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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 **1** Introduction

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

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

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

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

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

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

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

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

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

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

¹⁰² The non-linear model equations are :

1

10

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

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

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

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

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

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

Definitions and values of the parameters are given in Table 1. The sum of 109 these equations is null so the total amount of nitrogen, C_0 , is conserved : 110 $N + P_1 + P_2 + Z + D = C_0$. We chose a closed system and not a chemostat 111 because it is aimed at being embedded in a vertical model with nutrient fluxes 112 due to physics. In addition, it is more easily studied analytically. Each term 113 of these equations is a flux between two variables and is represented by an 114 arrow in Fig. 1. Phytoplankton growth is controlled by light (I) and nutrient 115 concentration (N) in the tank. The growth rate consists in 3 factors: $\mu_i,$ the 116 maximum growth rate (unit: day^{-1}), the Michaelis-Menten function that pa-117 rameterizes the nutrient limitation (dimensionless values comprised between 118 0 and 1) and the light limitation (dimensionless values comprised between 0119 and 1). This growth rate is multiplied by the phytoplankton concentration to 120 obtain the term of nutrient uptake in the phytoplankton equations 2 and 3. 121 The terms responsible for the decline of phytoplankton in equations 2 and 3 122 are respectively natural mortality and grazing. The formulation for the two 123 phytoplankton species is the same, P_1 and P_2 are only differentiated by their 124

maximal growth rate (μ_i) , their affinity for either nutrients (K_{Ni}) or light (K_{Ii}) .

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

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

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

Ranges for ingestion rates and half saturation constants for ingestion were 159 calculated according to Moloney and Field (1991), g varies from 6.30 day^{-1} 160 to 0.35 day^{-1} for predator size ranging from 10⁴ to 10⁹ pg C, and K_Z varies 161 from 0.46 to 3.56 mmol $N.m^{-3}$ for prey size ranging from 10^{-2} to $10^9 pg C$. 162 For β , the gross growth efficiency, Straile (1997) has shown that it is not that 163 different between protists and copepods with a global average of about 20-164 30 %. Mortality rates also scale with size across a large size spectrum from 165 protists to whales (McGurk, 1986). For microzooplankton or young stages 166 of copepods, Kiørboe (1997) found that mortality rates range from 0.02 to 167 $0.5 \ day^{-1}$, with most values $< 0.2 \ day^{-1}$. For adult copepods, average daily 168 mortality rates (ε) are around ~0.1 day⁻¹ (Hirst and Kiørboe, 2002). 169

The detritus concentration in equation 5 increases with the non-assimilated part of grazing along with the dead organisms. It decreases through remineralisation which transforms detritus into nutrients. Finally, the tank of nutrients in equation 1 is fed by detritus remineralisation and is emptied by phytoplankton uptake. Specific degradation of organic matter ranges from 0.003 day^{-1} to 0.44 day^{-1} at temperature ranging from 5 to 26°C (Newell et al., 1981; 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).

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

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

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

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

210 3 Intrinsic Ecosystem dynamics

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

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

216

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

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

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

This model is a general dynamical system : $\frac{dX}{dt} = f(X, \nu)$ where $X = (N, P_1, P_2, Z)$ 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 the state variable vector and the parameter vector. All components of X and ν are positive. Among the parameters of this model, I and C_0 can be classified apart. Indeed, C_0 and I vary artificially in this ecosystem model but vary in space and time in reality. Thus a detailed study of the state vector variations with C_0 and Iin 0D is essential to better explain the 3D observations from the sea surface where light is intense to the subsurface where nutrients are abundant.

Now we will first characterize the equilibria of this model and their stability, and then a sensitivity study of the ecosystem model dynamics will be conducted to extract the role of key parameters.

231 3.1 Equilibrium solutions and their stability

The purpose is to characterize analytically the equilibria and their stability 232 for this dynamical system in the whole parameter space defined by ν . In other 233 words, we are looking for the asymptotic behaviour of the system as $t \to \infty$. 234 The ecosystem structures corresponding to equilibria of the system are listed 235 in Table 2. Two types of equilibrium can be reached by the system : steady 236 equilibria (fixed points) and oscillatory regimes (limit cycles). In our case, 237 there are five possible fixed points with different ecosystem structures and 238 two possible limit cycles (see Table 2). Ecosystems n° 6 and n° 7, which in-230 volve phytoplankton coexistence, can not be achieved in such a model. All the 240 analytical determination of the domain of validity of fixed points, bifurcation 241 curves and intrinsic time scales are detailed in Appendix A. The question of 242 phytoplankton coexistence or segregation is dealt with, in Appendix B. 243

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

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

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

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

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

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

With the analytical study, time scales associated with each fixed point can be calculated as a function of light and amount of nutrients (Fig. 5). As expected, there are some differences between time scales associated with conditions of surface and of subsurface. At high light - low nutrient conditions often en²⁹⁸ 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).

