

# Working document

March 10, 2020

Preliminary idea: How can the terrestrial plant literature on seed bank be applied to phytoplankton coexistence?

## Introduction

The high biodiversity of plant communities is still an unresolved question for both experimental and theoretical ecologists. Both terrestrial plants and phytoplanktonic communities can present hundreds of species which seem to consume the same resources. Earlier theoreticians have proposed that environmental fluctuations only [ref] could sustain coexistence but further research showed that this could not explain the order of magnitude of species richness [ref]. Other mechanisms such as niche differentiation [ref], demography [ref] and life history traits [ref] have completed environmental variation and stochasticity as other explanations.

Analyses of coexistence in terrestrial plant communities often take into account several life stages [refs]. Considering at least two stages, seeds/juveniles and adults, different models have uncovered mechanisms that might explain long-term coexistence. Examples of such mechanisms are the bet-hedging strategy, the storage effect and the Janzen-Connell effect. Bet-hedging is a long-term strategy relying on the creation of seeds which can remain dormant for a long period of time (over a year, often much longer). Dormant seeds can tolerate harsher years during which adults cannot maintain, but they also reduce part of the population that could germinate from one year to another (in case of an annual plant). The storage effect has first been defined by the presence of a long-lived life stage and temporal variation in recruitment from this long-lived life stage that helps escape interspecific competition (Chesson, 1986; Cáceres, 1997). This has been later generalized as a negative correlation between the effect of the environment and the effect of competition (Ellner *et al.*, 2016). In good environmental conditions, competition from other individuals is stronger as seeds might germinate at the same time. Finally, models and experiments suggest that adults can have a negative effect on seed survival, through the Janzen-Connell effect (Comita *et al.*, 2014). Therefore, neglecting explicit modeling of this life stage can modify the understanding we have of the dynamics of the populations (Nguyen *et al.*, 2019).

Even though different coexistence mechanisms have been unveiled through the use of several life stages and a focus on the youngest stage (seeds) for terrestrial plants, aquatic plants, and more specifically phytoplanktonic algae, have not been modeled with the same precision. Although ecologists have proposed for a long time that the blooms may initiate after the resuspension and germination of seeds (Patrick, 1948; Marcus & Boero, 1998), it is unusual to see an explicit model of such process. The classical view behind phytoplankton dynamics is that bloom formation is mostly seasonal, due to the variation in light and temperature, assuming that there are always enough cells in the environment to duplicate. However, a recent review suggests that there might be more complexity behind phytoplanktonic seeds/cysts (Ellegaard & Ribeiro, 2018).

Phytoplankton communities in coastal environments may benefit from seed banks even more than the oceanic communities [REF-find back], as the distance to the bottom is lower. Similarly to the seed bank approach, Smayda (2002) has proposed the term “pelagic seed bank” to characterize the contribution of the ocean to coastal communities. This has been noticed for dinoflagellate especially [[ref Dinophysis, check what we have on diatoms]]. We can

wonder, however, to which extent the seed banks can contribute to the biodiversity in the ocean, especially in the long term. Indeed, spores are able to germinate again after tens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy, which can play a huge role on biodiversity in both oceanic and coastal environments.

Here we build on the work by Shoemaker & Melbourne (2016); Wisnoski *et al.* (2019), and previous findings in Picoche & Barraquand (2019, 2020), to examine the effect on coexistence and feedbacks from the different compartments (ocean, coastal water column and bottom).

## Methods

### Model

The model developed by Shoemaker & Melbourne (2016); Wisnoski *et al.* (2019) builds on a two-step discrete-time model: the abundances of cells present in the coastal or oceanic waters first increase following Beverton-Holt dynamics (eq. 1). The Beverton-Holt (BH) formulation is classical for discrete-time models of terrestrial plants and includes both maximum growth rates  $r_i(T)$  and the effects of positive and negative interactions  $\alpha_{ij}$  on said growth rates. In our models, the maximum achievable growth rate for one time step is dependant on both the species and the current temperature. During the same first step, the abundance of cells present at the bottom of the floor in coastal areas (hereafter called cysts) decreases because of cyst mortality ( $m$ ) and the burial resulting from sedimentation ( $\zeta$ ). During the second step, exchanges take place between the different compartments (eq. 2).

$$\begin{cases} N_{t+h,i,c/o} &= \frac{e^{r_i(T)} N_{t,i,c/o}}{1 + \sum_j \alpha_{ij,c/o} N_{t,j,c/o}} - l N_{t,i,c/o} \\ N_{t+h,i,b} &= N_{t,i,b} (1 - m - \zeta) \end{cases} \quad (1)$$

with  $r_i(T)$  was calibrated for this study (see SI for more information) and interactions are inferred from previous work on real data with a Multivariate AutoRegressive (MAR) model (Picoche & Barraquand, 2020). The shift from MAR to BH- matrices of interactions is described in SI.

$$\begin{cases} N_{t+1,i,c} &= N_{t+h,i,c} (1 - s_i - e) + \gamma N_{t+h,i,b} + e N_{t+h,i,o} \\ N_{t+1,i,o} &= N_{t+h,i,o} (1 - s'_i - e) + e N_{t+h,i,c} \\ N_{t+1,i,b} &= N_{t+h,i,b} (1 - \gamma) + s_i N_{t+h,i,c} \end{cases} \quad (2)$$

Parameters and state variables definitions are given in Table 1. Each compartment (ocean, coast, seed bank) contain  $10^3$  cells at the beginning of the simulation, which is run for 10000 time steps.

