove their distribution, their coexistence or segregation or if these
35 distributions were intrinsic to the biological system itself. Furthermore, the
36 dependence of conclusions on biological parameters of the ecosystem was un-
37 known. Anderson (2005), for instance, raises the question of the accuracy of
38 results given by complex ecosystem models when the system dynamics and
39 parameterisation sensitivity are not well known.

40 All these results motivate the following general question : Do ocean dynamics,
41 via advection and diffusion, affect the ecosystem structure especially with
42 respect to phytoplankton competition on a limited number of resources? To
43 address such a question, models are ideal tools; indeed, they allow a study
44 of dominant mechanisms, from ecosystem functioning to ocean dynamics. In
45 the present study we choose to focus on the effects of particular dynamical
46 process, vertical diffusion, on phytoplankton competition. Our strategy is as
47 follows: first gain knowledge of the intrinsic dynamics of a simple ecosystem
48 model (0D model) by means of an analytical study, and then use these results
49 to understand the effects of vertical diffusion on phytoplankton competition.

50 Up to now, simple ecosystem models with one phytoplankton species were
51 studied analytically. Franks et al. (1986) determined the equilibria of an NPZ

52 model (Wroblewski and O'Brien, 1976) and the sensitivity of equilibrium val-
53 ues to biological parameters and especially to phytoplankton growth rate.
54 Busenberg et al. (1990), with the same model, made a more detailed ana-
55 lytical study with rigorous calculations of equilibria and their linear stability
56 as a function of biological parameters. The studies of Edwards and Brindley
57 (1999) and Edwards (2001) also used analytical and numerical techniques to
58 determine the dynamical behaviour of their ecosystem and concentrated on
59 sensitivity to ecosystem parameters and in particular to zooplankton mor-
60 tality with NPZ and NPZD models of different complexity. The question of
61 competition dynamics between phytoplankton species within an ecosystem
62 model was addressed by Lima et al. (2002b). However their results were ob-
63 tained numerically through integration of model equations using Runge-Kutta
64 method. This approach is too expensive to allow a study of model parameter
65 sensitivity. Besides, it does not give characteristic time scales of the model in-
66 dependent of initial conditions. In the present study we choose to use a model
67 of intermediate level of complexity (NPPZD) to address the question of ma-
68 rine ecosystem structuring in an analytical way. Our model, though simple,
69 allows the investigation of phytoplankton competition within an ecosystem.

70 Hereafter we first describe our ecosystem model: equations and parameters.
71 This provides its domain of use and limits. With the mathematical tools of
72 dynamical systems, we determine the different equilibria (fixed points and
73 limit cycles), the transitions between them in the parameter space and the
74 intrinsic time scales associated with each equilibrium. Then we examine the
75 ecosystem model sensitivity to parameters with a particular focus on the in-
76 fluence of light and total amount of nutrient stock (particulate and dissolved).
77 After, the ecosystem model is embedded in a one-dimensional physical model
78 to determine the role of vertical diffusion and sedimentation on phytoplankton

79 competition. Finally, we discuss these results with a focus on ecosystem time
80 scales and their possible interactions with vertical diffusion and more generally
81 with ocean dynamics.

82 **2 Description of the ecosystem model**

83 The ecosystem model used here has 5 prognostic variables: N, P_1, P_2, Z, D
84 which are respectively nutrients, small phytoplankton, large phytoplankton
85 like diatoms, zooplankton, and detritus. This model is based on the structure
86 of classical NPZD models like those of Fasham et al. (1990), Denman and
87 Pena (1999), Busenberg et al. (1990), Lima et al. (2002b) and Olson and Hood
88 (1994). The first two models were used to study the seasonal cycle of plankton
89 dynamics in the oceanic mixed layer. The two following ones were used to
90 study the ecosystem structuring in the parameter space. The last one has the
91 simplest equations, which allow to calculate the equilibrium solutions. Then,
92 Olson and Hood (1994) coupled it with a one-dimensional dynamical model
93 and showed that idealised seasonal forcings can slow down the competitive
94 exclusion of one of the two phytoplankton species. Here, our model has an
95 intermediate level of complexity. The modelled ecosystem is aimed at a pelagic
96 environment. Only the autotroph level has two variables and therefore, it
97 allows to study phytoplankton competition. For seek of simplicity, we consider
98 nitrogen as the limiting element, acknowledging the fact that other elements
99 like phosphorus, silicon or iron can limit phytoplankton growth. The ecosystem
100 structure is outlined in Fig. 1. In this model each variable is quantified by its
101 equivalent scalar nitrogen concentration ($mmol N.m^{-3}$).

102 The non-linear model equations are :

$$103 \quad \frac{dN}{dt} = \tau D - \alpha_1 \frac{N}{K_{N1} + N} P_1 - \alpha_2 \frac{N}{K_{N2} + N} P_2 \quad (1)$$

$$104 \quad \frac{dP_1}{dt} = \left(\alpha_1 \frac{N}{K_{N1} + N} - m_p \right) P_1 - g \frac{P_1}{K_Z + P_1 + P_2} Z \quad (2)$$

$$105 \quad \frac{dP_2}{dt} = \left(\alpha_2 \frac{N}{K_{N2} + N} - m_p \right) P_2 - g \frac{P_2}{K_Z + P_1 + P_2} Z \quad (3)$$

$$106 \quad \frac{dZ}{dt} = \left[g \beta \frac{P_1 + P_2}{K_Z + P_1 + P_2} - \varepsilon \right] Z \quad (4)$$

$$107 \quad \frac{dD}{dt} = \left[g(1 - \beta) \frac{P_1 + P_2}{K_Z + P_1 + P_2} \right] Z + m_p(P_1 + P_2) + \varepsilon Z - \tau D \quad (5)$$

108 with $\alpha_1 = \mu_1(1 - \exp(\frac{-I}{K_{I1}}))$ et $\alpha_2 = \mu_2(1 - \exp(\frac{-I}{K_{I2}}))$.

109 Definitions and values of the parameters are given in Table 1. The sum of
 110 these equations is null so the total amount of nitrogen, C_0 , is conserved :
 111 $N + P_1 + P_2 + Z + D = C_0$. We chose a closed system and not a chemostat
 112 because it is aimed at being embedded in a vertical model with nutrient fluxes
 113 due to physics. In addition, it is more easily studied analytically. Each term
 114 of these equations is a flux between two variables and is represented by an
 115 arrow in Fig. 1. Phytoplankton growth is controlled by light (I) and nutrient
 116 concentration (N) in the tank. The growth rate consists in 3 factors: μ_i , the
 117 maximum growth rate (unit: day^{-1}), the Michaelis-Menten function that pa-
 118 rameterizes the nutrient limitation (dimensionless values comprised between
 119 0 and 1) and the light limitation (dimensionless values comprised between 0
 120 and 1). This growth rate is multiplied by the phytoplankton concentration to
 121 obtain the term of nutrient uptake in the phytoplankton equations 2 and 3.
 122 The terms responsible for the decline of phytoplankton in equations 2 and 3
 123 are respectively natural mortality and grazing. The formulation for the two
 124 phytoplankton species is the same, P_1 and P_2 are only differentiated by their

125 maximal growth rate (μ_i), their affinity for either nutrients (K_{N_i}) or light
126 (K_{I_i}).

127 Parameters vary according to species that are described in the ecosystem
128 model. Their range of variations must be defined to study model param-
129 eter sensitivity. Upper and lower limits for maximal growth rates can be
130 constrained using allometric laws. Maximal growth rates (μ_i) at 20°C range
131 from $\sim 0.2 \text{ day}^{-1}$ to 3 day^{-1} (see for example Banse, 1982; Moloney and
132 Field., 1989). In open ocean phytoplankton communities, K_{N_i} is usually $<$
133 1 mmol N.m^{-3} for nitrates (Harrison et al., 1996). We derive range of K_{I_i}
134 using data from Taguchi (1976) who studied the relationship between pho-
135 tosynthesis and cell size in marine diatoms. The range for K_{I_i} varies from
136 2 to 50 W.m^{-2} . Finally phytoplankton natural mortality (m_p), our default
137 value of 0.045 day^{-1} is in the range reported by Fasham et al. (1990) (mod-
138 elling study) and by Marbà et al. (2007) and Agustí et al. (1998) (estimates
139 of phytoplankton lysis).

140 In our model, a single zooplankton variable represents a herbivorous micro-
141 zooplankton. Its mass balance is governed by a growth term minus a mor-
142 tality term. The growth term is described by a Michaelis-Menten functional
143 response which depends on the maximal ingestion rate, g , and the half satu-
144 ration constant for ingestion, K_Z . In addition, part of the ingested food is not
145 transformed into biomass. In the model, this is taken into account with the
146 gross growth efficiency parameter, β , which is the ingested part of the grazed
147 phytoplankton after losses by excretion and fecal pellets. Finally, a linear loss
148 term (εZ) is used to represent natural mortality. It is a 'closure term' which
149 represents the consumption of zooplankton by higher predators. We consider
150 here a linear formulation for zooplankton natural mortality as was done by

151 Fasham et al. (1990), Busenberg et al. (1990) and Edwards and Brindley
152 (1999). Its value is equal or very close to the values of these three studies. We
153 chose a linear term instead of a quadratic one because we checked that it did
154 not change fundamentally our ecosystem dynamics in contrast to the results
155 of Steele and Henderson (1992). Indeed, we have similar results to those of
156 Edwards and Brindley (1999) with oscillations occurring across broader ranges
157 of parameters in linear than in quadratic formulation. In order to be able to
158 lead the analytical study as far as possible, we chose the linear term.

159 Ranges for ingestion rates and half saturation constants for ingestion were
160 calculated according to Moloney and Field (1991), g varies from 6.30 day^{-1}
161 to 0.35 day^{-1} for predator size ranging from 10^4 to 10^9 pg C , and K_Z varies
162 from 0.46 to $3.56 \text{ mmol N.m}^{-3}$ for prey size ranging from 10^{-2} to 10^9 pg C .
163 For β , the gross growth efficiency, Straile (1997) has shown that it is not that
164 different between protists and copepods with a global average of about 20-
165 30 %. Mortality rates also scale with size across a large size spectrum from
166 protists to whales (McGurk, 1986). For microzooplankton or young stages
167 of copepods, Kiørboe (1997) found that mortality rates range from 0.02 to
168 0.5 day^{-1} , with most values $< 0.2 \text{ day}^{-1}$. For adult copepods, average daily
169 mortality rates (ε) are around $\sim 0.1 \text{ day}^{-1}$ (Hirst and Kiørboe, 2002).

170 The detritus concentration in equation 5 increases with the non-assimilated
171 part of grazing along with the dead organisms. It decreases through remineral-
172 isation which transforms detritus into nutrients. Finally, the tank of nutrients
173 in equation 1 is fed by detritus remineralisation and is emptied by phytoplank-
174 ton uptake. Specific degradation of organic matter ranges from 0.003 day^{-1}
175 to 0.44 day^{-1} at temperature ranging from 5 to 26°C (Newell et al., 1981;
176 Biddanda and Pomeroy, 1988; Panagiotopoulos et al., 2002; Lønborg, 2009).

177 Here, the detritus remineralisation rate is set to 0.1 day^{-1} like Edwards (2001).

178 Each flux between two ecosystem variables is associated with one time scale,
179 which is defined by parameters. But the difficulty is to deduce a global charac-
180 teristic time scale from the combination of the whole set of parameters, which
181 would quantify the ability of the system to adapt to a new environment and
182 the rate at which it reacts. The mathematical tools of dynamical system the-
183 ory, described in the next section, will allow us to determine such a time scale
184 as a function of parameters.

185 The two phytoplankton species (see Table 1) have different preferences for
186 nutrients and light, two essential ingredients for photosynthesis. In the open
187 ocean, small phytoplankton species are rather encountered in nutrient-limited
188 environments. On the contrary, large species are rather adapted to conditions
189 propitious to blooms. Here, P_1 represents a picophytoplankton-like (e.g small
190 flagellates) better adapted to low-nutrient and high-light conditions while P_2
191 represents a nano- or micro-phytoplankton-like (for example diatoms) better
192 adapted to high-nutrient and low-light conditions (Margalef, 1958). So the
193 sea surface conditions better suit P_1 , and P_2 is better adapted to conditions
194 characteristic of subsurface. Indeed Fig. 2 shows the ratio between P_2 and P_1
195 growth rates as a function of light I and nutrients N . P_1 is actually stronger
196 (ratio lower than one) with rather high light intensity whereas P_2 is dominant
197 in low-light conditions.

198 This model is a simplified version of that used by Rivière and Pondaven (2006).
199 Our goal was to find a compromise between simplicity and realism to be able
200 to study the 0D model analytically. For this purpose, we modified the zoo-
201 plankton growth term by considering only the grazing of the two phytoplank-

202 ton species with fixed preferences. In this study, we want to focus on the
 203 bottom-up control of the phytoplankton species concentration by nutrients,
 204 so we consider a single zooplankton species that has a mean effect on the two
 205 phytoplankton species. It grazes as much P_1 as P_2 (same preference for the
 206 two species). The main difference with the original model of Rivière and Pon-
 207 daven (2006) is that the two phytoplankton species can not coexist anymore in
 208 homogeneous conditions (without physics). They are segregated in the whole
 209 parameter space as it will be shown in the following section.