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

$_{308}$ 3.3 Influence of biological parameters on the (I, C_0) equilibrium solutions

After studying the influence of external parameters (I, C_0) on ecosystem structuring, we investigate in the sensitivity of the system to biological parameters.

311 3.3.1 Sensitivity to the re-mineralisation rate τ

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

Let us consider the effects of varying re-mineralisation parameter τ from 10^{-3} to 1 day⁻¹, for a fixed light intensity of $I = 5 W.m^{-2}$ but two different total nitrogen concentrations : $C_0 = 1.2 \text{ mmol } N.m^{-3}$ and $C_0 = 4 \text{ mmol } N.m^{-3}$ ³²⁰ (Fig. 6).

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

Fig. 6b shows the case in which C_0 is increased to 4 mmol Nm⁻³. For the 338 default τ value (Fig. 3) the equilibrium was a limit cycle between N, P₂ and 339 Z. As τ is increased from this default value, this equilibrium remains stable 340 but the amplitude of oscillations increases. Inversely as τ is decreased the 341 periodic orbit collapses and the system reaches an $N^*P_2^*Z^*$ fixed point. Then 342 as τ decreases we observe two more bifurcations similar to the ones observed 343 in Fig. 6a with first a shift from P_2 to P_1 and then disappearance of Z giving 344 an $N^*P_1^*$ fixed point for very low values of τ . 345

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

358 3.3.2 Sensitivity to growth rates μ_1 and μ_2

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

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

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

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

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

and $N^*P_1^*Z^* \leftrightarrow N^*P_2^*Z^*$, and also of the Hopf bifurcation curves. The parameters g and β have therefore mainly an influence on the temporal behaviour of the system at equilibrium. Like the re-mineralisation parameter, they can influence phytoplankton competition mainly for medium light values (corresponding 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

Knowing the intrinsic ecosystem model dynamics, its associated time scales 402 and its sensitivity to parameters, we can now investigate the combined effect 403 of diffusion and sedimentation processes on ecosystem structuring and more 404 precisely on phytoplankton competition. For this purpose, we take exactly the 405 same ecosystem model with the default parameter set presented in Table 1 and 406 embed it into a simple physical model in which we define a profile of light, a 407 profile of vertical diffusivity (Edwards et al., 2000) and a sedimentation speed 408 on detritus. The important thing to notice is that light profile, diffusivity 409 profile and sedimentation are constant in time. The purpose is to study the 410 behaviour of the 1D model at equilibrium and to free ourselves of all temporal 411 forcing. If sedimentation and diffusion are turned off, we have at each depth 412 a OD ecosystem model running independently and following the behaviour 413 described on Fig. 3 (called hereafter 'OD spatialized model'). If they are turned 414 on, we have a 1D model with a vertical coupling of the different 0D simulations 415 by physical dynamics. 416

The diffusivity coefficient K_v is vertically homogeneous in a surface layer (from 10⁻⁵ up to 10⁻¹ $m^2 . s^{-1}$) representing an idealized mixed layer of depth varying between 50 to 200 m. It is equal to a classical background value below the 420 mixed layer $(K_v = 10^{-5} m^2 . s^{-1}).$

We chose to study the combined effect of diffusion and sedimentation and 421 not the two processes separately to have a more realistic vertical water col-422 umn. Without diffusion, the subsistence of an ecosystem at equilibrium is not 423 possible, because all the organic matter would be gradually drained out from 424 the euphotic layer. Furthermore, Hodges and Rudnick (2004) showed that the 425 subsurface chlorophyll maximum is conditioned by the sedimentation rate on 426 a biological compartment. Without sedimentation, organic matter gathers at 427 surface. We chose a default sedimentation speed of 1 $m.day^{-1}$ so that 90 % of 428 the organic matter is remineralised between 0 and 100 m in average. This is 420 consistent with export ratio found at the base of the euphotic zone in various 430 regions of the ocean (Schlitzer, 2000). 431

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

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

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

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

whereas the strong K_v (Fig. 9b) induces the competitive exclusion of P_2 . To analyse the mechanisms that lead to these results, we study the fluxes of biological variables as a function of time (not shown). The fluxes are integrated over a surface layer corresponding to the layer of P_1 dominance in 0D spatialized simulation, and over a subsurface layer where P_2 dominates in 0D.