Param	Name	Value (unit)
$N_{t,i,c/o/b}$	Abundances of species $i$ at time $t$ in the coast ( $c$ ) or ocean ( $o$ ) water column, or in the benthos ( $b$ )	NA (Number of cells)
$T$	temperature	NA (K)
$r_i(T)$	growth rate of species $i$	NA
$b_i$	Normalization constant for the thermal decay rate	( $K^3$ )
$\tau_0$	Reference temperature	293 (K) / 20 ( $^{\circ}C$ )
$a_r(\tau_0)$	Growth rate at reference temperature	$386(\frac{kg}{kg \times year})^1$
$E_r$	Activation energy	0.467 (eV)
$k$	Boltzmann's constant	$8.6173324 \cdot 10^{-5} (eV \cdot K^{-1})$
$A_i$	Niche area	15 [arbitrary], maybe species-dependent
$l$	loss of vegetative phytoplankton (predation, mortality...)	0.04 (Scranton & Vasseur, 2016)
$f_i(T)$	Fraction of the maximum rate achieved for the $i^{th}$ species	(NA)
$T_{min}$	Minimum thermal optimum	Will be calibrated
$T_{max}$	Maximum thermal optimum	Will be calibrated
$T_i^{opt}$	Optimal temperature for species $i$	Adapted from Picoche & Barraquand (2020)
$\alpha_{ij,c/o}$	interaction strength of species $j$ on $i$	Adapted from Picoche & Barraquand (2020)
$k_{c2o}$	conversion coefficient from coastal to oceanic interactions	1.5 [arbitrary]
$m$	cyst mortality	$\approx 10^{-4}/10^{-5}$ (McQuoid <i>et al.</i> , 2002)
$\zeta$	cyst burial	Will depend on the scenario
$s_i, s'_i$	sinking rate of species $i$ in a coastal environment	$0.3\beta(0.55, 1.25)$ (Passow, 1991)
$e$	exchange rate between ocean and coast	[40-100]% (Ascione Kenov <i>et al.</i> , 2015)
$\gamma$	germination + resuspension rate of species	$[0.1, 0.01, 0.001] * [10^{-5}, 0.1]$ (arbitrary)

Table 1: Definition of variable states and parameters

## Definition of parameter values

**Optimal temperature** Each species is defined by its own thermal optimum. However, the variability of this temperature is high, even within a single genus. Thermal optima will be determined with the observed dynamics of each species.

**Exchange rate** This parameter depends on the estuary. In the Arcachon Bay, the exchange rate for each tide has been estimated around 64% (Plus *et al.*, 2009)<sup>2</sup> In Marennes-Oléron, the renewal time is very low at the site we study, between 1 and 2.5 days (Ascione Kenov *et al.*, 2015).

**Cyst mortality and burial** As previously mentioned, cyst loss is a composite of cyst mortality and inaccessibility. McQuoid *et al.* (2002) provides values of mean and maximum depths at which cysts can still germinate for different species, leading to mortality values around  $10^{-4}/10^{-5}$  (for more details on the approximation of mortality rate from these depths, see SI).

However, cyst burial might be a prevailing phenomenon in driving phytoplanktonic dynamics. Even when seeds can be resurrected, they are not accessible after being buried. This value needs to be calibrated in our model.

**Sinking rate** According to Passow (1991) (who measured sinking rates in real conditions), rates can vary between 1 and 30% for the same species (*Chaetoceros* spp.), with a mean value for two diatom species of 10 (*Chaetoceros* and *Thalassiosira*). Values are much lower for the other species, around 1%.

Sinking rate values around 10% are consistent with the loss rate values in Wiedmann *et al.* (2016).

We can arbitrarily fix a beta distribution with mean value close to the one observed in both papers (between 9 and 10), and maximum around 30%, that is  $s \sim \beta(0.55, 1.25) * 0.3^3$ .

<sup>1</sup>As the final dimension of this variable is year-1, I don't think we have to convert to number of cells but I am still wondering about the usability of this parameter + we have to convert from year to day

<sup>2</sup>We need to have very good arguments to take into account only one tide per day.

<sup>3</sup>I do think this will need to be varied a lot

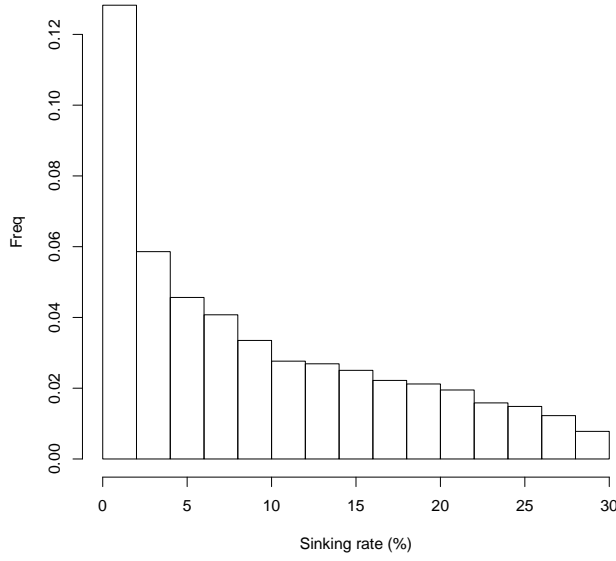


Figure 1: Possible distribution of sinking rates

**Germination/resuspension** Germination and resuspension might be difficult to differentiate, they are defined by the same parameters ( $\gamma = \text{resuspension} \times \text{germination}$ ). Even though we have no estimation of germination and resuspension rate, we can try several values.

