A metacommunity model for phytoplankton biodiversity maintenance with a seed bank and facilitative interactions

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Abstract

Life histories of all species include different stages in which an individual requirements and growth parameters differ, and contrasting growth strategies may be able to maintain the coexistence of a high number of species for long period of time. In most plants, seed formation is part of the reproductive cycle, leading to the establishment of seed banks in which individuals can resist harsher environmental conditions than more mature conspecifics. While the implications of this process on biodiversity have been studied in terrestrial plants, modeling of seed (or cyst) banks for phytoplankton has remained scarce and may prove useful in explaining the maintenance of a high number of species in aquatic environments. In this study, we build a metacommunity model of interacting phytoplankton taxa in a coastal environment, with exchanges with the ocean and a cyst bank. The functioning of the phytoplankton community is based on a previously analysed field data set, which include facilitative and competitive interactions between taxa, and is calibrated for the specificity of the metacommunity model. Other parameters are based on field studies and the sensitivity of the model on their varability is assessed. We consider two type of growth models, i.e. with and without a saturating effect of the interactions. Results are consistent between models and reveal that the presence of a cyst bank is necessary to maintain a high number of species in the community. Indeed, different life strategies lead to a higher vulnerability of certain taxa to extinction in specific moments of the year, which can only be buffered by their survival in the cyst stage. This may indicate the role of coastal environments in re-seeding oceanic regions, as opposed to the more common view of the oceans providing most individuals to the coast. Moreover, the cyst bank enables taxa to tolerate stronger impacts of other individuals as well as severe changes in the environment such as those predicted in the climate change context. This study therefore uncovers the importance of a cryptic life stage of phytoplankton taxa, which can inspire further investigations on the specific mechanisms governing this life stage.

Introduction

How the high biodiversity of plant communities maintains is still an unresolved question for both experimental and theoretical ecology. Terrestrial plants and phytoplanktonic communities can present hundreds of species relying on similar resources. Early theory has 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 explanation by the stochastic environmental variations and demographic processes.

Analyses of coexistence in terrestrial plant communities often take into account several life stages [refs cf. Adler paper]. 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 bet-hedging, 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 between individuals is stronger as seeds might germinate and therefore use the same resources 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, the life cycle of aquatic plants, and more specifically that of phytoplanktonic algae, have not been modeled with the same attention . Although ecologists have proposed for a long time that the blooms (peaks in abundances that can cover several orders of magnitude) may initiate after the resuspension and germination of phytoplanktonic resting cells, cysts, (Patrick, 1948; Marcus & Boero, 1998), it is unusal to see an explicit model of such process (but see Hinners *et al.*, 2019). The classical view behind phytoplankton dynamics is that bloom formation is mostly seasonal, due to the variation in light and temperature, assuming vegetative cells remaining in the environment can duplicate enough to attain bloom amplitude. However, a recent review (Ellegaard & Ribeiro, 2018) suggests that cysts might be another player .

Phytoplankton communities in coastal environments may benefit from seed banks (hereafter called cyst banks to remain consistent with phytoplankton terminology) even more than the oceanic communities [REF-find back], as the distance to the sea bottom is smaller allowing recolonization of the pelagic environment from the shallow sea bottom. In the open sea, cysts might arrive together with animals, but such events might be rarer in comparison. Also, and similarly to the seed bank approach in the terrestrial plant literature, Smayda (2002) has proposed the term "pelagic seed bank" to characterize the contribution of the ocean to coastal communities. This has been noticed for dinoflagellates especially [[ref Dinophysis, check what we have on diatoms]]. Conversely, in many other bloom-forming species the nutrient-rich coastal areas might function as a reservoir for the biodiversity in the ocean, especially in the long run. Indeed, cysts are able to germinate again after dozens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy, so they can have a long-term effect on biodiversity in both oceanic and coastal environments.

Here we build on multiple studies in plant and plankton ecology to investigate the effects of cyst banks on phytoplankton community dynamics. XXX [and we describe a little less the models and a little more what we do / what we find, which we can do later]

Methods

Models

Our models builds atop those developed by Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019) These discrete-time models are designed for metacommunities with multiple competing populations and unfold as follow: first, populations grow or decline according to a Beverton-Holt (BH) multispecies density-dependence (eqs. 1 and 3), and then, in a second step, exchanges occur between the different compartments or patches constituting the metacommunity (eq. 4).