They reveal that strong K_v induces quick nutrient injections into the mixed 478 layer but P_2 growth is too slow to consume enough of them. Therefore these 479 nutrients benefit P_1 which grows rapidly near the surface; P_1 growth is fol-480 lowed by that of Z. P_1 and Z propagate then downwards via diffusion; they 481 enter the layer suitable for P_2 and weaken it. Furthermore, since P_1 uses all 482 the nutrients in surface layer, the gradient in nutrients in the mixed layer is 483 maintained and nutrients keep being diffused to the surface layer. This has 484 again a negative feedback on P_2 which is more nutrient-limited and a positive 485 one on P_1 which keeps developing and spreading downwards. 486

For weak K_v , on the contrary, P_2 is sufficiently rapid to consume a great part 487 of the nutrients injected into the mixed layer. This limits the growth of P_1 and 488 allows the coexistence of the two phytoplankton species in the whole mixed 489 layer with a dominance of each of them in its prefered layer. Moreover, the in-490 tegrated fluxes at equilibrium reveal that growth rate of P_2 (respectively P_1) is 491 less than its loss rate in surface layer (respectively in subsurface layer). Indeed, 492 the diffusive flux maintains P_2 in surface layer (respectively P_1 in subsurface 493 layer). Thus, mixing allows a non-zero concentration of P_2 in the surface layer 494 (respectively P_1 in the subsurface layer) where these phytoplanktons can not 495 sustain their own population. In other words, there is a 'source' population 496 which spreads phytoplankton in a hostile habitat. We have therefore coexis-497 tence between the two species despite mixing, that is to say even if mixing 498 tends to create an isotropic environment without ecological niches that shel-499

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

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

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

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

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

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

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

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

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

In this study we considered a model with an intermediate level of complexity to 586 address the question of phytoplankton competition: two phytoplankton species 587 competing for one nutrient and light. Without external forcing (0D model), 588 light is a fixed parameter. There are more phytoplankton species than lim-580 iting resources. As a consequence, we observe a competitive exclusion of one 590 phytoplankton whatever the parameters in accordance with the competitive 591 exclusion principle (Hardin, 1960). In the 1D model things are less simple: the 592 fixed vertical gradient of light combined with the physical forcing induced by 593 vertical mixing may be thought as an "active" limiting factor. Therefore we 594 should expect a possible coexistence of the two phytoplankton species on the 595 two limiting factors. This is why we have also tested a three-phytoplankton 596 species model competing for the same two resources (light and nutrient) to 597 see if vertical mixing is always able to make these three phytoplankton species 598 coexist. The results are shown on Fig. 11. The ecosystem model used here is 590 very similar to the one previously studied but now with three phytoplankton 600 species: one better adapted to surface conditions, a second better adapted to 601 intermediate depths, and the third better adapted to even deeper depths. Pa-602

rameters of the three phytoplankton are indicated in Table 3. As expected, 603 the 0D model predicts a competitive exclusion of two phytoplankton species 604 at each point of the parameter space. But Fig. 11 reveals a coexistence of the 605 three phytoplankton species together over the mixed layer which confirms our 606 preceding results : the effect of vertical mixing is able to maintain a greater 607 number of phytoplankton species than the number of limiting resources. There-608 fore, this one-dimensional process is another potential answer to the 'paradox 600 of plankton' in the sense that it is able to prevent the competitive exclusion 610 of one or more phytoplankton species at equilibrium. 611

This two or three species coexistence at equilibrium can be explained by the 612 coupling between mixing and biological dynamics. Let us describe the differ-613 ent time scales inherent in the system and then discuss the possible influence 614 of turbulent vertical injections of nutrients in the mixed layer. The ecosys-615 tem time scales determined in the analytical study (Fig. 5) were 1-5 days 616 in surface layer, and 10-20 days in subsurface. The ecosystem could also un-617 dergo self-sustained oscillations with periods of about 50 days. Concerning 618 one-dimensional dynamics, a diffusivity coefficient of 10^{-4} to $10^{-2} m^2 s^{-1}$ cor-610 responds to time scales of around 100 to 1 days respectively if we consider a 620 vertical length scale of 25 m corresponding to the scale of the nutrient gradient. 621 These similar time scales show that, in the mixed layer, diffusion may interact 622 with ecosystem dynamics and couple the ecosystems at different depths. This 623 explains the strong sensitivity of the ecosystem structuring to the diffusivity 624 value revealed by 1D simulations. 625