Germination can be 1%, 0.1%, 0.01%. From McQuoid *et al.* (2002), we can assume that there is a temperature threshold for germination (but this cannot explain a lot of long-term dormancy) and the existence of such threshold is confirmed by the review by Agrawal (2009). We use a temperature threshold at 15°C. Photoperiodicity does not seem to have a strong effect according to Agrawal (2009)(but see Eilertsen *et al.* (1995)), and might be mingled with seasonal variation in temperature.

Resuspension values vary from one publication to another: in Fransz & Verhagen (1985), resuspension rate of sediments is evaluated around  $5.10^{-5} \text{ day}^{-1}$  in winter and decreases in summer (there is a link between resuspension/sinking and light extinction coefficient). In Kowe *et al.* (1998), resuspension rate of diatoms is evaluated around  $1.9.10^{-5} \text{ day}^{-1}$ , with a maximum sinking rate of  $0.085 \text{ day}^{-1}$ . In Le Pape *et al.* (1999), resuspension rate of sediments and dead diatoms is  $0.002 \text{ day}^{-1}$ . In this paper, we will examine values between  $10^{-5}$  (stratified water column) to 0.1 (highly mixed environment).

## Calibration

Groups of species (Table 2), interaction matrices (Fig. 7) and realistic environmental conditions are taken from one of the sites (Auger) considered in a previous analysis based on field data (Picoche & Barraquand, 2020), which shows the longest time-series for the most common groups of species.

Code	Taxa
CHA	<i>Chaetoceros</i>
DIT	<i>Ditylum</i>
GUI	<i>Guinardia</i>
LEP	<i>Leptocylindrus</i>
NIT	<i>Nitzschia+Hantzschia</i>
PLE	<i>Pleurosigma+Gyrosigma</i>
PRO	<i>Prorocentrum</i>
PRP	<i>Protoperidinium+Archaeperidinium+Peridinium</i>
PSE	<i>Pseudo-nitzschia</i>
SKE	<i>Skeletonema</i>
THP	<i>Thalassiosira+Porosira</i>

Table 2: Name and composition of the groups of species present in our reference site, based on Hernández Fariñas *et al.* (2015).

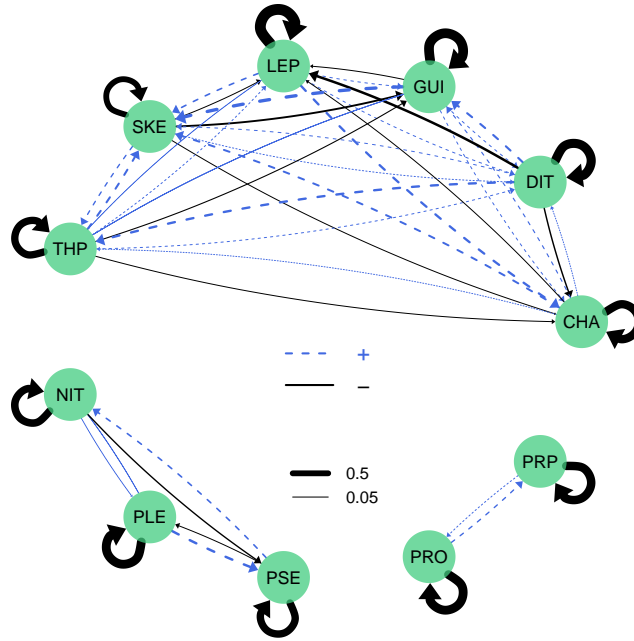


Figure 2: Description of the interaction networks in our reference site, with negative interactions in solide black lines and positive interactions in dashed blue lines. Edge linewidth is proportional to the decimal logarithm of interaction strengths.

Observations of abundances, growth rates and phenologies are used to calibrate the model.

The parameters that need to be calibrated are the following:

1. thermal optimal (mostly with the phenologies)  $T_i^{opt}$
2. sinking rates  $s_i$

The sensivity of the model to certain parameters needs to assessed before going further with other parameters.

1. germination x resuspension  $\gamma$

## Scenarios

Scenarios can be proposed to study the effect of a seed bank on coexistence of species, by

1. removing such seed bank (by setting seed mortality/burial to 1)
2. changing the exchanges between the coast and the ocean ( $e=0$ )

Final richness and average abundance/biomass productivity (to link with ecosystem functions<sup>4</sup>) can be diagnostics.

### Expected results WARNING: FIGURES ARE NOT BASED ON REAL RESULTS

We can make 2 a-priori hypotheses: removing the seed bank would increase the sensitivity to competition, i.e. decrease the maximum sustainable interspecific competition strength, and decrease the resilience of the community confronted to changes in the environment (Fig. 3).