In this paper, individuals are phytoplanktonic cells that move between the upper layer of coastal water, its bottom layer where a cyst bank accumulates and the ocean. Only oceanic and coastal pelagic cells are subject to BH-density dependence. Cysts are only affected by mortality m and burial due to sedimentation ζ. The different populations are field-inspired morphotypes accounting for the most frequent genera observed along the French coast (Picoche & Barraquand, 2020) and will hereafter be called taxa. Parameters and state variables are defined in Table 1.

The BH formulation of multispecies population dynamics is a Lotka-Volterra competition equivalent for discrete-time models, and is often used to represent terrestrial plant population/community dynamics. In this model, the maximum achievable growth rate is modified by both competitive and facilitative interactions, which translates into positive and negative α_{ij} coefficients respectively. We first use the classical multispecies Beverton-Holt model (model I, eq. 1). We subsequently defined saturating interactions (model II, eq. 3). More specifically, in our case, the first step of the first model is written as

$$\begin{cases} N_{t',i,c} &= \frac{\exp(r_i(T))N_{t,i,c}}{1+\sum_j \alpha_{ij}N_{t,j,c}} - lN_{t,i,c} \\ N_{t',i,o} &= \frac{\exp(r_i(T))N_{t,i,o}}{1+k_{c2o}\sum_j \alpha_{ij}N_{t,j,o}} - lN_{t,i,o} \\ N_{t',i,b} &= N_{t,i,b}(1-m-\zeta) \end{cases} \tag{1}$$

where the intrinsic growth rate $r_i(T)$ is a taxon-specific function of the temperature (see eq. 2), the interaction coefficients α_{ij} are the strength of the effect of taxon j on taxon i, and the loss term l accounts for lethal processes such a natural mortality, predation or parasitism. First estimate of interaction coefficients are inferred from our previous work on coastal data with Multivariate AutoRegressive (MAR) models (Picoche & Barraquand, 2020). How to shift from MAR- to BH-interaction matrices is described in the SI. We later calibrate this coefficient to an empirical dataset, since MAR models were applied at a different timescale.

In model I, we assume that competition for nutrients is stronger in the ocean than along the coast [ref], thus a coefficient $k_{c2o} > 1$ is applied to competitive interactions.

The growth rate $r_i(T)$ is a modified version of the formula by Scranton & Vasseur (2016) (eq. 2).

$$\begin{aligned} r_i(T) &= E(T)f_i(T) \qquad (2) \\ \text{where } E(T) &= d \times 0.81e^{0.0631T_{^\circ c}} \\ \text{and } f_i(T) &= \begin{cases} \exp(-|T_K - T_{K,i}^{opt}|^3/b_i), & T_K \leq T_{K,i}^{opt} \\ \exp(-5|T_K - T_{K,i}^{opt}|^3/b_i), & T > T_{K,i}^{opt} \end{cases} \end{aligned}$$

where $r_i(T)$ can be decomposed in two parts: the taxon-independent metabolism part $E(T)$ and the taxon-specific niche part $f_i(T)$. The metabolism part describes the maximum achievable growth rate based on Bissinger *et al.* (2008), as an update of the formula by Eppley (1972) used in Scranton & Vasseur (2016). This maximum daily growth rate is weighted by the daylength d as no growth occurs at night. The niche part $f_i(T)$ describes the decrease in growth rate due to the difference between the temperature in the environment and the taxon-specific thermal optimum $T_{K,i}^{opt}$, and is controlled by the specific thermal decay b_i which depends of the niche width. Parameterisation is detailed in the SI.

In model II, oceanic and coastal dynamics are governed by eq. 2.

$$N_{t',i,c/o} = \frac{\exp(r_i(T))N_{t,i,c/o}}{1 + \sum_{j\in\mathbb{C}} \frac{a_C N_{t,j,c/o}}{H_{ij}+N_{t,j,c/o}} + \sum_{j\in\mathbb{F}} \frac{a_F N_{t,j,c/o}}{H_{ij}+N_{t,jc/o}}} - lN_{t,i,c/o} \tag{3}$$

where a_C and a_F are the maximum competition and facilitation strengths, respectively, with $\mathbb{C}$ and $\mathbb{F}$ the sets of competitors and facilitators of taxon i. We use here similar notations to Qian & Akçay (2020), but have different parameters that vary between taxa. Indeed, the half-saturation coefficients H_{ij} are here variable between taxa, since it did not make sense biologically for this quantity to be fixed (e.g., in a resource competition context, different species are expected to feel resource limitations at different concentrations of nutrients and at different number of competitors). . How to use parameter estimates from model I to specify model II is described in the SI.