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

first one corresponds for instance to wind-induced gyres with horizontal scales 620 of a few thousand kilometers and with vertical time scales of the order of 100-630 1000 days (around 300 days according to Flierl and McGillicuddy, 2002). The 631 second one corresponds to phenomena like eddies or meanders, characterized 632 by length scale of about 100 km and time scales of 10-100 days (Klein and 633 Lapeyre, 2009). The last class results from the interaction between mesoscale 634 structures which forms filaments characterized by strong gradients on scales of 635 10 km. The time scale of nutrient injections in these filaments is about 1 day 636 (Klein and Lapevre, 2009). The comparison of these time scales with biolog-637 ical ones indicates how efficient the coupling between physical and biological 638 dynamics can be. 639

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

predominance of pico- and nano- phytoplankton in oligotrophic areas of theLevantine basin (eastern Mediterranean).

Deeper in the ocean, conclusions seem to be less simple. Physics and biology 658 evolve approximately at the same rate. Our ecosystem model, at equilibrium, 650 predicts either a fixed point with an associated time scale of 10-20 days or 660 self-sustained oscillations with a 50-day period. But ocean dynamics might 661 disguise these potential oscillations (Koszalka et al., 2007). It might account 662 for the very few observations of fluctuations of the deep chlorophyll maximum. 663 Only Huisman et al. (2006) reported such sustained oscillations in oligotrophic 664 waters of subtropical Pacific Ocean and ascribed it to intrinsic ecosystem 665 dynamics (and not to seasonal forcing). 666

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

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

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

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

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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
Phytoplanktons			
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
Zooplankton			
g	1.5	day^{-1}	Maximum ingestion rate
Kz	1.4	$mmol \ N.m^{-3}$	Half saturation constant for ingestion
eta	0.2		Gross Growth Efficiency for P_1 and P_2
ε	0.06	day^{-1}	Mortality rate
Detritus			
τ	0.1	day^{-1}	Specific remineralisation rate
Table 1 Econystom model -	aramata	na	
cosystem 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 ${\cal P}_1$
				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 ${\cal P}_3$
				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
Tabl	e 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 equilibrium (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 $1.2 \ mmol \ N.m^{-3}$, (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 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 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) $K_v = 10^{-3} m^2 . s^{-1}$, (b) $K_v = 10^{-2} m^2 . s^{-1}$. 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 (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 $mmol \ N.m^{-3})$ 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 $K_v = 10^{-3} m^2 . s^{-1}$. 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

It can be easily shown that for such an ecosystem, no trivial equilibrium can 924 be attained if N = 0 or $N = P_1 = P_2 = 0$ (in other words phytoplankton 925 needs nutrients to survive and zooplankton needs phytoplankton to survive). 926 A fixed point (defined by $f(X, \nu) = 0$) becomes unstable if any eigenvalue 927 of its Jacobian matrix has a real part which becomes positive as parameters 928 vary. The condition for this change of sign can be translated into a relation 929 between the parameters (here C_0 and I for instance). This relation defines a 930 bifurcation curve between two equilibria. When this change of sign occurs for 931 a single eigenvalue, the new equilibrium is a fixed point and the bifurcation is 932 called transcritical. When it occurs for a pair of complex conjugate eigenvalues, 933 the new attractor is a limit cycle reached via a Hopf bifurcation. When a fixed 934 point is stable, the smallest inverse of the negative real part of its eigenvalues 935 defines the *e*-folding time T. When the equilibrium is slightly perturbed, T is 936 the time needed for this perturbation to decrease by a factor e in the return to 937 equilibrium. State variables at a fixed point will be referred to with the symbol 938 ;*; . 939

Fixed point $n^{\circ}1$: This is the trivial "no life" equilibrium $(N^* = C_0, P_1^* = P_2^* = Z^* = 0)$ corresponding for instance to the deep ocean or the nutrient depleted surface layer. This fixed point is defined in the whole parameter space 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

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

 \cap

946

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

947 $\lambda_3=- au$

948 $\lambda_4 = -\varepsilon$

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

Here, depending on the ecosystem parameter values, either $T = 1/\tau$ or $T = 1/\varepsilon$ or $T > 1/m_p$. Given the permitted values (discussed before), we can say that $T = 1/\tau$ over a large part of the parameter space. With the default parameter values (Table 1), this time scale is $T = 1/\tau = 10$ days. The dynamics of this no-life fixed point is mainly controlled by the remineralisation process, and logically its associated time scale depends on τ except for very high zooplankton or phytoplankton mortality rates. Moreover τ only defines the time scale for the system to reach the equilibrium without playing any role in the bifurcation towards other fixed points, according to bifurcation parameters λ_1 and λ_2 .