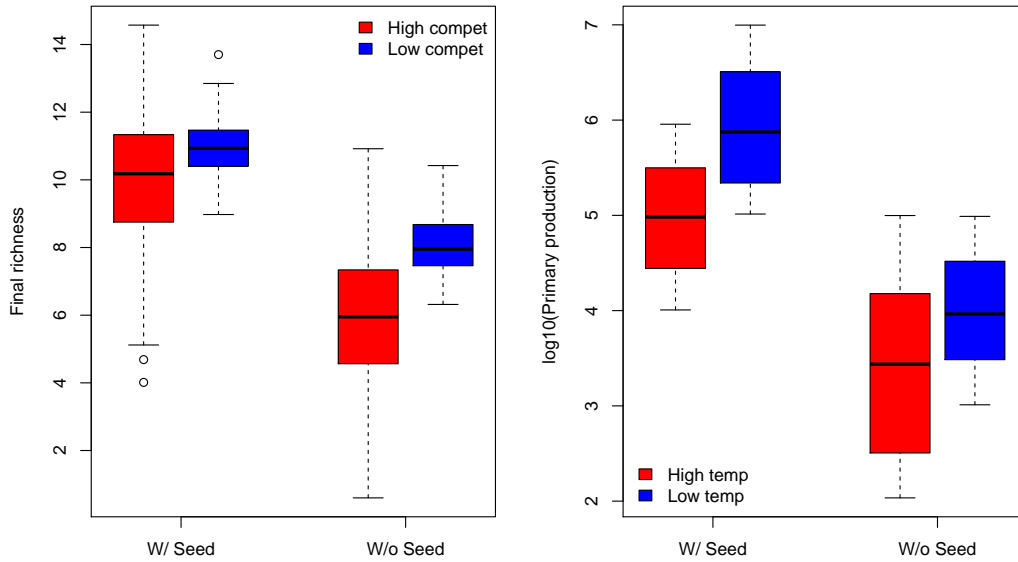


Figure 3: Expected changes in tolerance (stable richness) to interspecific competition and increase in temperature with and without seed banks

Fig. 4 gives a more precise view of the possible interactions of seed mortality and exchange between the coast and the ocean.

<sup>4</sup>Might be too dangerous to try and talk about increase in temperature and change in phytoplankton abundances.

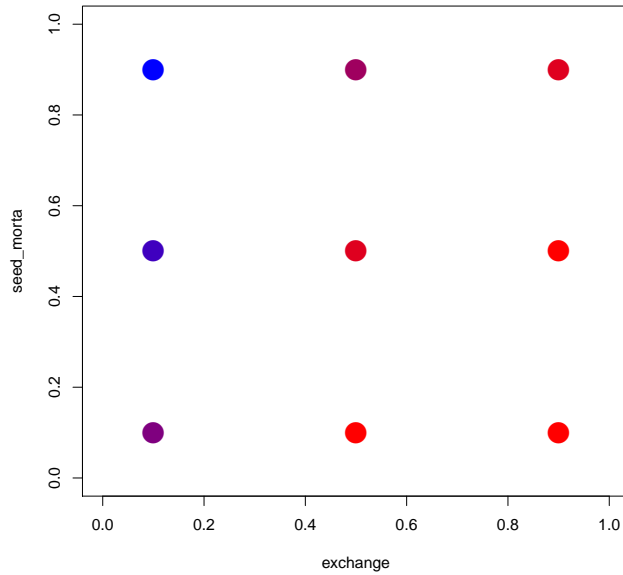


Figure 4: Expected changes in community richness in the ocean for different values of seed mortality/burial (=access to the seed compartment) and exchange with the ocean. Point color indicates richness, from low (blue) to high (red).

## Going further

We may need/be interested in

1. defining niches in different ways. Keeping the same area but changing width and eight of the niche OR Generalist vs specialists OR keeping the same niches
2. using a density-dependent mortality
3. using a delay in the exchange rate to implicitly represent a transfer to populations farther away
4. using much more species (100) and/or explicitly accounting for more population than only coast/ocean (more transitions between compartments)

## Results

### Quadratic programming

Using quadratic programming(see SI) as a way to tune interaction strengths<sup>5</sup> on the observed abundances leads to changes in parameter values (Fig. 5). Some interactions can be multiplied by 80 after re-calibration (LEP/GUI) while most of the parameters at least keep their order of magnitude.

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<sup>5</sup>I have not really formalized how we could do that with growth rates, as they are not fixed through time and do not depend on only one mean parameter. For now, calibration only applies to interactions.