After growth and mortality happen, exchanges take place between the three compartments during the second step of the model (eq. 4).

$$\begin{cases} N_{t+1,i,c} &= (1-s_i-e)N_{t',i,c} + \gamma N_{t',i,b} + eN_{t',i,o} \\ N_{t+1,i,o} &= (1-s_i-e)N_{t',i,o} + eN_{t',i,c} \\ N_{t+1,i,b} &= (1-\gamma)N_{t',i,b} + s_i N_{t',i,c} \end{cases} \tag{4}$$

Param	Name	Value (unit)	Status
$N_{t,i,c/o/b}$	Abundance of taxon i at time t in the coast (c) or ocean (o), or in the coastal benthos (b)	NA (Number of cells)	Dynamic
$T_{K/°C}$	Temperature	NA ($K/°C$)	Dynamic
$r_i(T)$	Growth rate of taxon i	NA	Dynamic
b_i	Thermal decay	Field-based, taxon-specific (K^3)	Calibrated
T_i^{opt}	Optimal temperature for taxon i	Field-based, taxon-specific (K)	Calibrated
d	Daylength	0.5 (%)	Fixed
$\alpha_{ij,c/o}$	Interaction strength of taxon j on i in model I	Field-based, taxon-specific (Cells^{-1})	Calibrated
k_{c2o}	Ocean/Coast interaction strength ratio in model I	1.5	Fixed
a_C/a_F	Maximum competitive/facilitative interaction strength in model II	Field-based, taxon-specific (NA)	Calibrated
H_{ij}	Half-saturation for the interaction strength of taxon j on i in model II	Field-based, taxon-specific (Cells)	Calibrated
s_i	Sinking rate of taxon i	$\{0.1; \mathbf{0.3}; 0.5\}\beta(0.55, 1.25)$	Fixed
e	Exchange rate between ocean and coast	0.4; 0 in scenario	Scenario
l	Loss rate of vegetative phytoplanktonic cells	$0.04; 0.1; \mathbf{0.2}$	Fixed
m	Cyst mortality rate	$\approx 10^{-4}/\mathbf{10^{-5}}$; $1-\zeta$ in scenario	Scenario
ζ	Cyst burial rate	$10^{-3}, \mathbf{10^{-2}}, 10^{-1}$	Fixed
γ	Germination × Resuspension rate	$10^{-3}, \mathbf{10^{-2}}, 10^{-1} \times 10^{-5}, 10^{-3}, \mathbf{10^{-1}}$	Fixed

Table 1: Definition of main state variables and parameters of the models. Calibrated parameters are either directly estimated on data for this study or parameters for which initial estimates exist, but are improved through calibration. Fixed values or distributions are estimated from the literature and references are given in the main text. When a range of values is given, the bold numbers indicate the reference values while the others are used to test the sensitivity of the model. Scenario parameters are the parameters which are used to build ecological scenarii.

Each compartment (ocean, coast, seed bank) contains 10^3 cells at the beginning of the simulation, and is run for 1000 time steps. .

Parameterisation

Empirical dataset used for calibration

[[Write here]]

Parameter definition and values

Loss rate The loss rate of vegetative cells can be attributed to natural mortality, predation or parasitism. A maximum value of 0.2 is fixed for the model.

Sinking rate Phytoplanktonic particles have a higher density than water and cannot swim to prevent sinking (although see Reynolds (2006) for a discussion on the settling of phytoplanktonic cells compared to inorganic particles). Sinking is mostly affected by hydrodynamics, but at the species-level, size, shape and colony-formation capacity are key determinants of the particle floatation. In this model, the sinking rate of each taxon is drawn from a beta distribution with a mean value of 9%, and a maximum around 30%, that is $s \backsim 0.3\beta(0.55, 1.25)$ (see Fig. SXX), adapted from observations by Passow (1991) and Wiedmann *et al.* (2016).

Exchange rate The exchange rate between the ocean and the coast depends on the shape and location of the coast (estuary, cape, ...). At our calibration site (see section SXX), the renewal time ranges between 1 and 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily rate between 40 and 100 %.

Cyst mortality and burial Cyst loss is the result of cyst mortality m and burial by sedimentation ζ. Mortality values range between 10^{-5} and 10^{-4} per day (more details on the approximation of mortality rates from McQuoid *et al.* (2002) are given in the SI). However, cyst burial by sedimentation might be a prevailing phenomenum in driving phytoplanktonic dynamics. Once cysts have been buried, they are not accessible for resuspension even if they could have germinated if put in an accessible location. Burial depends on the hydrodynamics of the site, but also on biotic processes (i.e., bioturbation) and anthropogenic disturbances such as fishing or leisure activities (e.g., jet skiing). This parameter is thus heavily dependent on the environmental context and varies here between 0.001 and 0.1 per day.