210 3 Intrinsic Ecosystem dynamics

211 The ecosystem model under focus here is a nonlinear system with 5 equations
 212 and 5 variables (equations 1 to 5). Because the system is closed it can be
 213 reduced to 4 equations and 4 variables using the relation $D = C_0 - N - P_1 -$
 214 $P_2 - Z$, so that the system becomes:

$$215 \quad \frac{dN}{dt} = \tau(C_0 - N - P_1 - P_2 - Z) - \alpha_1 \frac{N}{K_{N1} + N} P_1 - \alpha_2 \frac{N}{K_{N2} + N} P_2 \quad (6)$$

$$216 \quad \frac{dP_1}{dt} = \left(\alpha_1 \frac{N}{K_{N1} + N} - m_p \right) P_1 - g \frac{P_1}{K_Z + P_1 + P_2} Z \quad (7)$$

$$217 \quad \frac{dP_2}{dt} = \left(\alpha_2 \frac{N}{K_{N2} + N} - m_p \right) P_2 - g \frac{P_2}{K_Z + P_1 + P_2} Z \quad (8)$$

$$218 \quad \frac{dZ}{dt} = \left[g\beta \frac{P_1 + P_2}{K_Z + P_1 + P_2} - \varepsilon \right] Z \quad (9)$$

219 This model is a general dynamical system : $\frac{dX}{dt} = f(X, \nu)$ where $X = (N, P_1, P_2, Z)$
 220 and $\nu = (I, C_0, \tau, \mu_1, \mu_2, K_{I1}, K_{I2}, K_{N1}, K_{N2}, m_p, g, K_Z, \varepsilon, \beta)$ are respectively
 221 the state variable vector and the parameter vector. All components of X and
 222 ν are positive.

223 Among the parameters of this model, I and C_0 can be classified apart. Indeed,
224 C_0 and I vary artificially in this ecosystem model but vary in space and time
225 in reality. Thus a detailed study of the state vector variations with C_0 and I
226 in 0D is essential to better explain the 3D observations from the sea surface
227 where light is intense to the subsurface where nutrients are abundant.

228 Now we will first characterize the equilibria of this model and their stabil-
229 ity, and then a sensitivity study of the ecosystem model dynamics will be
230 conducted to extract the role of key parameters.

231 3.1 *Equilibrium solutions and their stability*

232 The purpose is to characterize analytically the equilibria and their stability
233 for this dynamical system in the whole parameter space defined by ν . In other
234 words, we are looking for the asymptotic behaviour of the system as $t \rightarrow \infty$.
235 The ecosystem structures corresponding to equilibria of the system are listed
236 in Table 2. Two types of equilibrium can be reached by the system : steady
237 equilibria (fixed points) and oscillatory regimes (limit cycles). In our case,
238 there are five possible fixed points with different ecosystem structures and
239 two possible limit cycles (see Table 2). Ecosystems n° 6 and n° 7, which in-
240 volve phytoplankton coexistence, can not be achieved in such a model. All the
241 analytical determination of the domain of validity of fixed points, bifurcation
242 curves and intrinsic time scales are detailed in Appendix A. The question of
243 phytoplankton coexistence or segregation is dealt with, in Appendix B.

244 The main conclusion from this analytical study is: whatever the parameter
245 values, the two phytoplankton species can not coexist in our model at equi-
246 librium: one of them is always excluded from the system. Without zooplank-

247 ton this result is a consequence of the competitive exclusion principle. With
248 zooplankton this result can be interpreted as a consequence of the fixed pref-
249 erences applied to the phytoplankton. Indeed, if one species is favoured and
250 develops much more than the other, zooplankton does not take into account
251 this dominance and still grazes the same proportion of each species. Zooplank-
252 ton does not control the species in excessive number and does not spare the
253 other. As we aim to study the effect of diffusion on phytoplankton competi-
254 tion, this model choice is important: it is the most unfavourable case for the
255 two phytoplanktons to coexist.

256 *3.2 Equilibria and associated time scales as a function of light (I) and total* 257 *nitrogen (C_0)*

258 With the dynamical system theory, we explored analytically the ecosystem
259 equilibria in the whole parameter space. Here, we study the ecosystem struc-
260 ture at equilibrium and the associated time scales as a function of light (I)
261 and total nitrogen (C_0), the other parameters being set to their default value
262 (Table 2). These two parameters have a large range of variation in ocean. At
263 first order, they only vary along the vertical, light is decreasing with depth
264 while nutrient concentration is usually increasing down to the nitracline. Nev-
265 ertheless they also vary horizontally through combined advection and diffusion
266 processes for nutrients and, through shading due to phytoplankton for light.
267 In that sense the possible values for I and C_0 define a 2D parameter space
268 in which the ecosystem can achieve different equilibria. Our 0D study will
269 provide preliminary and indicative information for the 1D model to follow.

270 Fig. 3 sums up the different equilibrium solutions on a bifurcation diagram

271 as a function of I and C_0 . As expected, varying parameters I and C_0 causes
272 deep changes in stability of equilibrium solutions. Two types of bifurcation
273 are observed on this diagram: transcritical bifurcations (solid lines on Fig.
274 3) and Hopf bifurcations (dashed lines on Fig. 3). Fixed points are white
275 areas whereas limit cycles are grey areas on Fig. 3. Each equilibrium is in-
276 dicated by the emergent variables. Fig. 4 gives the amplitude of each vari-
277 able at fixed points in the same parameter space. These figures illustrate the
278 main results obtained by the analytical study. First, phytoplankton species
279 do not coexist. P_1 survives for high values of I and P_2 for low values of I .
280 Therefore, P_1 is expected to dominate in surface layers and P_2 in subsurface.
281 Secondly, no zooplankton is observed for low values of C_0 . Thirdly, as soon as
282 the zooplankton emerges, concentration of the subsisting phytoplankton re-
283 mains constant, illustrating zooplankton control of phytoplankton which im-
284 plies an increase of zooplankton concentration as total nitrogen (C_0) or light
285 (I) increases. Edwards and Brindley (1999) had the same feature in their
286 model with linear zooplankton mortality. Lastly, large values of total nitrogen
287 lead to self-sustained oscillations between nutrient, subsisting phytoplankton
288 and zooplankton. These oscillations occur for parameter ranges corresponding
289 closely to subsurface chlorophyll maximum in the ocean. This kind of oscil-
290 lations have already been observed with an ecosystem model by Lima et al.
291 (2002b). As a global view of the (I, C_0) bifurcation diagram, we can conclude
292 that phytoplankton emergence is mainly managed by I whereas zooplankton
293 emergence and temporal behaviour is mainly managed by C_0 .

294 With the analytical study, time scales associated with each fixed point can be
295 calculated as a function of light and amount of nutrients (Fig. 5). As expected,
296 there are some differences between time scales associated with conditions of
297 surface and of subsurface. At high light - low nutrient conditions often en-

298 countered in surface layers, time scales to reach equilibrium range from 1 to
299 5 days which is quite fast. The ecosystem is very reactive at sea surface. At
300 low light - high nutrient conditions characteristic of subsurface layers, time
301 scales are an order higher (10 – 20 days) and the ecological system is likely to
302 undergo self-sustained oscillations with periods of about 50 days (not shown).

303 This shows that ecosystem time scales will be very different from the surface
304 to the deep ocean. Ocean dynamics is expected to play an important role on
305 3D ecosystem structuring through parameters I and C_0 , and it is likely to
306 interact with ecosystem dynamics through the coupling of their time scales as
307 it will be dealt with in the discussion.

308 *3.3 Influence of biological parameters on the (I, C_0) equilibrium solutions*

309 After studying the influence of external parameters (I, C_0) on ecosystem struc-
310 turing, we investigate in the sensitivity of the system to biological parameters.

311 *3.3.1 Sensitivity to the re-mineralisation rate τ*

312 In the real ocean, re-mineralisation associated with sinking is an important
313 process in subsurface chlorophyll maximum dynamics. In our system, re-
314 mineralisation time scale can be thought of as a time scale related to the
315 system closure. This time scale is supposed to be important in our model
316 concerning the competition process between the two phytoplankton species.

317 Let us consider the effects of varying re-mineralisation parameter τ from 10^{-3}
318 to 1 day^{-1} , for a fixed light intensity of $I = 5 \text{ W.m}^{-2}$ but two different total
319 nitrogen concentrations : $C_0 = 1.2 \text{ mmol N.m}^{-3}$ and $C_0 = 4 \text{ mmol N.m}^{-3}$

320 (Fig. 6).

321 For $C_0 = 1.2 \text{ mmol } N.m^{-3}$ the system was reaching a fixed point of type
322 $N^*P_2^*Z^*$ with default value of $\tau = 0.1 \text{ day}^{-1}$ (Fig. 3). On Fig. 6a, we observe
323 that as τ increases from this value, no more bifurcation is observed, only the
324 amplitude of N and Z increases. As τ decreases from its default value, two
325 consecutive bifurcations are observed: first a new fixed point is achieved with
326 a shift from P_2 to P_1 giving an $N^*P_1^*Z^*$ equilibrium and then another fixed
327 point appears for very low τ values in which zooplankton disappears giving an
328 $N^*P_1^*$ equilibrium. The shift from P_2 to P_1 as τ decreases can be explained as
329 follows: for low re-mineralisation rates the process of re-mineralisation from
330 detritus to nutrients is very slow inducing a drop in nutrient stocks at the
331 equilibrium which is more favourable to small phytoplankton P_1 . When τ tends
332 to 0, the $N^*P_1^*$ fixed point remains stable according to eigenvalues λ_1 and λ_2
333 calculated in the preceding section which remain negative, and N remains
334 constant whereas P_1 decreases towards 0 according to equations A.1 and A.2.
335 In that case re-mineralisation is so slow that it can not balance uptake and
336 thus, at equilibrium, detritus concentration increases while P_1 concentration
337 decreases.

338 Fig. 6b shows the case in which C_0 is increased to $4 \text{ mmol } Nm^{-3}$. For the
339 default τ value (Fig. 3) the equilibrium was a limit cycle between N , P_2 and
340 Z . As τ is increased from this default value, this equilibrium remains stable
341 but the amplitude of oscillations increases. Inversely as τ is decreased the
342 periodic orbit collapses and the system reaches an $N^*P_2^*Z^*$ fixed point. Then
343 as τ decreases we observe two more bifurcations similar to the ones observed
344 in Fig. 6a with first a shift from P_2 to P_1 and then disappearance of Z giving
345 an $N^*P_1^*$ fixed point for very low values of τ .

346 In conclusion, the increase of τ tends to destabilize the system giving rise to
 347 oscillations when total nitrogen concentration is sufficient. Large values of τ
 348 are favourable to a dominance of P_2 , whereas low τ values are favourable to
 349 a dominance of P_1 . Moreover large values of τ tend to increase biodiversity
 350 giving rise to a coexistence of phytoplankton and zooplankton. If we refer to
 351 the (I, C_0) bifurcation diagram of Fig. 3 we checked in the analytical study
 352 (see Appendix A) that an increase of τ values has no influence on bifurcation
 353 lines $N^* \leftrightarrow N^*P_1^*$, $N^* \leftrightarrow N^*P_2^*$ and $N^*P_1^* \leftrightarrow N^*P_2^*$, whereas it tends to
 354 translate downwards all the remaining bifurcation curves. It is able to influence
 355 phytoplankton competition mainly for medium light values, corresponding to
 356 neighborhood of the bifurcation lines $N^*P_1^*Z^* \leftrightarrow N^*P_2^*Z^*$ and $NP_1Z \leftrightarrow$
 357 NP_2Z (limit cycles).

358 3.3.2 Sensitivity to growth rates μ_1 and μ_2

359 The sensitivity of the model to the growth rates μ_1 and μ_2 is illustrated on
 360 the bifurcation diagram of Fig. 7 in which I is set to $5 W.m^{-2}$ and C_0 is set to
 361 $1.2 mmol N.m^{-3}$. We can distinguish 5 regions. The first region corresponds to
 362 small values of μ_1 and μ_2 for which phytoplankton growth is too slow for them
 363 to subsist (fixed point n°1 in Table 2 for which eigenvalues λ_1 and λ_2 remain
 364 negative). When μ_1 or μ_2 are increased, fixed point n°1 loses its stability giving
 365 rise to fixed point n°2 or n°3 respectively (see Table 2). Further, if we keep
 366 increasing μ_1 or μ_2 , fixed point n°4 or n°5 appears. For low C_0 value chosen
 367 on Fig. 7 neither μ_1 nor μ_2 values are able to give rise to a Hopf bifurcation.
 368 For higher C_0 values, this is observed (not shown).