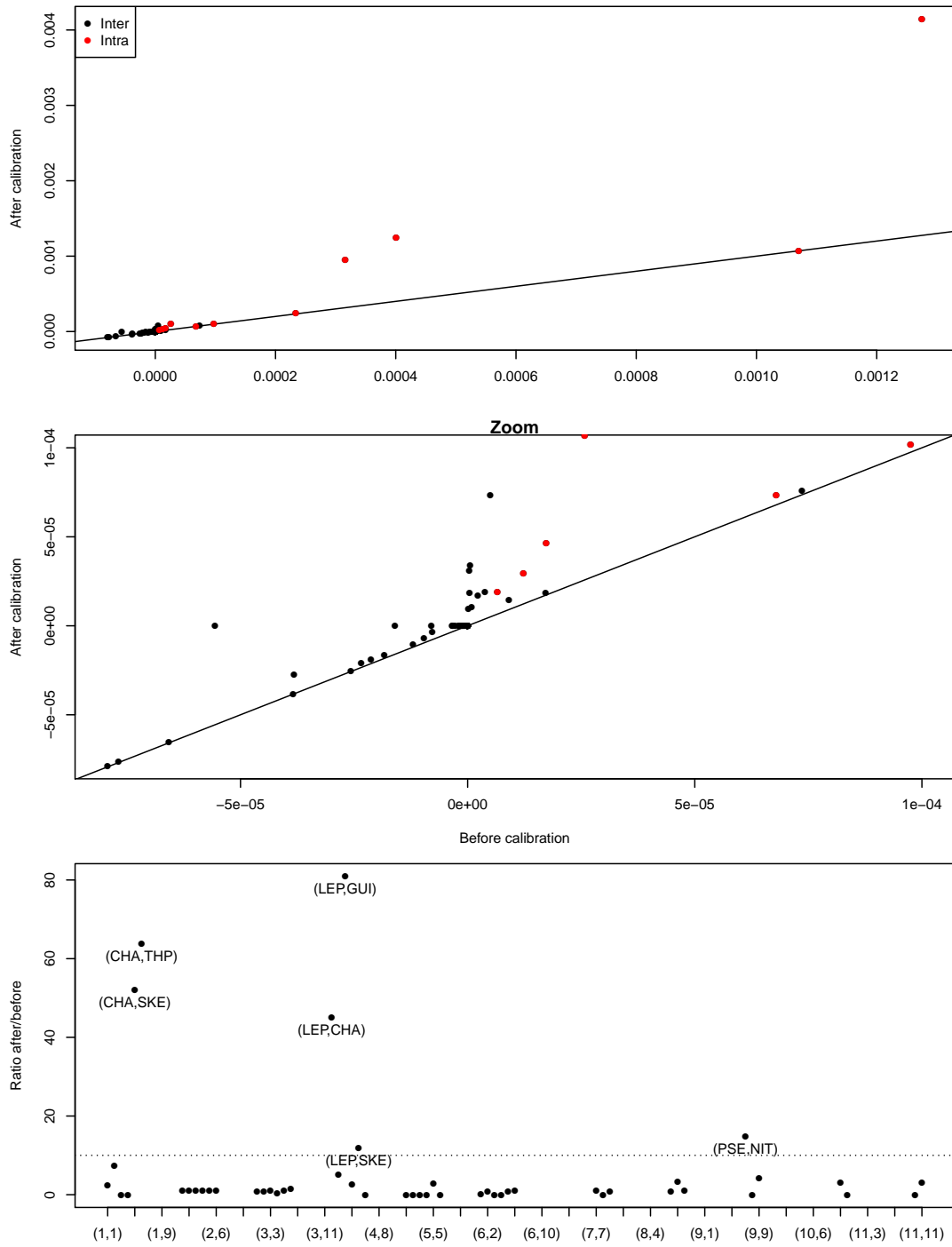


Figure 5: Changes in interaction strengths after calibration by quadratic programming. The middle panel is a zoom on interspecific interaction strengths. The bottom panel shows the ratio of parameter values after and before quadratic programming.

## Phytoplankton dynamics

Average abundances seem to be respected but blooms do not appear clearly (Fig. 6). The variation in abundances due to seasonality is, for now, underestimated. Species with a lower thermal optima such as *Skeletonema* miss their two blooms.



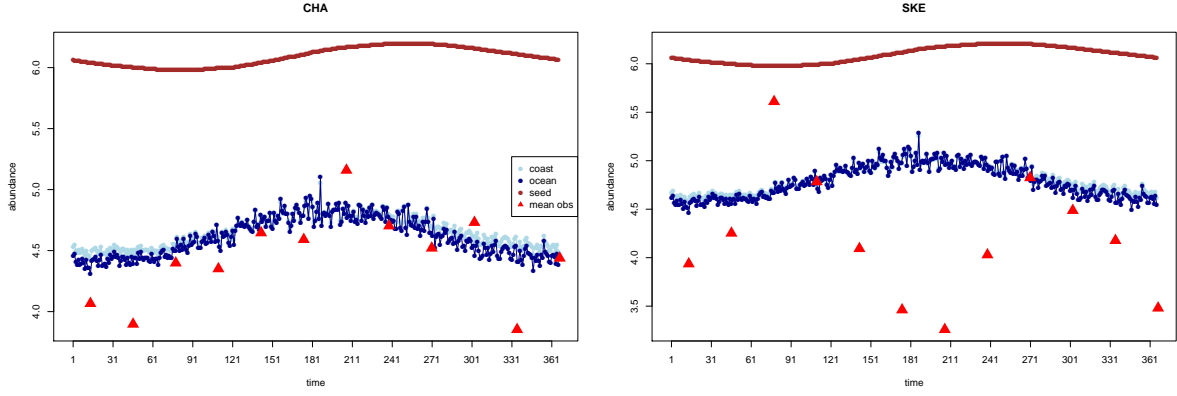


Figure 6: Examples of phytoplankton dynamics (Chaetoceros on the left, Skeletonema on the right)

Thermal optima need to be redesigned in relation to niche area. For now, species with a preference for low temperatures also have a wider niches which buffers their growth. A distinction between generalists and specialists species (Hernández Fariñas *et al.*, 2015). could emerge from the modification of the growth rate formula.