Germination/resuspension Germination and resuspension are both needed for cyst to get back to the water column ($\gamma =$ resuspension$\times$germination). Following McQuoid *et al.* (2002) and Agrawal (2009), we assume a temperature threshold: germination is triggered by temperatures going above 15°C. As actual rates of germination are not easily deduced from the literature, a set of credible values are tested (1%, 0.1%, 0.01%). Similarly, resuspension values are seldom computed for phytoplanktonic cells, but models for other particles such as sediments can be used. In this paper, we explore values between 10^{-5} (stratified water column) to 0.1 (highly mixed environment).

Parameter calibration

In addition to phenology parameters whose estimation process is described in the SI, the 49 non-null interactions that form the community matrix of the model are calibrated on field-data. These interactions are computed from previous models (Picoche & Barraquand, 2020, see SI for details on the equations) but need to be adjusted to take into account the differences in structure and time-step between studies.

The calibration procedure consisted in lauching 1000 simulations, each characterized by a specific set of interaction coefficients. More precisely, for each simulation, each interaction coefficient (α_{ij} in model I, H_{ij} in model II) has the same probability of keeping its value, being increased or decreased by 10%, or being halved or doubled. The abundances of the coastal compartment are then extracted over the last 2 years of the simulation and compared to observations to compute the following summary statistics:

- average abundance $f_1 = \sqrt{\frac{1}{S}\sum_i^S \left(\bar{N}_{i,obs} - \bar{N}_{i,sim}\right)^2}$ where S is the number of taxa.
- amplitude of the cycles $f_2 = \sqrt{\frac{1}{S}\sum_i^S \left[(\max(N_{i,obs}) - \min(N_{i,obs})) - (\max(N_{i,sim}) - \min(N_{i,sim}))\right]^2}$
- period of the bloom. The year is divided in 3 periods, i.e. summer, winter and the spring/autumn group (as taxa blooming in these periods can appear in either or both seasons). We give a score of 0 if the taxon blooms in the same period as its observed counterpart and 1 otherwise.

Simulations with taxon extinction are discarded. Models are ranked according to their performance for each summary statistic and the set of interactions with the best rank in every category is kept throughout the rest of the simulation.

Sensitivity analysis Certain parameters, which were evaluated from the literature, may be site- or model- specific, or vary over one order of magnitude, e.g. rates of sinking s, resuspension/germination γ, cyst mortality m and burial ζ, as well as the loss rate l. The dependence between variation in values and outputs of present models needs to be investigated before drawing conclusions for specific ecological scenarii. The set of tested values for each parameter is given in Table 1. Variations in average abundances and amplitudes at the community- and taxon levels for the last 2 years of simulations are the major model diagnostics.

Scenarii

The effect of the seed bank on biodiversity and community dynamics can be evaluated through the response to disturbance with and without the seed compartment. We evaluated two main disturbances:

1. interaction strength variation
2. temperature change, either in mean value or variability

1.

2.

Results

Phytoplankton dynamics

The classical Beverton-Holt (model I) and saturating interaction (model II) formulations led to similar satisfactory results. They both reproduced the main characteristics of phytoplanktonic dynamics, that is the presence of one or two blooms during the year with a range of abundances covering several orders of magnitude and the timing of these blooms. At the Auger site, abundances increase in spring and can last over part of summer, or start in autumn, which is what we obtained in the models. Annual mean abundance of the various taxa was also well reproduced. That said, in some cases abundances could be lower than expected and the variation in abundances due to seasonality was underestimated (Fig. 1). In all cases, saturating interactions led to higher abundances than mass-action interactions throughout the year (Fig. SXXX).