369 In conclusion, μ_1 and μ_2 are likely to make the system undergo bifurcations
 370 between fixed points (transcritical bifurcation) and even between a fixed point

371 and a limit cycle (Hopf bifurcation, not shown). But their influence is all the
 372 same quite limited. Indeed, for $C_0 < \frac{m_p + \tau}{\tau} \frac{\varepsilon K}{g\beta - \varepsilon}$, growth rates just determine the
 373 transition between fixed points N^* and $N^*P_i^*$. Elsewhere in parameter space,
 374 given their domain of variation, μ_1 and μ_2 do not influence much the stable
 375 equilibria except close to transition lines of (I, C_0) bifurcation diagram. As
 376 expected μ_1 and μ_2 essentially play a role in the competition between the two
 377 phytoplankton species. If we refer to the (I, C_0) bifurcation diagram (Fig. 3),
 378 values of μ_1 and μ_2 act mainly on bifurcation curves which characterize a shift
 379 in the phytoplankton composition ($N^*P_1^* \leftrightarrow N^*P_2^*$ and $N^*P_1^*Z^* \leftrightarrow N^*P_2^*Z^*$).
 380 If μ_1 is increased, these curves move to the left on Fig. 3 in the (I, C_0) space,
 381 and conversely if μ_2 is increased.

382 3.3.3 Sensitivity to gross growth efficiency and ingestion rate (β and g)

383 The gross growth efficiency β for P_1 and P_2 , and the maximum ingestion
 384 rate g appear in the grazing term and define its intensity. The bifurcation
 385 diagram as a function of these two parameters is presented on Fig. 8. The
 386 bifurcation curves have a hyperbolic signature, which suggests that the prod-
 387 uct $g\beta$ plays an essential role in bifurcation parameter. This is the case for
 388 $\lambda_5 = g\beta \frac{P_1^*}{K_Z + P_1^*} - \varepsilon$ (see Appendix A) whose zero curve is drawn on Fig. 8
 389 (bifurcation $N^*P_1^* \leftrightarrow N^*P_1^*Z^*$). The product $g\beta$ has a quite important influ-
 390 ence on the type of equilibrium solution (fixed point or limit cycle) reached
 391 by the system. If it is small, grazing is too weak so that zooplankton sub-
 392 sists. On the contrary, if it is important the system loses its stability and
 393 oscillations between variables occur. The global effect of βg on the general
 394 bifurcation diagram of Fig. 3 is as follows: an increase of βg induces a down-
 395 ward translation of bifurcation curves $N^*P_1^* \leftrightarrow N^*P_1^*Z^*$, $N^*P_2^* \leftrightarrow N^*P_2^*Z^*$

396 and $N^*P_1^*Z^* \leftrightarrow N^*P_2^*Z^*$, and also of the Hopf bifurcation curves. The param-
397 eters g and β have therefore mainly an influence on the temporal behaviour
398 of the system at equilibrium. Like the re-mineralisation parameter, they can
399 influence phytoplankton competition mainly for medium light values (corre-
400 sponding to neighborhood of the bifurcation curve $N^*P_1^*Z^* \leftrightarrow N^*P_2^*Z^*$).

401 **4 The ecosystem model behaviour in 1D diffusive dynamics**

402 Knowing the intrinsic ecosystem model dynamics, its associated time scales
403 and its sensitivity to parameters, we can now investigate the combined effect
404 of diffusion and sedimentation processes on ecosystem structuring and more
405 precisely on phytoplankton competition. For this purpose, we take exactly the
406 same ecosystem model with the default parameter set presented in Table 1 and
407 embed it into a simple physical model in which we define a profile of light, a
408 profile of vertical diffusivity (Edwards et al., 2000) and a sedimentation speed
409 on detritus. The important thing to notice is that light profile, diffusivity
410 profile and sedimentation are constant in time. The purpose is to study the
411 behaviour of the 1D model at equilibrium and to free ourselves of all temporal
412 forcing. If sedimentation and diffusion are turned off, we have at each depth
413 a OD ecosystem model running independently and following the behaviour
414 described on Fig. 3 (called hereafter ‘OD spatialized model’). If they are turned
415 on, we have a 1D model with a vertical coupling of the different OD simulations
416 by physical dynamics.

417 The diffusivity coefficient K_v is vertically homogeneous in a surface layer (from
418 10^{-5} up to $10^{-1} m^2.s^{-1}$) representing an idealized mixed layer of depth varying
419 between 50 to 200 m . It is equal to a classical background value below the

420 mixed layer ($K_v = 10^{-5} \text{ m}^2 \cdot \text{s}^{-1}$).

421 We chose to study the combined effect of diffusion and sedimentation and
422 not the two processes separately to have a more realistic vertical water col-
423 umn. Without diffusion, the subsistence of an ecosystem at equilibrium is not
424 possible, because all the organic matter would be gradually drained out from
425 the euphotic layer. Furthermore, Hodges and Rudnick (2004) showed that the
426 subsurface chlorophyll maximum is conditioned by the sedimentation rate on
427 a biological compartment. Without sedimentation, organic matter gathers at
428 surface. We chose a default sedimentation speed of $1 \text{ m} \cdot \text{day}^{-1}$ so that 90 % of
429 the organic matter is remineralised between 0 and 100 m in average. This is
430 consistent with export ratio found at the base of the euphotic zone in various
431 regions of the ocean (Schlitzer, 2000).

432 The light profiles used here are exponentially decreasing, $I = I_0 \exp(\lambda z)$. I_0 is
433 the surface irradiance. λ is the extinction coefficient and is set to 0.04 m^{-1} .
434 The euphotic depth is defined as the depth where light is 1% of the surface
435 irradiance. Here, we have a euphotic layer of 115 m depth. In this 1D config-
436 uration, the two phytoplankton species move in the light and total nitrogen
437 gradients. All the simulations we discuss here are run until equilibrium.

438 In this study, we mainly vary the mixed layer depth, the diffusivity coefficient
439 K_v and also the light profile, because in 0D light is essential to determine
440 which phytoplankton species will survive. An idealized initial profile of nu-
441 trients based on tanh function is used. It is calibrated such as the nitracline
442 depth is the same as the mixed layer depth. Initially nutrient are scarce in
443 the mixed layer and abundant below. We first present the results for a winter
444 case with a 200 m mixed layer and a surface irradiance of $111 \text{ W} \cdot \text{m}^{-2}$ corre-
445 sponding to midlatitudes (Campbell and Aarup, 1989). On Fig. 9, the verti-

446 cal ecosystem structuring is presented at equilibrium for two configurations
447 with a mixed layer depth of 200 m and a diffusivity coefficient of respectively
448 $10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$ (Fig. 9a) and $10^{-2} \text{ m}^2 \cdot \text{s}^{-1}$ (Fig. 9b). On Fig. 9a, the two phyto-
449 plankton species coexist in the whole mixed layer whereas on Fig. 9b, there
450 is a competitive exclusion of P_2 . The first conclusion is that the combined
451 diffusion and sedimentation processes can allow the coexistence of the two
452 phytoplankton species at equilibrium which was absolutely impossible in 0D.
453 Secondly, the result of the competition is very dependent on the diffusivity
454 value resulting in competitive exclusion or coexistence of phytoplanktons.

455 To understand the mechanisms that lead to these different outcomes, Fig. 9c,d
456 present the profiles that would be obtained without diffusion and sedimenta-
457 tion in the two cases ('0D spatialized model'). We take care to have the same
458 C_0 profile as the one reached at the end of the previous 1D simulations. In
459 practice, to obtain Fig. 9c,d, we run a new simulation from the C_0 profile of
460 each balanced 1D simulation but this time, by cutting diffusion and sedimen-
461 tation. Therefore, at each depth, the system reaches an equilibrium predicted
462 by 0D analytical study. In the two cases, the '0D spatialized' simulations give
463 the same kind of results i.e. the subsistence of P_1 in surface layers and P_2 be-
464 low. The two phytoplankton species are maintained by zooplankton to a fixed
465 concentration as described in the analytical study. To compare 0D predictions
466 for light and amount of nutrients found along the water column and the 1D
467 results, the corresponding (I, C_0) couples at each depth are reported on the
468 bifurcation diagram established in the 0D analytical study (Fig. 9e,f). In 0D
469 spatialized configuration, there is segregation of the two phytoplankton species
470 with each profile of total nitrogen. But when the diffusion and sedimentation
471 are turned on, we have totally different vertical ecosystem structuring: the
472 weak K_v (Fig. 9a) induces the coexistence of the two phytoplankton species

473 whereas the strong K_v (Fig. 9b) induces the competitive exclusion of P_2 . To
474 analyse the mechanisms that lead to these results, we study the fluxes of bio-
475 logical variables as a function of time (not shown). The fluxes are integrated
476 over a surface layer corresponding to the layer of P_1 dominance in 0D spatial-
477 ized simulation, and over a subsurface layer where P_2 dominates in 0D.
478 They reveal that strong K_v induces quick nutrient injections into the mixed
479 layer but P_2 growth is too slow to consume enough of them. Therefore these
480 nutrients benefit P_1 which grows rapidly near the surface; P_1 growth is fol-
481 lowed by that of Z . P_1 and Z propagate then downwards via diffusion; they
482 enter the layer suitable for P_2 and weaken it. Furthermore, since P_1 uses all
483 the nutrients in surface layer, the gradient in nutrients in the mixed layer is
484 maintained and nutrients keep being diffused to the surface layer. This has
485 again a negative feedback on P_2 which is more nutrient-limited and a positive
486 one on P_1 which keeps developing and spreading downwards.
487 For weak K_v , on the contrary, P_2 is sufficiently rapid to consume a great part
488 of the nutrients injected into the mixed layer. This limits the growth of P_1 and
489 allows the coexistence of the two phytoplankton species in the whole mixed
490 layer with a dominance of each of them in its preferred layer. Moreover, the in-
491 tegrated fluxes at equilibrium reveal that growth rate of P_2 (respectively P_1) is
492 less than its loss rate in surface layer (respectively in subsurface layer). Indeed,
493 the diffusive flux maintains P_2 in surface layer (respectively P_1 in subsurface
494 layer). Thus, mixing allows a non-zero concentration of P_2 in the surface layer
495 (respectively P_1 in the subsurface layer) where these phytoplanktons can not
496 sustain their own population. In other words, there is a ‘source’ population
497 which spreads phytoplankton in a hostile habitat. We have therefore coexis-
498 tence between the two species despite mixing, that is to say even if mixing
499 tends to create an isotropic environment without ecological niches that shel-

500 ter the weak species. And the magnitude of mixing makes the system shift
501 between coexistence (intermediate mixing) or exclusion (strong mixing).

502 To complement these results retaining a winter mixed layer of 200 m depth,
503 the surface irradiance is diminished to $50 W.m^{-2}$ and then to $13 W.m^{-2}$ which
504 corresponds respectively to latitudes between 40 and 50° and polar latitudes
505 (Campbell and Aarup, 1989). With these light profiles, P_2 is favoured over a
506 thicker layer if we refer to 0D bifurcation diagram (see Fig. 3). For a surface
507 irradiance of $50 W.m^{-2}$, the results are the same as those previously shown. For
508 a surface irradiance of $13 W.m^{-2}$ (polar case), P_2 does exclude P_1 competitively
509 when the diffusivity coefficient is set to $10^{-2} m^2.s^{-1}$. It is what is expected
510 from the 0D study.

511 After having shown the importance of the mixing magnitude in a winter case,
512 we take a shallower mixed layer (30-50 m) associated to a summer light profile
513 (surface irradiance of $230 W.m^{-2}$). In this case, there is a vertical segregation
514 (not shown): P_1 in the mixed layer and P_2 in the subsurface maximum. It is
515 interesting to see that the mixed layer plays the role of an ecological niche for
516 P_1 . Each phytoplankton is sheltered from the other and can develop itself in
517 its part of the water column.

518 Last, we checked that we obtained the same results as Edwards et al. (2000)
519 who noticed a vanishing of oscillations when the ecosystem model was spatial-
520 ized vertically. Mixing and sedimentation actually couple biological dynamics
521 along vertical dimension. In our model, this has indeed a stabilizing effect on
522 water column and limit cycles, predicted by 0D dynamics, become fixed points
523 in 1D configuration.

524 To conclude on this 1D study, combined diffusion and sedimentation can al-

525 low coexistence of two species of phytoplankton at equilibrium even if there is
526 always competitive exclusion in 0D. Furthermore, the value of the diffusivity
527 coefficient is essential. Indeed, there is a threshold value for which the cou-
528 pled system shifts from coexistence in the whole mixed layer to a competitive
529 exclusion of P_2 .

530 **5 Discussion**

531 The dynamics of an NPPZD ecosystem model was examined in the param-
532 eter space. The ecosystem structure, the type of equilibrium reached by the
533 system (fixed point or limit cycle) and the value of each ecosystem variable
534 at each fixed point has been obtained for each parameter set. This allowed
535 us to deduce the parameter sensitivity and to conclude on the role of each
536 parameter in ecosystem dynamics. Light intensity and total amount of nitro-
537 gen matter turn out to be the more important parameters. Because of their
538 domain of variation, they allow a large variety of ecosystem structures and a
539 large range of equilibrium values for each variable. Once a detailed knowledge
540 of the 0D ecosystem dynamics was obtained, the model was embedded in a
541 vertical environment. It allowed us to study the combined effect of diffusive
542 physics and sedimentation of detritus. Diffusion and sedimentation turned out
543 to have an important role in the ecosystem structure along the water column.
544 They change the phytoplankton distribution and especially allow the coexis-
545 tence of the two phytoplankton species at a same depth in the water column.
546 1D dynamics has also a stabilizing effect on the intrinsic oscillations displayed
547 by a vertically-distributed ecosystem model.