## Supplementary Information

### Growth rate

Phytoplanktonic growth rates are highly variable, in situ or in experimental conditions. As an example of such variability appears in Balzano *et al.* (2011). For ten strains of one genus only (Skeletonema), and in the same experimental conditions, Balzano *et al.* (2011) have been able to detect growth rates between 0.5 and 1.25 day<sup>-1</sup>, which corresponds more generally to the values found in the literature (between 0.2 and 1.78 for diatoms in Reynolds (2006), even reaching 3 in the meta-analysis of 308 experiments by Edwards *et al.* (2015); this can be much lower for dinoflagellates). These growth rates are maximum, fixed values for isolated species in laboratory conditions. Most of the time, they correspond to fixed temperature conditions, or to only a small set of values. These observations therefore cannot accomodate realistic, seasonal environment.

In this context, Bissinger *et al.* (2008) based their study on a seminal work by Eppley (1972) to compute the maximum possible growth rate depending on the temperature. The relationship between temperature and growth rate, evaluated on a large database<sup>6</sup>, is then  $r(T) = 0.81e^{0.0631T}$ , with  $T$  in °C. This represents the daily growth rate under a continuous irradiance and can therefore be at least halved because mean daylight is around 12 hours. In this case, growth rates vary between 0.5 and 1.9, in line with previous observations. However, these values only illustrate a maximum, exponential growth which cannot be realistic for species which actually show different niche temperatures.

Scranton & Vasseur (2016) designed an equation that distinguished different niches based on optimal temperature.

$$\begin{aligned}
 r_i(T) &= a_r(\tau_0)e^{E_r \frac{(T-\tau_0)}{kT\tau_0}} f_i(T) \\
 \text{where } f_i(T) &= \begin{cases} e^{-|T-T_i^{opt}|^3/b_i}, & T \leq T_i^{opt} \\ e^{-5|T-T_i^{opt}|^3/b_i}, & T > T_i^{opt} \end{cases} \\
 \text{and } b_i &\text{ is defined by numerically solving } \int r_i(\tau)d\tau = A
 \end{aligned} \tag{3}$$

<sup>6</sup>1,501 data points from several studies

However, the niches described by this growth function are too narrow, corresponding to values close to 0 for temperatures in which phytoplankton can normally grow. The meta-analysis by Edwards *et al.* (2016) allows to correct, at least qualitatively the growth rates obtained with Scranton & Vasseur (2016).

By increasing the niche area in Scranton & Vasseur (2016) as well as directly increasing the final growth rate by 0.25, thermal niches seem closer to other values in the literature (Fig. 7).

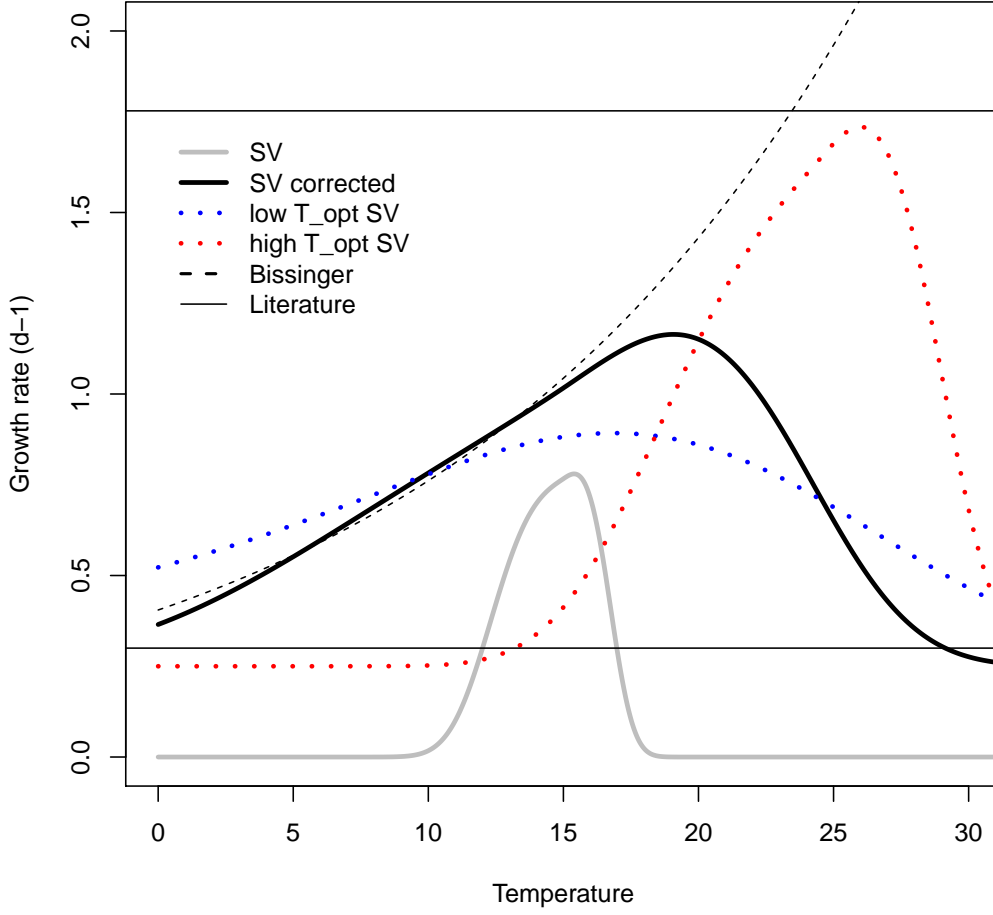


Figure 7: Comparison of growth rate formula

### Community matrix: correspondence between Multivariate Autoregressive and Beverton-Holt models

Certain *et al.* (2018)<sup>7</sup> showed that MAR and Beverton-Holt interaction coefficients, respectively  $b_{ij}$  and  $\alpha_{ij}$ , could map once abundances at equilibrium  $N_i^*$  are defined.

$$\begin{cases} b_{ii} - 1 = \frac{-\alpha_{ii}N_i^*}{1 + \sum_l \alpha_{il}N_l^*} \\ b_{ij, i \neq j} = \frac{-\alpha_{ij}N_j^*}{1 + \sum_l \alpha_{il}N_l^*} \end{cases}$$

Let's define  $f_A(i) = \sum_l \alpha_{il}N_l^*$ .