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

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

979

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

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:

 ε ,

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

983

$$\lambda_6 = \alpha_2 \frac{1}{K_{N2} + N^*} - m_p,$$

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

 N^*

984

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

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

 $_{987}$ $~\lambda_5$ and λ_6 are the bifurcation parameters (they are real and are likely to change

sign) unlike λ_7 and λ_8 whose real part is always negative. λ_5 is responsible for the transition to fixed point $N^*P_1^*Z^*$ and λ_6 for the transition to fixed point $N^*P_2^*$. λ_5 controls the growth of zooplankton whereas λ_6 manages the competition between phytoplankton species. Contrary to λ_5 , bifurcation parameter λ_6 is independent of the total amount of nitrogen in the system (C_0). This means that without zooplankton, only light, and not background nitrogen 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
$$sign(\lambda_5) = sign\left(\left(\frac{g\beta}{\varepsilon} - 1\right)\frac{\tau}{m_p + \tau}\left(C_0 - \frac{K_{N1}m_p}{\alpha_1 - m_p}\right) - K_Z\right)$$

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

1004 Concerning bifurcation parameter λ_6 we have :

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

It shows that fixed point $N^*P_1^*$ will tend to destabilize more quickly towards $N^*P_2^*$ if parameters K_{N1}, K_{I1} and μ_2 are large and parameters K_{N2}, K_{I2} and μ_1 are small. These parameters define the affinity of each phytoplankton species for light and nutrients and therefore the phytoplankton competitiviveness according to the surrounding environment (nutrients and light availabil1011 ity).

1023

1024

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

¹⁰¹⁷ *Fixed points* $n^{\circ}4$ and $n^{\circ}5$: 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
$$N^* = -\frac{a - C_0 + b\alpha_1}{2} + \sqrt{\frac{(a - C_0 + b\alpha_1)^2}{4} - (d - K_{N1}C_0)}$$
(A.3)

$$P_1^* = \frac{\varepsilon K_Z}{g\beta - \varepsilon} \tag{A.4}$$

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

With, $a = K_{N1} + P_1^* \left(1 - \frac{\beta}{\varepsilon} m_p\right)$, $b = P_1^* \left(\frac{\beta}{\varepsilon} + \frac{1}{\tau}\right)$, $d = P_1^* K_{N1} - \frac{\beta}{\varepsilon} m_p K_{N1} P_1^*$ This fixed point is defined when $d = K_{N1} C_0 \le 0$ (equivalently $C_0 \ge \frac{\varepsilon K}{\varepsilon} (1 - \frac{\varepsilon K}{\varepsilon})$

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

The equilibrium value P_1^* only depends on zooplankton parameters: neither parameters that define phytoplankton features nor I and C_0 have an influence on the equilibrium phytoplankton value. It means that as soon as Zdevelops, it totally controls phytoplankton concentration. The more efficient zooplankton is, that is to say the greater $g\beta/\varepsilon$ is, the lower phytoplankton 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
$$\lambda_9 = \alpha_2 \frac{N^*}{K_{N2} + N^*} - \alpha_1 \frac{N^*}{K_{N1} + N^*}$$

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

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

$$\lambda^{3} + \lambda^{2} [Z^{*} (V - W) + U + \tau] + \lambda [Z^{*} ((U + \tau) (V - W) + UW + \beta VWP_{1}) + U (m_{p} + \tau)] + Z^{*}\beta V [(U + \tau) WP_{1} + U\tau] = 0$$

1049 with

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

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

will be discussed in the following section. We only mention here that for the 1054 default parameter set (Table 1) and all the values of C_0 and I considered 1055 here, one of these eigenvalues is responsible for the transition towards fixed 1056 point $N^*P_1^*$ while the other two are complex conjugates with a real part that 105 change sign when parameters vary. These last two eigenvalues are thus bifurca-1058 tion parameters associated with a classical Hopf bifurcation. This bifurcation 1059 is characterized by a transition towards a limit cycle with the ecosystem struc-1060 ture NP_1Z when the real part of the eigenvalues becomes positive. Identically, 1061 from fixed point $n^{\circ}5$, we find the same types of bifurcations, either towards 1062 fixed point n°4, or toward fixed point n°3, or towards an NP_2Z limit cycle. 1063

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

¹⁰⁸¹ they are subject to turbulent ocean dynamics.

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¹⁰⁸³ B Segregation of the two phytoplankton species

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

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

¹⁰⁹¹ which is equivalent to:

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

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

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

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

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

1109

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

1110 which implies :

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

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

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

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