548 We showed that the diffusivity coefficient K_v in the mixed layer determines

549 the outcome of the competition between the two phytoplankton species. More
 550 precisely, there is a threshold value beyond which one of the two species is
 551 competitively excluded. This competition result can be described by the clas-
 552 sical diversity index of Shannon-Weaver H' as well. It is defined by $H' =$
 553 $-\sum_{i=1}^2 \frac{P_i}{P_1+P_2} \log_2 \frac{P_i}{P_1+P_2}$. It varies between 0 and 1. This index is generally used
 554 with many species of phytoplankton. In our case, it is averaged in the mixed
 555 layer and it gives a quantification of coexistence (close to $H' = 1$) and exclu-
 556 sion or vertical segregation ($H' = 0$) and thus a new highlight of the results.
 557 The Shannon-Weaver index, averaged within the mixed layer, is plotted on
 558 Fig. 10a as a function of diffusivity. It shows an increase of H' with K_v be-
 559 tween 10^{-5} to $2.10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$ and a sharp decrease towards zero as soon as K_v
 560 exceeds a threshold value of $2.10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$. This indicates a bifurcation of the
 561 1D system between a fixed point with coexistence of the two phytoplankton
 562 species and a fixed point with competitive exclusion. Moreover, the maximum
 563 of H' is almost correlated with the maximum of total biomass ($P_1 + P_2 + Z + D$)
 564 in the system (Fig. 10b). It is slightly shifted from $1.10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$. These model
 565 results are in line with enclosure experiments of Flöder and Sommer (1999)
 566 who showed that species diversity index H' reaches a maximum at intermedi-
 567 ate level of disturbance (mixing).

568 Our '0D spatialized model' (Fig. 9c,d) shows that the two phytoplankton
 569 species are vertically segregated. Both of them survive at different levels be-
 570 cause of the heterogeneity of the environmental conditions (I and C_0 vary
 571 along depth). Introducing vertical diffusion tends to mix this vertical distri-
 572 bution of phytoplankton and thus it is reasonable to expect a coexistence of
 573 the two phytoplankton species at a same depth. In the winter case, when the
 574 mixed layer is deeper than the euphotic layer, the two phytoplankton species
 575 have to face each other, with two solutions: either they coexist or one dies.

576 We showed that the outcome crucially depends on the value of diffusivity.
577 If mixing is sufficiently weak (below a threshold value) phytoplankton almost
578 does not feel the vertical gradients in 'physical parameters' (namely I and C_0).
579 Each phytoplankton species develops in its preferential part of the mixed layer
580 and then slowly diffuses in the whole mixed layer. Thus the two phytoplank-
581 ton species coexist. If, on the contrary, mixing is sufficiently intense, light and
582 total nitrogen received by the two phytoplankton species have an amplitude
583 that is about the average of I and C_0 in the mixed layer. In this case, physical
584 and biological dynamics decouple and the results become identical to those of
585 the 0D model (competitive exclusion).

586 In this study we considered a model with an intermediate level of complexity to
587 address the question of phytoplankton competition: two phytoplankton species
588 competing for one nutrient and light. Without external forcing (0D model),
589 light is a fixed parameter. There are more phytoplankton species than lim-
590 iting resources. As a consequence, we observe a competitive exclusion of one
591 phytoplankton whatever the parameters in accordance with the competitive
592 exclusion principle (Hardin, 1960). In the 1D model things are less simple: the
593 fixed vertical gradient of light combined with the physical forcing induced by
594 vertical mixing may be thought as an "active" limiting factor. Therefore we
595 should expect a possible coexistence of the two phytoplankton species on the
596 two limiting factors. This is why we have also tested a three-phytoplankton
597 species model competing for the same two resources (light and nutrient) to
598 see if vertical mixing is always able to make these three phytoplankton species
599 coexist. The results are shown on Fig. 11. The ecosystem model used here is
600 very similar to the one previously studied but now with three phytoplankton
601 species: one better adapted to surface conditions, a second better adapted to
602 intermediate depths, and the third better adapted to even deeper depths. Pa-

603 rameters of the three phytoplankton are indicated in Table 3. As expected,
604 the 0D model predicts a competitive exclusion of two phytoplankton species
605 at each point of the parameter space. But Fig. 11 reveals a coexistence of the
606 three phytoplankton species together over the mixed layer which confirms our
607 preceding results : the effect of vertical mixing is able to maintain a greater
608 number of phytoplankton species than the number of limiting resources. There-
609 fore, this one-dimensional process is another potential answer to the ‘paradox
610 of plankton’ in the sense that it is able to prevent the competitive exclusion
611 of one or more phytoplankton species at equilibrium.

612 This two or three species coexistence at equilibrium can be explained by the
613 coupling between mixing and biological dynamics. Let us describe the differ-
614 ent time scales inherent in the system and then discuss the possible influence
615 of turbulent vertical injections of nutrients in the mixed layer. The ecosys-
616 tem time scales determined in the analytical study (Fig. 5) were 1-5 days
617 in surface layer, and 10-20 days in subsurface. The ecosystem could also un-
618 dergo self-sustained oscillations with periods of about 50 days. Concerning
619 one-dimensional dynamics, a diffusivity coefficient of 10^{-4} to $10^{-2} m^2.s^{-1}$ cor-
620 responds to time scales of around 100 to 1 days respectively if we consider a
621 vertical length scale of 25 *m* corresponding to the scale of the nutrient gradient.
622 These similar time scales show that, in the mixed layer, diffusion may interact
623 with ecosystem dynamics and couple the ecosystems at different depths. This
624 explains the strong sensitivity of the ecosystem structuring to the diffusivity
625 value revealed by 1D simulations.

626 Lastly, if we consider a three-dimensional environment, time scales correspond-
627 ing to turbulent vertical injections can be estimated. To schematize, we classify
628 oceanic motions in three scales: large scale, mesoscale and submesoscale. The

629 first one corresponds for instance to wind-induced gyres with horizontal scales
630 of a few thousand kilometers and with vertical time scales of the order of 100-
631 1000 days (around 300 days according to Flierl and McGillicuddy, 2002). The
632 second one corresponds to phenomena like eddies or meanders, characterized
633 by length scale of about 100 km and time scales of 10-100 days (Klein and
634 Lapeyre, 2009). The last class results from the interaction between mesoscale
635 structures which forms filaments characterized by strong gradients on scales of
636 10 km. The time scale of nutrient injections in these filaments is about 1 day
637 (Klein and Lapeyre, 2009). The comparison of these time scales with biolog-
638 ical ones indicates how efficient the coupling between physical and biological
639 dynamics can be.

640 Ecosystem time scales were diagnosed in the analytical study (Fig. 5). At
641 large scale and in surface layers, ecosystem dynamics is therefore expected to
642 be much faster than ocean dynamics so the ecosystem feels the evolution of
643 physical environment as a change in initial conditions. Immediately, it reacts
644 to the perturbation and reaches a new fixed point. Thus, the 0D ecosystem
645 model predictions concerning phytoplankton competition should be similar to
646 in situ data in a weakly turbulent domain. Our model predicts a dominance
647 of the small species (picophytoplankton P_1), which is in accordance with data
648 collected during several surveys. Indeed, Claustre et al. (1994) reported a
649 dominance of cyanobacteria and flagellates (nano- and pico- phytoplankton)
650 in surface layers in the areas adjacent to the front between Mediterranean and
651 Atlantic waters whereas the frontal zone was diatom-dominated. Dandonneau
652 et al. (2006) also showed a clear dominance of picophytoplankton (75%) at
653 sea surface of South Pacific subtropical gyre (highly oligotrophic region). The
654 results of Vidussi et al. (2001) also confirm this clear dominance and stability
655 of small phytoplankton species in surface waters at large scale. They show the

656 predominance of pico- and nano- phytoplankton in oligotrophic areas of the
657 Levantine basin (eastern Mediterranean).

658 Deeper in the ocean, conclusions seem to be less simple. Physics and biology
659 evolve approximately at the same rate. Our ecosystem model, at equilibrium,
660 predicts either a fixed point with an associated time scale of 10-20 days or
661 self-sustained oscillations with a 50-day period. But ocean dynamics might
662 disguise these potential oscillations (Koszalka et al., 2007). It might account
663 for the very few observations of fluctuations of the deep chlorophyll maximum.
664 Only Huisman et al. (2006) reported such sustained oscillations in oligotrophic
665 waters of subtropical Pacific Ocean and ascribed it to intrinsic ecosystem
666 dynamics (and not to seasonal forcing).

667 At meso- and submeso- scale, data are still too scarce and scattered for us to
668 be able to draw a conclusion. According to a few studies (Fryxell et al., 1985;
669 Vidussi et al., 2001; Jeffrey and Hallegraeff, 1980) it seems that at sea surface,
670 at eddy edge, there is a shift in size of the phytoplankton community structure
671 towards small species (pico- and nano-phytoplankton). But these observations
672 are difficult to relate to biological and physical time scales.

673 At eddy centre, there is no rule either. Phytoplankton dominance depends on
674 the class of motion (cyclone, anticyclone, mode-water eddy) and on the eddy
675 age (Claustre et al., 1994; Fryxell et al., 1985; Vidussi et al., 2001; Sweeney
676 et al., 2003; Vaillancourt et al., 2003; Jeffrey and Hallegraeff, 1980). This
677 variety of ecosystem size distribution in eddy centre seems to support the hy-
678 pothesis that physics and biology are indivisible at this scale. Ecosystems are
679 presumably never at equilibrium. At meso- and submeso-scale, high biodiver-
680 sity observed may thus be explained by non-equilibrium conditions imposed by
681 physical forcing. Ocean submeso- and mesoscale structures should play a role

682 of shelter for less-competitive species and thus allow them to survive (Bracco
683 et al., 2000; Pasquero et al., 2004).

684 The purpose of this study was to focus on the dynamics of an NPPZD ecosys-
685 tem and on its behaviour when submitted to mixing, and particularly in terms
686 of phytoplankton competition. The spatially extended and coupled system ex-
687 hibits a wider range of ecosystem structures, allowing for instance coexistence
688 between the two phytoplankton species over the first 200 meters of the water
689 column. This provides an additional solution to the ‘paradox of the plankton’,
690 complementing the overview drawn up by Roy and Chattopadhyay (2007).
691 The examination of physical and biological time scales allowed us to conclude
692 on the likely coupling between ecosystem and ocean dynamics in three dimen-
693 sions, except in weakly-turbulent ocean surface layers. Further work has to
694 be done in new numerical process studies using simplified three-dimensional
695 ocean dynamics models, including 3D advection (at mesoscale and subme-
696 soscale) and interactions with mixed layer dynamics for instance. These new
697 process studies should complement our conclusions issued from the timescale
698 analysis, in particular concerning the influence of fine scale dynamical struc-
699 tures on phytoplankton competition within an ecosystem.