<sup>7</sup>Corrected in the Appendices of Picoche & Barraquand (2020)

$$b_{ij}(1 + f_A(i)) = -\alpha_{ij}N_j^*$$

We then sum on columns (on  $j$ ).

$$\begin{aligned} \sum_j [b_{ij}(1 + f_A(i))] &= -f_A(i) \\ \Leftrightarrow -f_A(i)(1 + \sum_j b_{ij}) &= \sum_j b_{ij} \\ \Leftrightarrow f_A(i) &= -\frac{\sum_j b_{ij}}{(1 + \sum_j b_{ij})} \\ \Leftrightarrow \alpha_{ij} &= -\frac{1}{N_j^*} b_{ij} \left(1 - \frac{\sum_j b_{ij}}{1 + \sum_j b_{ij}}\right) \\ \Leftrightarrow \alpha_{ij} &= -\frac{1}{N_j^*} \frac{b_{ij}}{1 + \sum_j b_{ij}} \end{aligned}$$

This gives an exact correspondance between  $\alpha_{ij}$  and  $b_{ij}$ .

### Quadratic programming

Even though we could directly use the values obtained previously, the switch to another model with a different timestep and the strong uncertainty for all parameters, among other factors of variability, are motivations to calibrate the model more precisely. Maynard *et al.* (2019) have already shown that such an additional calibrations of parameter could lead to more realistic simulations. Following their example, we use quadratic programming (Bazaraa *et al.*, 2013), applied to interaction matrices and growth rates<sup>8</sup>.

The quadratic programming algorithm aims at finding  $\mathbf{x}$  that minimizes  $\|\mathbf{C}\mathbf{x} - \mathbf{d}\|^2$  under the constraints  $\mathbf{E}\mathbf{x} = \mathbf{f}$  and  $\mathbf{G}\mathbf{x} \geq \mathbf{h}$ .

Here,  $\mathbf{C} = \mathbf{I}$ ,  $\mathbf{d} = [\text{vec}(\mathbf{A}^T) \wedge \mathbf{r}']$  where  $\mathbf{A}$  is the interaction matrix,  $\mathbf{r}' = -(\mathbf{e}^r - \mathbf{1})$  is the vector of growth rates,  $\mathbf{E}$  is built so that we verify the equality  $\mathbf{A}\mathbf{N}^* + \mathbf{r}' = 0$  where  $\mathbf{N}^*$  is the vector of abundance at equilibrium (more precisely, here, average abundance values over the whole time series), and  $\mathbf{G}, \mathbf{h}$  so that  $\mathbf{r} > 0$  (genera have a positive growth rate when taken in isolation) and  $\forall i, a_{ii} > 0$  (negative density-dependence, individuals from the same genus compete with each other).

### Mortality in the sediment

McQuoid *et al.* (2002) present maximum and mean depth at which germination of diatoms and dinoflagellates occurred in sediments. They also present sediment datation according to depth. Depth can therefore be related to maximum and mean age of phytoplankton before death.

Assuming  $m$  is the probability of mortality,  $m$  follows a geometric law, i.e.,  $m$  is the probability distribution of the number of days needed for a phytoplankton spore to die. The expectancy for the life duration (the number of days without dying) is  $\frac{1}{m} \Leftrightarrow m = \frac{1}{L_{mean}}$  where  $L_{mean}$  is the average life duration.

Another way to look at the process is that life expectancy  $L$  follows the distribution  $p(L > l) = e^{-ml}$ . With maximum values, we can arbitrarily choose that for these values  $p(L > l_{max}) = 0.05$ . In this,  $m = -\frac{\ln(p(L > l_{max}))}{l_{max}}$ .

In both cases,  $m \propto 10^{-4} \text{d}^{-1}$ .

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<sup>8</sup>Actually, Maynard et al. 2019 uses a Least Square Inverse Problem solver, with a package (limSolve::lsei) that also offers quadratic programming