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752 as (b) 35

- 753 10 (a) Vertical mean of Shannon-Weaver Diversity index H as
754 a function of diffusivity coefficient K_v ; Mixed layer depth of
755 200 m (b) Total biomass ($P_1 + P_2 + Z + D$ in $mmol N.m^{-3}$)
756 as a function of diffusivity coefficient K_v 36
- 757 11 1D simulation with 3 phytoplankton species: Vertical profile
758 of P_1 , P_2 and P_3 at equilibrium with a 200 m depth mixed
759 layer and $K_v = 10^{-3} m^2.s^{-1}$. P_1 (solid line) is better adapted
760 to surface conditions, P_2 (dashed line) to intermediate depths
761 and P_3 (dashed dotted line) to even deeper depths. 37

Parameter	Value	Unit	Description
<i>Phytoplanktons</i>			
μ_1	1.9	day^{-1}	Maximal P_1 growth rate
μ_2	1.5	day^{-1}	Maximal P_2 growth rate
K_{N1}	0.15	$mmol N.m^{-3}$	Half saturation constant of P_1 for nutrient uptake
K_{N2}	0.6	$mmol N.m^{-3}$	Half saturation constant of P_2 for nutrient uptake
K_{I1}	30	$W.m^{-2}$	P_1 affinity for light
K_{I2}	5	$W.m^{-2}$	P_2 affinity for light
m_p	0.045	day^{-1}	Phytoplankton mortality rate
<i>Zooplankton</i>			
g	1.5	day^{-1}	Maximum ingestion rate
K_z	1.4	$mmol N.m^{-3}$	Half saturation constant for ingestion
β	0.2		Gross Growth Efficiency for P_1 and P_2
ε	0.06	day^{-1}	Mortality rate
<i>Detritus</i>			
τ	0.1	day^{-1}	Specific remineralisation rate

Table 1
Ecosystem model parameters

n°	Ecosystem structure	Temporal behaviour
1	N	Fixed Point
2	NP_1	Fixed Point
3	NP_2	Fixed Point
4	NP_1Z	Fixed Point and Limit Cycle
5	NP_2Z	Fixed Point and Limit Cycle
6	NP_1P_2	-
7	NP_1P_2Z	-

Table 2
The different nonlinear equilibria of the ecosystem model

Parameter	Value	Unit	Description
μ_1	1.7	day^{-1}	Maximal P_1 growth rate
μ_2	1.7	day^{-1}	Maximal P_2 growth rate
μ_3	1.3	day^{-1}	Maximal P_3 growth rate
K_{N1}	0.15	$mmol N.m^{-3}$	Half saturation constant of P_1 for nutrient uptake
K_{N2}	0.4	$mmol N.m^{-3}$	Half saturation constant of P_2 for nutrient uptake
K_{N3}	1	$mmol N.m^{-3}$	Half saturation constant of P_3 for nutrient uptake
K_{I1}	25	$W.m^{-2}$	P_1 affinity for light
K_{I2}	5	$W.m^{-2}$	P_2 affinity for light
K_{I3}	1	$W.m^{-2}$	P_3 affinity for light

Table 3

3 phytoplankton ecosystem model: Parameters of the three phytoplankton species P_1 , P_2 , P_3 . All the other parameters are the same as in Table 1

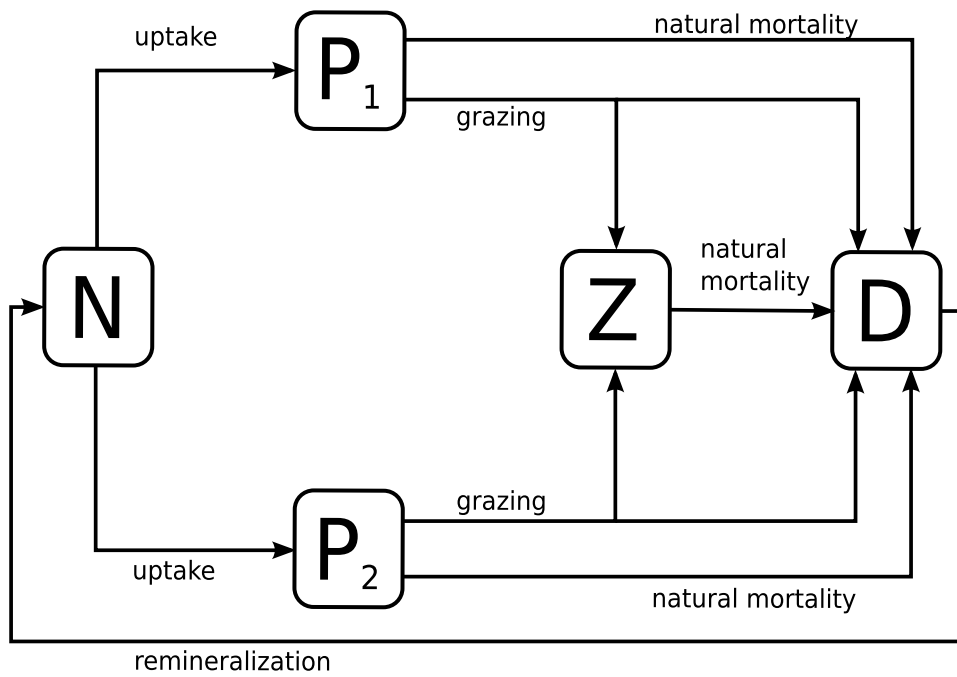


Fig. 1. Structure of the five-component ecosystem model: nitrate (N), small phytoplankton (P_1), large phytoplankton (P_2), zooplankton (Z) and detritus (D).

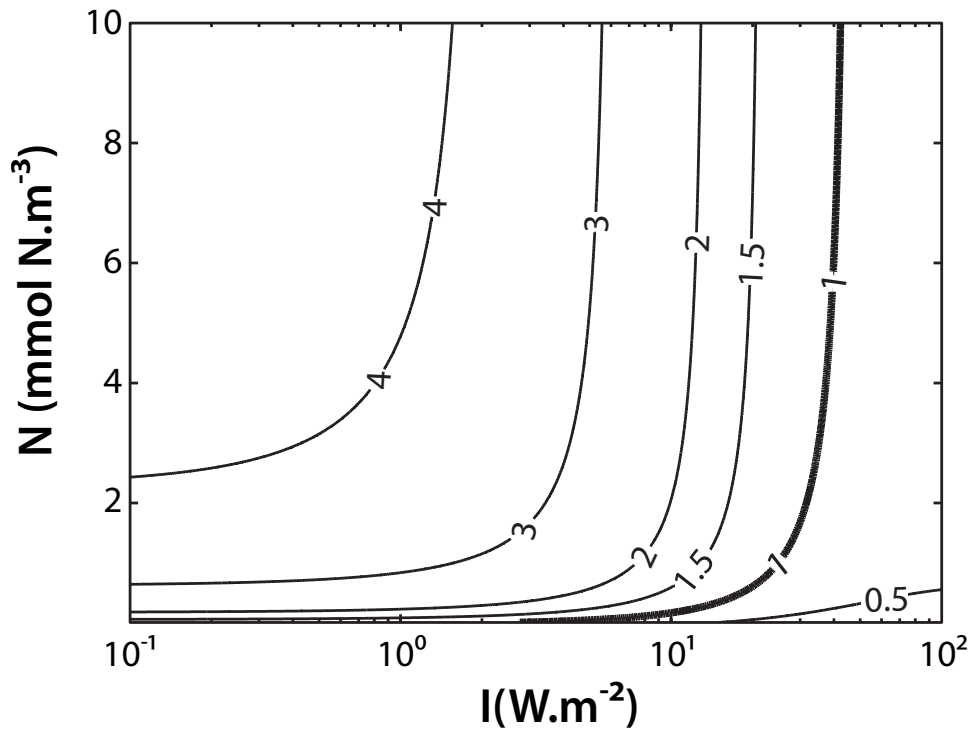


Fig. 2. Ratio between P_2 and P_1 effective growth rates as a function of light (I) and concentration of nutrients (N).

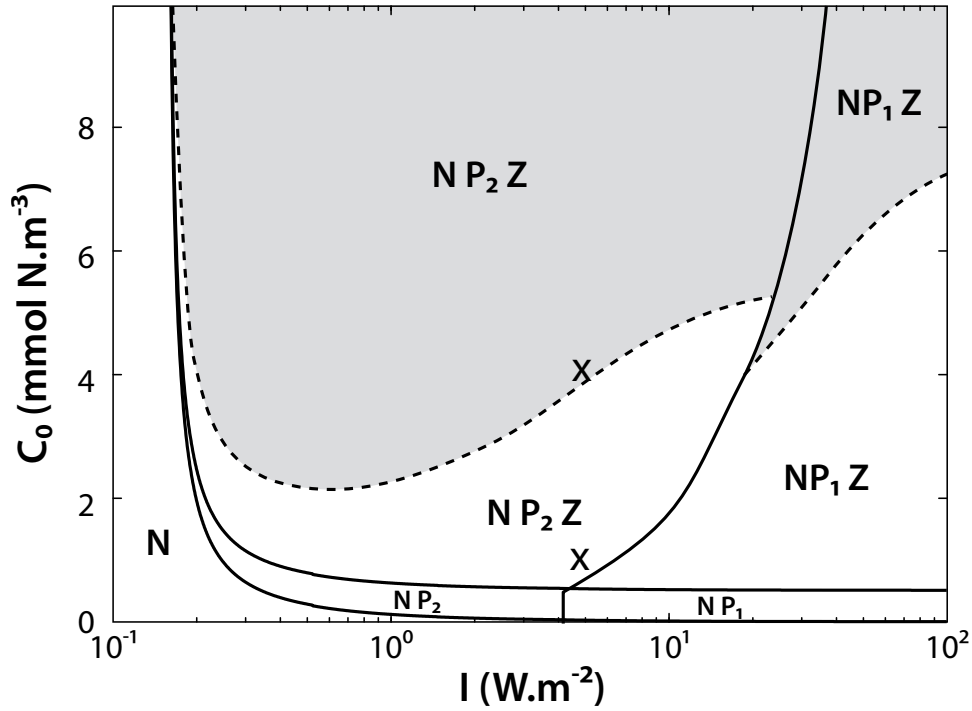


Fig. 3. Bifurcation diagram as a function of light I ($W.m^{-2}$) and total amount of nitrogen matter C_0 ($mmol N.m^{-3}$) for the default biological parameters given in Table 1. Grey areas indicate limit cycle equilibria (other equilibria are fixed points). The two crosses indicate the location of (I, C_0) couples used to explore the sensitivity of the model to other parameters.

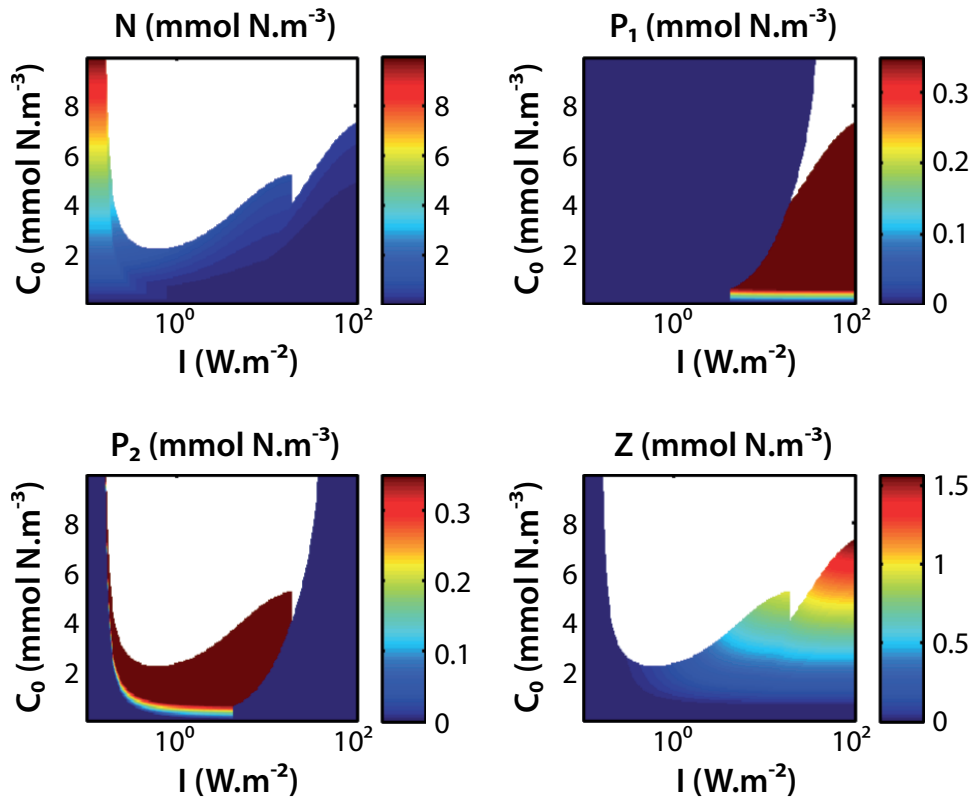


Fig. 4. Equilibrium values of N , P_1 , P_2 and Z as a function of light I and total amount of nitrogen matter C_0 . Biological parameters are default parameters given in Table 1.

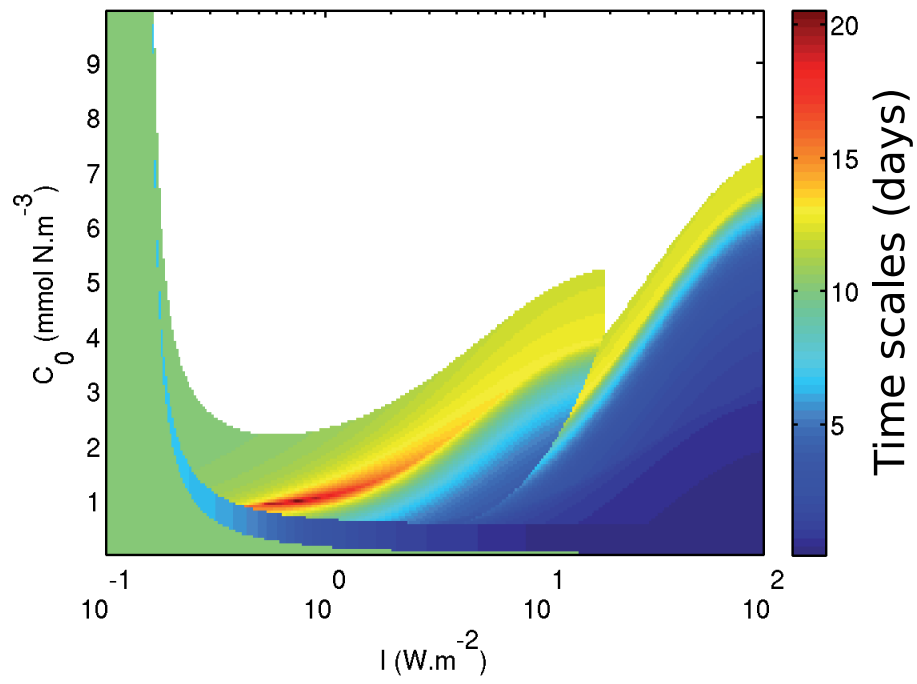


Fig. 5. Time scales (days) of the ecosystem model at fixed points as a function of light I ($W.m^{-2}$) and total amount of nitrogen C_0 ($mmol N.m^{-3}$).