## References

- Agrawal, S.C. (2009). Factors affecting spore germination in algae - review. *Folia Microbiol*, 54, 273–302.
- Ascione Kenov, I., Muttin, F., Campbell, R., Fernandes, R., Campuzano, F., Machado, F., Franz, G. & Neves, R. (2015). Water fluxes and renewal rates at Pertuis d’Antioche/Marennes-Oléron Bay, France. *Estuarine, Coastal and Shelf Science*, 167, 32–44.
- Balzano, S., Sarno, D. & Kooistra, W.H.C.F. (2011). Effects of salinity on the growth rate and morphology of ten *Skeletonema* strains. *Journal of Plankton Research*, 33, 937–945.
- Bazaraa, M.S., Sherali, H.D. & Shetty, C.M. (2013). *Nonlinear programming: theory and algorithms*. John Wiley & Sons.
- Bissinger, J., Montagnes, D., Harples, J. & Atkinson, D. (2008). Predicting marine phytoplankton maximum growth rates from temperature: Improving on the Eppley curve using quantile regression. *Limnology and Oceanography*, 53, 487–493.
- Cáceres, C.E. (1997). Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proceedings of the National Academy of Sciences*, 94, 9171–9175.
- Certain, G., Barraquand, F. & Gårdmark, A. (2018). How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution*, 9, 1975–1995.
- Chesson, P. (1986). Environmental variation and the coexistence of species. In: *Community ecology* (eds. Diamond, J. & Case, T.). Harper & Row, New-York, chap. 14, pp. 240–256.
- Comita, L., Queenborough, S., Murphy, S., Eck, J., Xu, K., Krishnadas, M., Beckman, N. & Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, 102, 845–856.
- Edwards, K., Thomas, M., Klausmeier, C. & Litchman, E. (2015). Light and growth in marine phytoplankton: allometric, taxonomic, and environmental variation: Light and growth in marine phytoplankton. *Limnology and Oceanography*, 60, 540–552.
- Edwards, K., Thomas, M., Klausmeier, C. & Litchman, E. (2016). Phytoplankton growth and the interaction of light and temperature: A synthesis at the species and community level: Light-Temperature Interactions. *Limnology and Oceanography*, 61, 1232–1244.
- Eilertsen, H., Sandberg, S. & Tøllefsen, H. (1995). Photoperiodic control of diatom spore growth; a theory to explain the onset of phytoplankton blooms. *Mar. Ecol. Prog. Ser.*, 116, 303–307.
- Ellegaard, M. & Ribeiro, S. (2018). The long-term persistence of phytoplankton resting stages in aquatic ‘seed banks’. *Biological Reviews*, 93, 166–183.
- Ellner, S., Snyder, R. & Adler, P. (2016). How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters*, 19, 1333–1342.
- Eppley, R. (1972). Temperature and phytoplankton growth in the sea. 70.
- Fransz, H. & Verhagen, J. (1985). Modelling research on the production cycle of phytoplankton in the Southern Bight of the North Sea in relation to riverborne nutrient loads. *Netherlands Journal of Sea Research*, 19, 241–250.

- Hernández Fariñas, T., Bacher, C., Soudant, D., Belin, C. & Barillé, L. (2015). Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. *Estuarine, Coastal and Shelf Science*, 159, 15–27.
- Kowe, R., Skidmore, R., Whitton, B. & Pinder, A. (1998). Modelling phytoplankton dynamics in the River Swale, an upland river in NE England. *Science of The Total Environment*, 210, 535–546.
- Le Pape, O., Jean, F. & Ménesguen, A. (1999). Pelagic and benthic trophic chain coupling in a semi-enclosed coastal system, the Bay of Brest (France): a modelling approach. *Mar. Ecol. Prog. Ser.*, 189, 135–147.
- Marcus, N. & Boero, F. (1998). Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography*, 43, 763–768.
- Maynard, D.S., Wootton, J.T., Serván, C.A. & Allesina, S. (2019). Reconciling empirical interactions and species coexistence. *Ecology Letters*, 22, 1028–1037.
- McQuoid, M.R., Godhe, A. & Nordberg, K. (2002). Viability of phytoplankton resting stages in the sediments of a coastal Swedish fjord. *European Journal Phycology*, 37, 191–201.
- Nguyen, V., Buckley, Y.M., Salguero-Gómez, R. & Wardle, G.M. (2019). Consequences of neglecting cryptic life stages from demographic models. *Ecological Modelling*, 408, 108723.
- Passow, U. (1991). Species-specific sedimentation and sinking velocities of diatoms. *Mar. Biol.*, 108, 449–455.
- Patrick, R. (1948). Factors effecting the distribution of diatoms. *Bot. Rev.*, 14, 473–524.
- Picoche, C. & Barraquand, F. (2019). How self-regulation, the storage effect, and their interaction contribute to coexistence in stochastic and seasonal environments. *Theoretical Ecology*.
- Picoche, C. & Barraquand, F. (2020). Strong self-regulation and widespread facilitative interactions between genera of phytoplankton. preprint, bioRxiv.
- Plus, M., Dumas, F., Stanisière, J.Y. & Maurer, D. (2009). Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. *Continental Shelf Research*, 29, 1008–1013.
- Reynolds, C.S. (2006). *The ecology of phytoplankton*. Cambridge University Press.
- Sanyal, A., Larsson, J., van Wirdum, F., Andrén, T., Moros, M., Lönn, M. & Andrén, E. (2018). Not dead yet: Diatom resting spores can survive in nature for several millennia. preprint, bioRxiv.
- Scranton, K. & Vasseur, D.A. (2016). Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. *Theoretical Ecology*, 9, 353–363.
- Shoemaker, L.G. & Melbourne, B.A. (2016). Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology*, 97, 2436–2446.
- Smayda, T.J. (2002). Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as “pelagic seed banks”. *Harmful Algae*, 1, 95–112.
- Wiedmann, I., Reigstad, M., Marquardt, M., Vader, A. & Gabrielsen, T. (2016). Seasonality of vertical flux and sinking particle characteristics in an ice-free high arctic fjord-Different from subarctic fjords? *Journal of Marine Systems*, 154, 192–205.
- Wisnoski, N.I., Leibold, M.A. & Lennon, J.T. (2019). Dormancy in metacommunities. *The American Naturalist*, 194, 135–151.