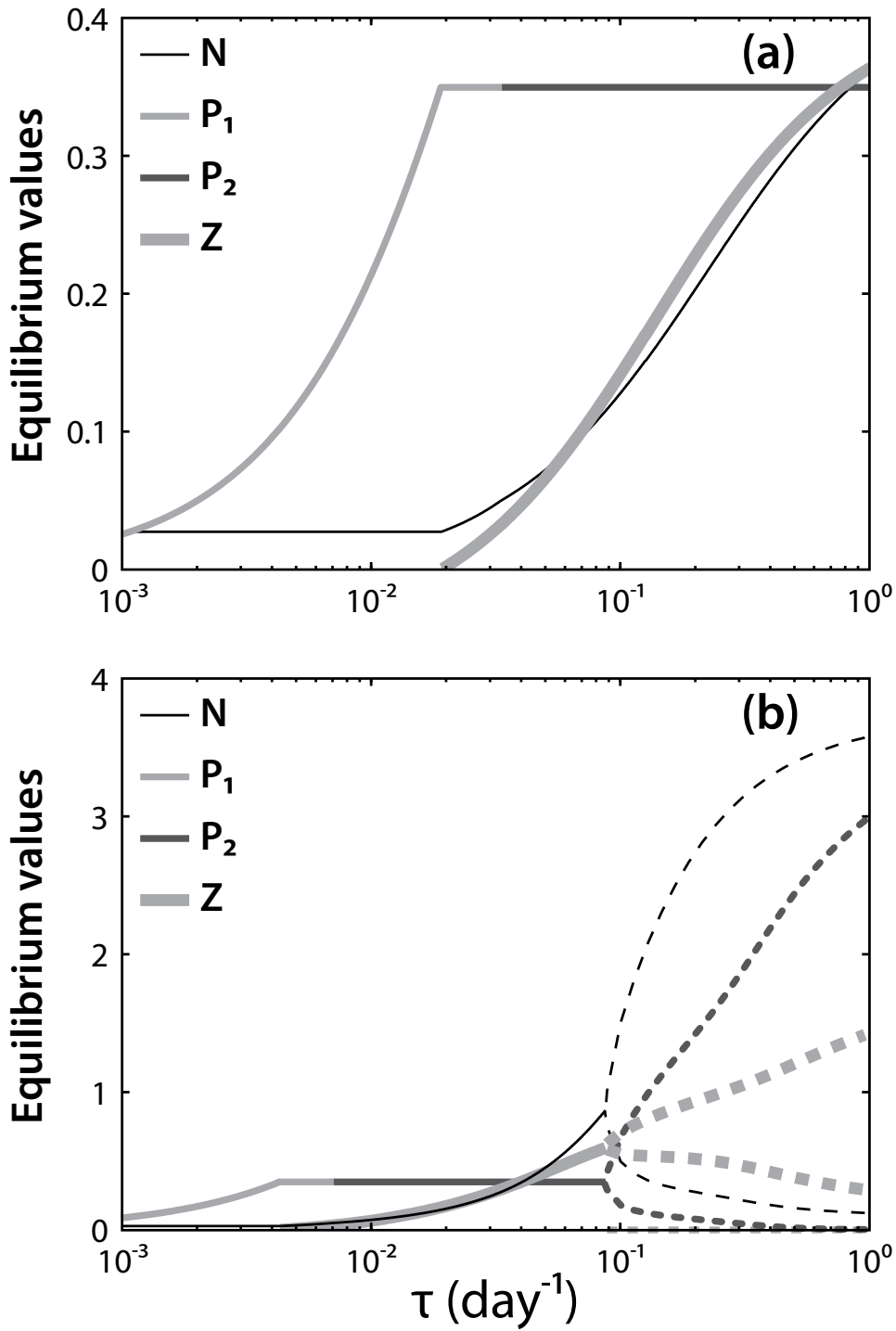


Fig. 6. Equilibrium values (mmol N.m^{-3}) of N , P_1 , P_2 and Z as a function of re-mineralisation parameter τ ; I set to 5 W.m^{-2} and (a) C_0 set to $1.2 \text{ mmol N.m}^{-3}$, (b) C_0 set to 4 mmol N.m^{-3} . The fixed points are represented with solid lines, minimum and maximum values of limit cycles are represented with dashed lines. All the other biological parameters are default parameters given in Table 1.

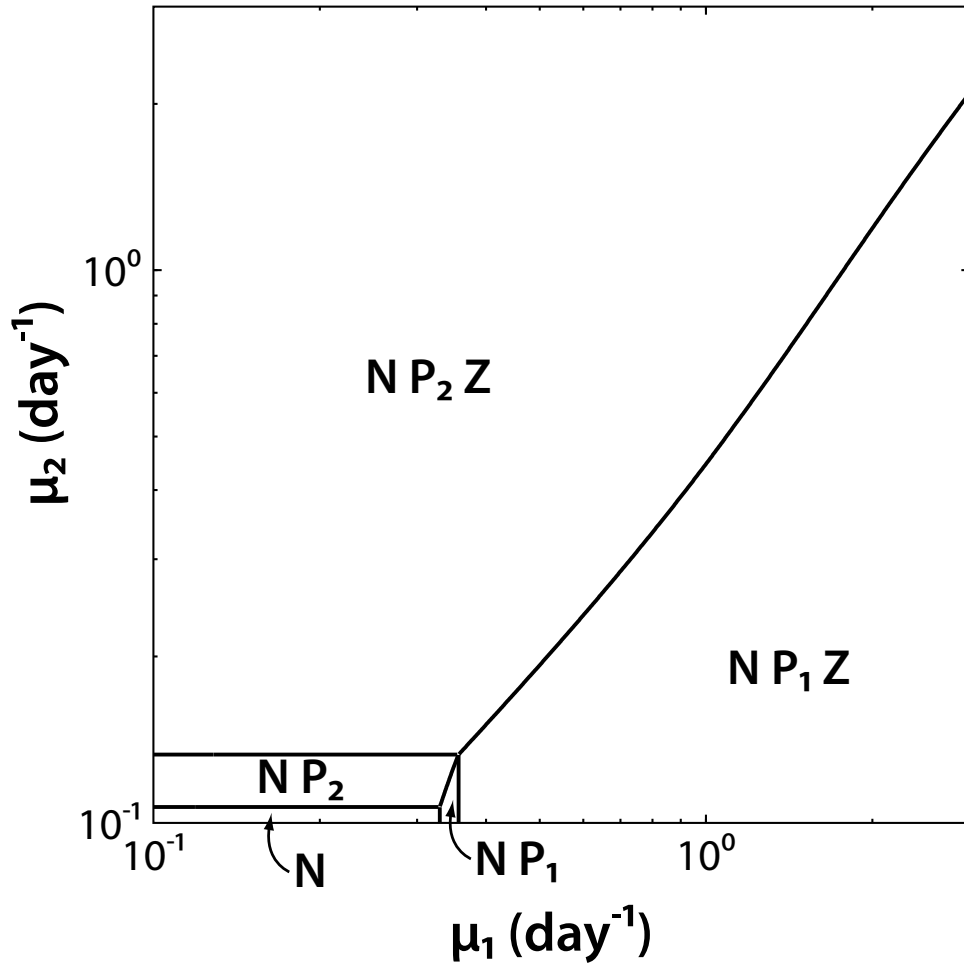


Fig. 7. Bifurcation diagram as a function of phytoplankton growth rates μ_1 and μ_2 ; I set to 5 W.m^{-2} , C_0 set to $1.2 \text{ mmol N.m}^{-3}$. All the other biological parameters are default parameters given in Table 1.

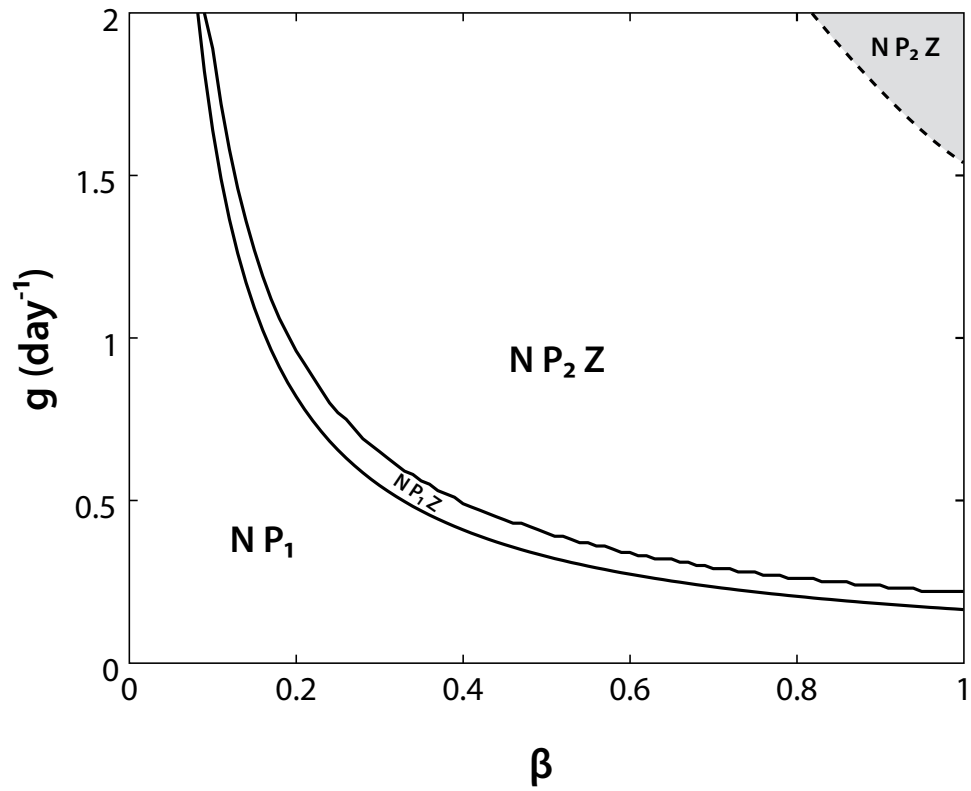


Fig. 8. Bifurcation diagram as function of zooplankton parameters: gross growth efficiency β and maximum ingestion rate g ; I set to 5 W.m^{-2} , C_0 set to $1.2 \text{ mmol N.m}^{-3}$. Grey areas indicate limit cycle equilibrium (other equilibria are fixed points).

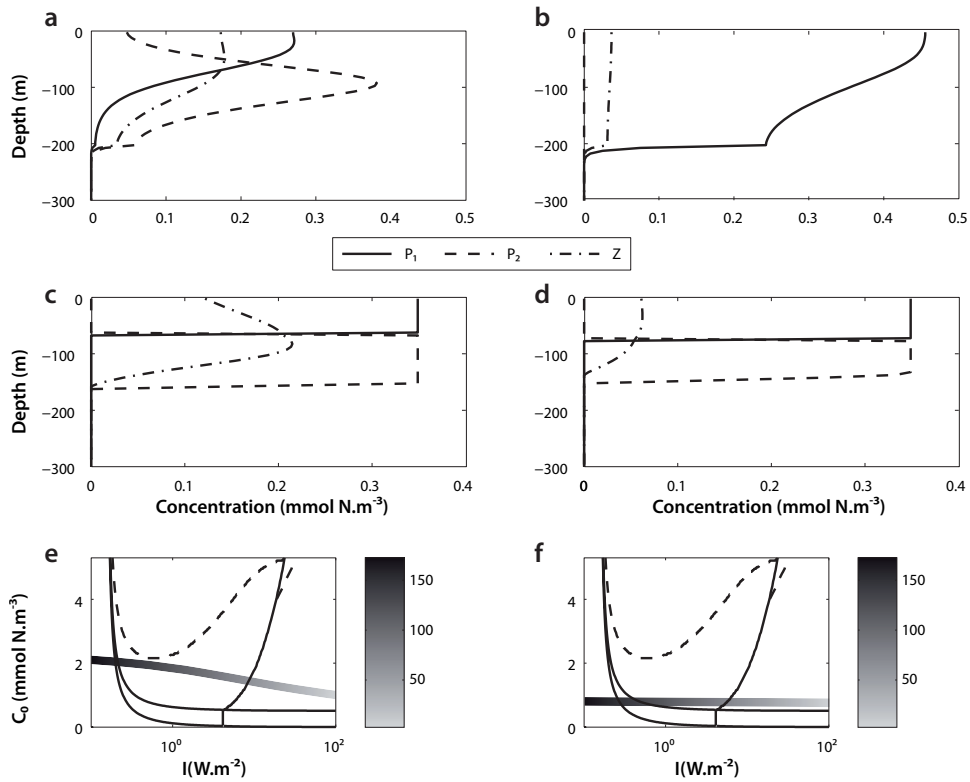


Fig. 9. Top panels: Ecosystem structuring in 1D simulations with a 200 m depth mixed layer. Profiles of P_1 (solid line), P_2 (dashed line) and Z (dashed-dotted line) at equilibrium with diffusivity coefficient in the mixed layer: (a) $K_v = 10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$, (b) $K_v = 10^{-2} \text{ m}^2 \cdot \text{s}^{-1}$. Middle panels: Ecosystem structuring in 0D spatialized simulations. Profiles of P_1 (solid line), P_2 (dashed line) and Z (dashed-dotted line) at equilibrium: (c) C_0 profile same as (a), (d) No mixing and C_0 profile same as (b). Bottom panels: Bifurcation diagram with (I, C_0) couples at each depth: (e) C_0 profile same as (a), (f) C_0 profile same as (b)

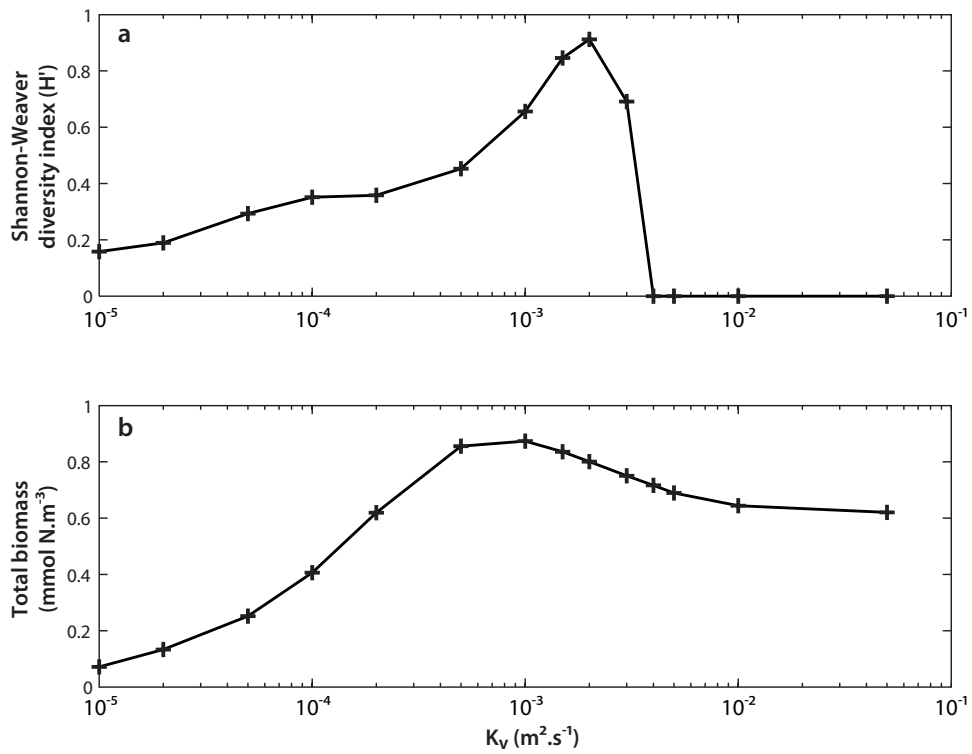


Fig. 10. (a) Vertical mean of Shannon-Weaver Diversity index H as a function of diffusivity coefficient K_v ; Mixed layer depth of 200 m (b) Total biomass ($P_1 + P_2 + Z + D$ in $\text{mmol N} \cdot \text{m}^{-3}$) as a function of diffusivity coefficient K_v

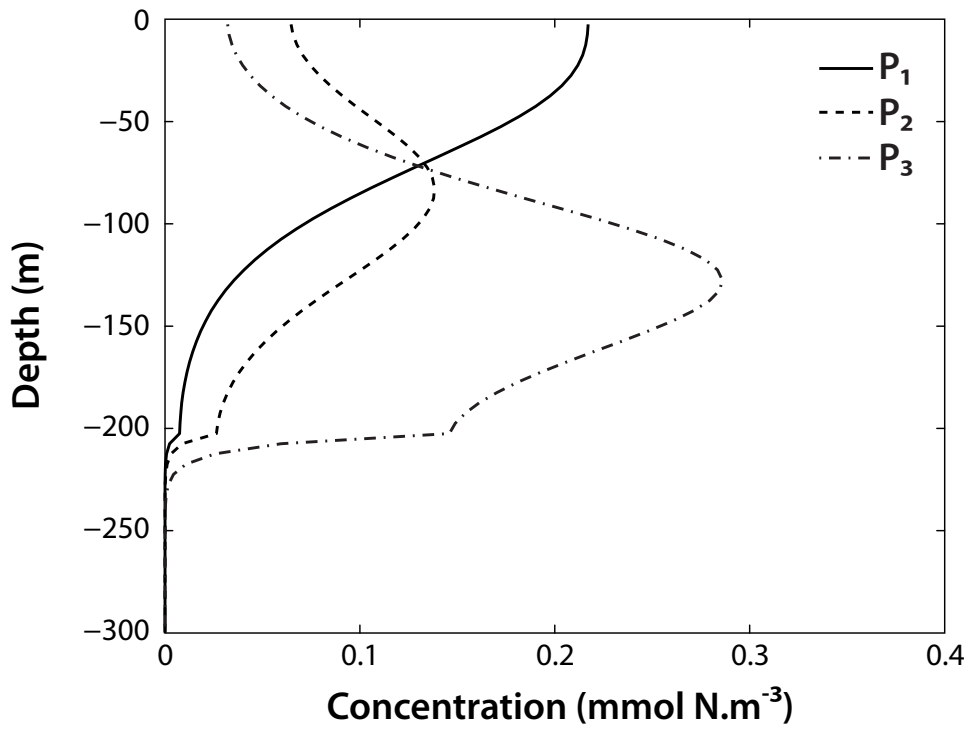


Fig. 11. 1D simulation with 3 phytoplankton species: Vertical profile of P_1 , P_2 and P_3 at equilibrium with a 200 m depth mixed layer and $K_v = 10^{-3} \text{ m}^2 \cdot \text{s}^{-1}$. P_1 (solid line) is better adapted to surface conditions, P_2 (dashed line) to intermediate depths and P_3 (dashed dotted line) to even deeper depths.

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922 Appendix

923 A Calculation of the equilibria

924 It can be easily shown that for such an ecosystem, no trivial equilibrium can
925 be attained if $N = 0$ or $N = P_1 = P_2 = 0$ (in other words phytoplankton
926 needs nutrients to survive and zooplankton needs phytoplankton to survive).
927 A fixed point (defined by $f(X, \nu) = 0$) becomes unstable if any eigenvalue
928 of its Jacobian matrix has a real part which becomes positive as parameters
929 vary. The condition for this change of sign can be translated into a relation
930 between the parameters (here C_0 and I for instance). This relation defines a
931 bifurcation curve between two equilibria. When this change of sign occurs for
932 a single eigenvalue, the new equilibrium is a fixed point and the bifurcation is
933 called transcritical. When it occurs for a pair of complex conjugate eigenvalues,
934 the new attractor is a limit cycle reached via a Hopf bifurcation. When a fixed
935 point is stable, the smallest inverse of the negative real part of its eigenvalues
936 defines the e -folding time T . When the equilibrium is slightly perturbed, T is
937 the time needed for this perturbation to decrease by a factor e in the return to
938 equilibrium. State variables at a fixed point will be referred to with the symbol
939 $'*$.

940 **Fixed point n° 1:** This is the trivial "no life" equilibrium ($N^* = C_0, P_1^* =$
941 $P_2^* = Z^* = 0$) corresponding for instance to the deep ocean or the nutrient
942 depleted surface layer. This fixed point is defined in the whole parameter space
943 but becomes unstable as soon as any phytoplankton species is able to develop.

944 The eigenvalues of the Jacobian matrix at this fixed point are the following:

$$945 \quad \lambda_1 = \alpha_1 \frac{C_0}{K_{N1} + C_0} - m_p$$

$$946 \quad \lambda_2 = \alpha_2 \frac{C_0}{K_{N2} + C_0} - m_p$$

$$947 \quad \lambda_3 = -\tau$$

$$948 \quad \lambda_4 = -\varepsilon$$

949 Among them, the first two (λ_1 and λ_2) are the bifurcation parameters (they
950 are real and can change sign) unlike the last two (λ_3 and λ_4) which are always
951 real negative because of the ecosystem parameter positivity. λ_1 is associated
952 with a bifurcation towards fixed point $N^*P_1^*$ whereas λ_2 is associated with
953 a bifurcation towards fixed point $N^*P_2^*$. Thus these two bifurcation parame-
954 ters are fundamental to understand the competition between phytoplankton
955 species : as soon as λ_1 (respectively λ_2) becomes positive, P_1 (respectively P_2)
956 emerges and excludes P_2 (respectively P_1). As expected, parameters μ_i , K_{Ni} ,
957 and K_{Ii} , which define the phytoplankton competitiveness for light and nutri-
958 ents, constrain the emergence of one or the other phytoplankton. The fixed
959 point destabilizes all the faster as the values of parameters C_0 , I , μ_1 and μ_2
960 are higher or K_{N1} , K_{N2} , K_{I1} , K_{I2} and m_p are lower.

961 Here, depending on the ecosystem parameter values, either $T = 1/\tau$ or $T =$
962 $1/\varepsilon$ or $T > 1/m_p$. Given the permitted values (discussed before), we can say
963 that $T = 1/\tau$ over a large part of the parameter space. With the default pa-
964 rameter values (Table 1), this time scale is $T = 1/\tau = 10$ days. The dynamics
965 of this no-life fixed point is mainly controlled by the remineralisation process,
966 and logically its associated time scale depends on τ except for very high zoo-
967 plankton or phytoplankton mortality rates. Moreover τ only defines the time

968 scale for the system to reach the equilibrium without playing any role in the
 969 bifurcation towards other fixed points, according to bifurcation parameters λ_1
 970 and λ_2 .

971 **Fixed points n° 2 and n° 3:** They consist of $N^*P_1^*$ and $N^*P_2^*$. Because P_1
 972 and P_2 (with their associated parameters) play symmetric roles in equations 6
 973 to 9, results concerning any of these fixed points can be easily deduced from the
 974 other by exchanging subscripts 1 and 2. This is why we only analyse fixed point
 975 n°2 : $N^*P_1^*$ (supposing that P_1 outclasses P_2 , that is to say $\lambda_1 = \alpha_1 \frac{C_0}{K_{N1}+C_0} - m_p$
 976 becomes positive first). In that case the equilibrium point reached by the
 977 dynamical system is the following:

$$978 \quad N^* = \frac{K_{N1}m_p}{\alpha_1 - m_p} \quad (\text{A.1})$$

$$979 \quad P_1^* = \frac{\tau}{m_p + \tau}(C_0 - N^*) \quad (\text{A.2})$$

980 This fixed point exists if and only if $C_0 > \frac{K_{N1}m_p}{\alpha_1 - m_p}$.

981 The Jacobian matrix eigenvalues at this equilibrium are:

$$982 \quad \lambda_5 = g\beta \frac{P_1^*}{K_Z + P_1^*} - \varepsilon,$$

$$983 \quad \lambda_6 = \alpha_2 \frac{N^*}{K_{N2} + N^*} - m_p,$$

$$984 \quad \lambda_7 = -\frac{\tau + A_1}{2} + \sqrt{\left(\frac{\tau + A_1}{2}\right)^2 - A_1(m_p + \tau)},$$

$$985 \quad \lambda_8 = -\frac{\tau + A_1}{2} - \sqrt{\left(\frac{\tau + A_1}{2}\right)^2 - A_1(m_p + \tau)}$$

986 With $A_1 = \alpha_1 \frac{K_{N1}}{(K_{N1} + N^*)^2}$

987 λ_5 and λ_6 are the bifurcation parameters (they are real and are likely to change

988 sign) unlike λ_7 and λ_8 whose real part is always negative. λ_5 is responsible for
 989 the transition to fixed point $N^*P_1^*Z^*$ and λ_6 for the transition to fixed point
 990 $N^*P_2^*$. λ_5 controls the growth of zooplankton whereas λ_6 manages the compe-
 991 tition between phytoplankton species. Contrary to λ_5 , bifurcation parameter
 992 λ_6 is independent of the total amount of nitrogen in the system (C_0). This
 993 means that without zooplankton, only light, and not background nitrogen
 994 concentration, controls competition between phytoplanktons.

995 Let us now study in more detail the sensitivity of these two bifurcation pa-
 996 rameters to parameter values. Concerning bifurcation parameter λ_5 we have:

$$997 \quad \text{sign}(\lambda_5) = \text{sign} \left(\left(\frac{g\beta}{\varepsilon} - 1 \right) \frac{\tau}{m_p + \tau} \left(C_0 - \frac{K_{N1}m_p}{\alpha_1 - m_p} \right) - K_Z \right)$$

998 If $g\beta/\varepsilon < 1$ the fixed point is always stable (λ_5 is always negative) and the
 999 zooplankton is not sufficiently efficient to develop. $g\beta/\varepsilon$ is the ratio between
 1000 the assimilation rate of zooplankton and its mortality rate and thus represents
 1001 the efficiency of the zooplankton species. When $g\beta/\varepsilon > 1$ the fixed point can
 1002 destabilize and then cross the bifurcation towards the $N^*P_1^*Z^*$ fixed point as
 1003 τ , C_0 , I , $g\beta/\varepsilon$ increase or K_{N1} , K_{I1} , K_Z , m_p decrease.

1004 Concerning bifurcation parameter λ_6 we have :

$$1005 \quad \text{sign}(\lambda_6) = \text{sign} \left(\frac{K_{N1}}{\alpha_1 - m_p} - \frac{K_{N2}}{\alpha_2 - m_p} \right)$$

1006 It shows that fixed point $N^*P_1^*$ will tend to destabilize more quickly towards
 1007 $N^*P_2^*$ if parameters K_{N1} , K_{I1} and μ_2 are large and parameters K_{N2} , K_{I2}
 1008 and μ_1 are small. These parameters define the affinity of each phytoplankton
 1009 species for light and nutrients and therefore the phytoplankton competitivene-
 1010 ss according to the surrounding environment (nutrients and light availabil-

1011 ity).

1012 Let us discuss now the time scale T associated to this fixed point. We have $T >$
 1013 $1/\varepsilon$ (according to λ_5) or $T > 1/m_p$ (according to λ_6) or $T < \left(\frac{1}{2}\left(\tau + \frac{(\alpha_2 - m_p)^2}{\alpha_2 K_{N2}}\right)\right)^{-1}$
 1014 (according to λ_8). According to the parameter domain of variation, except for
 1015 very low values of τ , the e -folding time is given by the real part of λ_8 . It can
 1016 be noticed that, in that case, the intrinsic time scale is independent of light.

1017 **Fixed points n° 4 and n° 5:** They correspond to $N^*P_1^*Z^*$ or $N^*P_2^*Z^*$. They
 1018 appear if eigenvalue λ_5 (with the right choice of subscripts 1 and 2) managing
 1019 zooplankton development becomes positive. As in the previous paragraph we
 1020 only analyse fixed point $N^*P_1^*Z^*$. The other one can be deduced easily by
 1021 interchanging subscripts 1 and 2. Values at equilibrium are the following:

$$1022 \quad N^* = -\frac{a - C_0 + b\alpha_1}{2} + \sqrt{\frac{(a - C_0 + b\alpha_1)^2}{4} - (d - K_{N1}C_0)} \quad (\text{A.3})$$

$$1023 \quad P_1^* = \frac{\varepsilon K_Z}{g\beta - \varepsilon} \quad (\text{A.4})$$

$$1024 \quad Z^* = \frac{\beta}{\varepsilon} \left(\alpha_1 \frac{N^*}{K_{N1} + N^*} - m_p \right) P_1^* \quad (\text{A.5})$$

1025 With, $a = K_{N1} + P_1^* \left(1 - \frac{\beta}{\varepsilon} m_p\right)$, $b = P_1^* \left(\frac{\beta}{\varepsilon} + \frac{1}{\tau}\right)$, $d = P_1^* K_{N1} - \frac{\beta}{\varepsilon} m_p K_{N1} P_1^*$

1026 This fixed point is defined when $d - K_{N1}C_0 \leq 0$ (equivalently $C_0 \geq \frac{\varepsilon K}{g\beta - \varepsilon} \left(1 - \frac{\beta}{\varepsilon} m_p\right)$), $\frac{g\beta}{\varepsilon} > 1$ and $N^* \geq \frac{K_{N1}m_p}{\alpha_1 - m_p}$.

1028 The equilibrium value P_1^* only depends on zooplankton parameters: neither
 1029 parameters that define phytoplankton features nor I and C_0 have an influ-
 1030 ence on the equilibrium phytoplankton value. It means that as soon as Z
 1031 develops, it totally controls phytoplankton concentration. The more efficient
 1032 zooplankton is, that is to say the greater $g\beta/\varepsilon$ is, the lower phytoplankton
 1033 concentration is at equilibrium. And whatever the phytoplankton efficiency,

1034 zooplankton is going to balance it by eating more or less phytoplankton. The
 1035 more food zooplankton finds, the more it eats. This is in agreement with the
 1036 results of Edwards and Brindley (1999) with linear zooplankton mortality. An
 1037 important implication is that phytoplankton value at the equilibrium is the
 1038 same whatever species emerges (P_1^* or P_2^*), so that phytoplankton character-
 1039 istics will only affect zooplankton and nutrient concentrations.

1040 Among the four Jacobian matrix eigenvalues related to this equilibrium, one
 1041 can easily be obtained analytically:

$$1042 \quad \lambda_9 = \alpha_2 \frac{N^*}{K_{N2} + N^*} - \alpha_1 \frac{N^*}{K_{N1} + N^*}$$

1043 This bifurcation parameter is always real and changes sign as parameters
 1044 vary. It is clearly related to a bifurcation towards fixed point $N^*P_2^*Z^*$. Thus it
 1045 governs the competition between phytoplanktons in presence of zooplankton,
 1046 that is to say the switch between the two phytoplankton species.

1047 The three other eigenvalues are given by the following third degree equation :
 1048

$$\begin{aligned} &\lambda^3 + \lambda^2 [Z^* (V - W) + U + \tau] \\ &\quad + \lambda [Z^* ((U + \tau) (V - W) + UW + \beta VW P_1) + U (m_p + \tau)] \\ &\quad + Z^* \beta V [(U + \tau) W P_1 + U \tau] = 0 \end{aligned}$$

1049 with

$$1050 \quad U = \frac{K_{N1} \alpha_1 P_1^*}{(K_{N1} + N^*)^2} \quad V = \frac{g K_Z}{(K_z + P_1^*)^2} \quad W = \frac{\varepsilon}{\beta P_1^*}$$

1051 whose solutions via Cardan formulae are too complicated to provide a clear
 1052 interpretation of their analytical form. They are computed numerically from
 1053 these formulae. The sensitivity of these eigenvalues to parameter variations

1054 will be discussed in the following section. We only mention here that for the
1055 default parameter set (Table 1) and all the values of C_0 and I considered
1056 here, one of these eigenvalues is responsible for the transition towards fixed
1057 point $N^*P_1^*$ while the other two are complex conjugates with a real part that
1058 change sign when parameters vary. These last two eigenvalues are thus bifurca-
1059 tion parameters associated with a classical Hopf bifurcation. This bifurcation
1060 is characterized by a transition towards a limit cycle with the ecosystem struc-
1061 ture NP_1Z when the real part of the eigenvalues becomes positive. Identically,
1062 from fixed point n°5, we find the same types of bifurcations, either towards
1063 fixed point n°4, or toward fixed point n°3, or towards an NP_2Z limit cycle.

1064 Such self-sustained oscillations are usual in ecosystem models (Huisman and
1065 Weissing, 1999; Lima et al., 2002b; Edwards and Brindley, 1999; Edwards,
1066 2001). They still raise numerous questions and debates among ecologists about
1067 the existence of such oscillations. But lately, a few publications set forth a dif-
1068 ferent view. First, the deep chlorophyll maximum was shown to commonly
1069 develop oscillations in temperate region (Huisman et al., 2006) whereas they
1070 are usually considered as stable features. This shows that it is possible to find
1071 sustained fluctuations of biogeochemical variables. In addition, McCauley and
1072 Murdoch (1987) observed internally-driven cycles in riparian ecosystems. Evi-
1073 dence of marine phytoplankton oscillations (chaos) was also very recently given
1074 in the context of a long term laboratory mesocosm experiment with constant
1075 external conditions (Benincà et al., 2008). Besides, according to Huisman and
1076 Weissing (1999), such oscillations are a potential solution to the paradox of the
1077 plankton (Hutchinson, 1961). They may allow coexistence between numerous
1078 phytoplankton species with a very limited number of mineral resources. Last,
1079 Koszalka et al. (2007), in a numerical study, showed that oscillations present
1080 in 0D are attenuated or somewhat concealed in Eulerian measurements when

1081 they are subject to turbulent ocean dynamics.

1082

1083 B Segregation of the two phytoplankton species

1084 We now study the question of coexistence of the two phytoplankton species,
1085 that is to say, ecosystem structures n°6 and n°7 in Table 2. The question is:
1086 with such a model, is it possible that the two species stably coexist somewhere
1087 in parameter space? First, let us consider the case of fixed points. If we sup-
1088 pose that a fixed point without zooplankton but with $P_1^* \neq 0$ and $P_2^* \neq 0$
1089 simultaneously exists, then equations 7 and 8 give:

$$1090 \quad \alpha_1 \frac{N^*}{K_{N1} + N^*} - m_p = 0 \quad \text{and} \quad \alpha_2 \frac{N^*}{K_{N2} + N^*} - m_p = 0$$

1091 which is equivalent to:

$$1092 \quad N^* = \frac{K_{N1} m_p}{\alpha_1 - m_p} = \frac{K_{N2} m_p}{\alpha_2 - m_p}$$

1093 This means that without zooplankton, we can not find a fixed point with a
1094 coexistence of P_1 and P_2 except on the curve defined by $\frac{K_{N1}}{\alpha_1 - m_p} - \frac{K_{N2}}{\alpha_2 - m_p} = 0$
1095 which is exactly the bifurcation curve $\lambda_6 = 0$ between equilibria n°2 ($N^* P_1^*$)
1096 and n°3 ($N^* P_2^*$). If we define variables $\bar{P} = P_1 + P_2$ and $P' = P_1 - P_2$, defining
1097 the symmetric and asymmetric parts of the total phytoplankton, it can be
1098 shown that on this bifurcation curve, $\bar{P} = \frac{\tau(C_0 - N^*)}{m_p + \tau}$ whatever the value of P' ,
1099 $|P'| \leq \bar{P}$. Elsewhere each fixed point without zooplankton verifies $P' = \pm \bar{P}$
1100 which means $P_1 = 0$ or $P_2 = 0$.

1101 This is consistent with the competitive exclusion principle (Hutchinson, 1961;
 1102 Passarge and Huisman, 2002) which states that at equilibrium the number of
 1103 coexisting species can not exceed the number of limiting resources. Here, only
 1104 variable N is limiting, thus phytoplankton species can not coexist without a
 1105 predator in the system.

1106 If we suppose now that a fixed point exists with $P_1^* \neq 0$, $P_2^* \neq 0$ and $Z^* \neq 0$,
 1107 then equations 7 and 8 give:

$$1108 \quad \alpha_1 \frac{N^*}{K_{N1} + N^*} - m_p - g \frac{1}{K_Z + \bar{P}^*} Z^* = 0$$

$$1109 \quad \alpha_2 \frac{N^*}{K_{N2} + N^*} - m_p - g \frac{1}{K_Z + \bar{P}^*} Z^* = 0$$

1110 which implies :

$$1111 \quad \alpha_1 \frac{N^*}{K_{N1} + N^*} - \alpha_2 \frac{N^*}{K_{N2} + N^*} = 0$$

1112 This means that at a fixed point in the presence of zooplankton P_1 and P_2
 1113 cannot coexist, except on the bifurcation curve defined by $\lambda_9 = 0$ between the
 1114 fixed points n°4 ($N^*P_1^*Z^*$) and n°5 ($N^*P_2^*Z^*$). It can be shown that on this
 1115 bifurcation curve, $\bar{P} = \frac{K_Z \varepsilon}{g\beta - \varepsilon}$ whatever the value of P' , $|P'| \leq \bar{P}$. Elsewhere
 1116 each fixed point without zooplankton verifies $P' = \pm \bar{P}$ which means $P_1 = 0$
 1117 or $P_2 = 0$.

1118 The second way for phytoplankton species to coexist at equilibrium is to os-
 1119 cillate. Is it possible for our dynamical system to reach a limit cycle with
 1120 N, P_1, P_2 or N, P_1, P_2, Z ? First, the limit cycle without zooplankton (NP_1P_2)
 1121 may appear either from a fixed point or another limit cycle. The first case
 1122 which comes immediately to mind is a bifurcation from fixed point NP_1P_2 to
 1123 the corresponding limit cycle. As this fixed point does not exist, this transi-

1124 tion is not possible. The second case is a bifurcation from fixed points $N^*P_i^*$
1125 or $N^*P_i^*Z^*$ to the limit cycle, with $i = 1$ or 2 . It is not possible because no
1126 eigenvalues of the Jacobian matrix has been found before for such a bifurca-
1127 tion. And the last case would be a transition of the system towards another
1128 limit cycle than that considered. This would require a projection of the system
1129 on a Poincaré map with determination of the eigenvalues in this new basis.
1130 But the calculation is too complex to be solved analytically. Such a transi-
1131 tion is, however, unlikely, since in no part of the parameter explored (beyond
1132 that presented here) did we find a limit cycle with co-existence of P_1 and P_2 .
1133 The same reasoning can be conducted for the limit cycle with zooplankton
1134 (NP_1P_2Z) to attain the same conclusions.