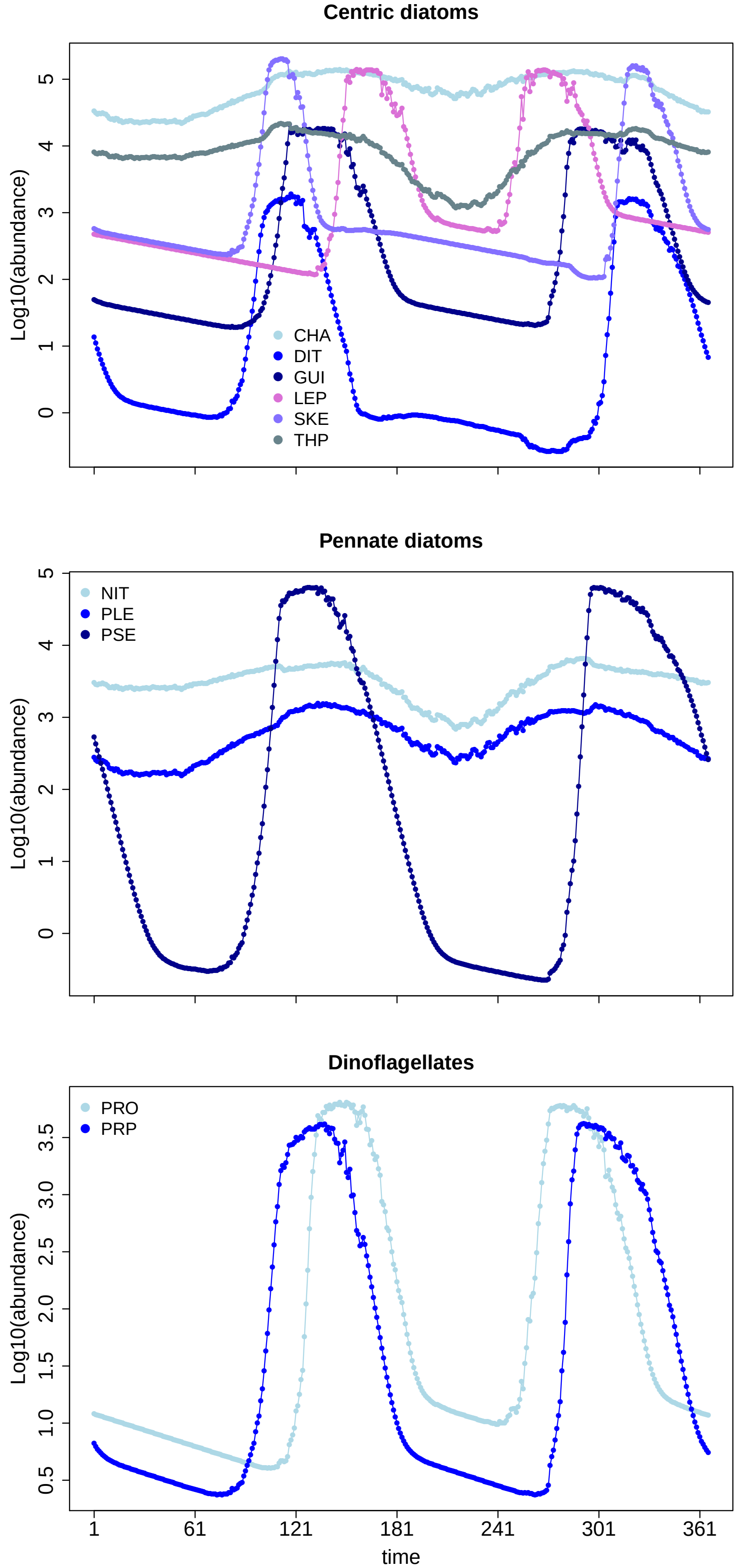

Figure 1: Simulated phytoplankton dynamics for a year in model I. Each panel corresponds to a cluster of interactions.

Sensitivity analysis to fixed parameter set

Total phytoplankton dynamics were not strongly affected by changes in the parameter values (Fig. 2). As values varied in a plausible range, the average change in abundance on the coast between the reference simulation and the simulations varied between -4.6 and 1.9% for model I and between -4.2 and 1.1% for model II, with similar deviations (same sign and magnitude) in the two models. The only parameter that led to a substantially different result between the two models was the resuspension parameter (leading to a different value of the parameter γ in Eq. 4) which, when decreased, led to an increase in abundance of approximately 1.9% in model I while it was only 0.9% in model II. In the two models, the decrease in mortality rate of vegetative cells m had the more impact of the final average abundance, leading to an increase in abundances. The exchange rate between the ocean and the coast had much less effect on the coastal average abundance.

On the other hand, the decimal logarithm of the maximum to minimum ratio of abundance (i.e., the order of magnitude of the range of abundances for each taxa) was more affected by changes in parameters and could vary by -39.4 to 18.6% in model I, and between -41.2% and 23.02% in model II. Results were qualitatively the same in the two models, with a decrease in cyst burial being the main driver of the decrease in amplitude, and a decrease in resuspension leading to an increase in amplitude.

In three cases (cyst burial rate set to 0.1, resuspension to 10^{-5} or the exchange rate set to 0), the final richness of the community decreased from 11 to 4. Extant taxa were the same in all simulations (CHA, THP, NIT, PSE). In a specific case (resuspension set to 0.001), a taxon periodically disappeared from the ocean, to be subsequently re-seeded by the coastal population.

With all parameters, except the sinking rate, an increase in abundance was linked with a decrease in amplitude

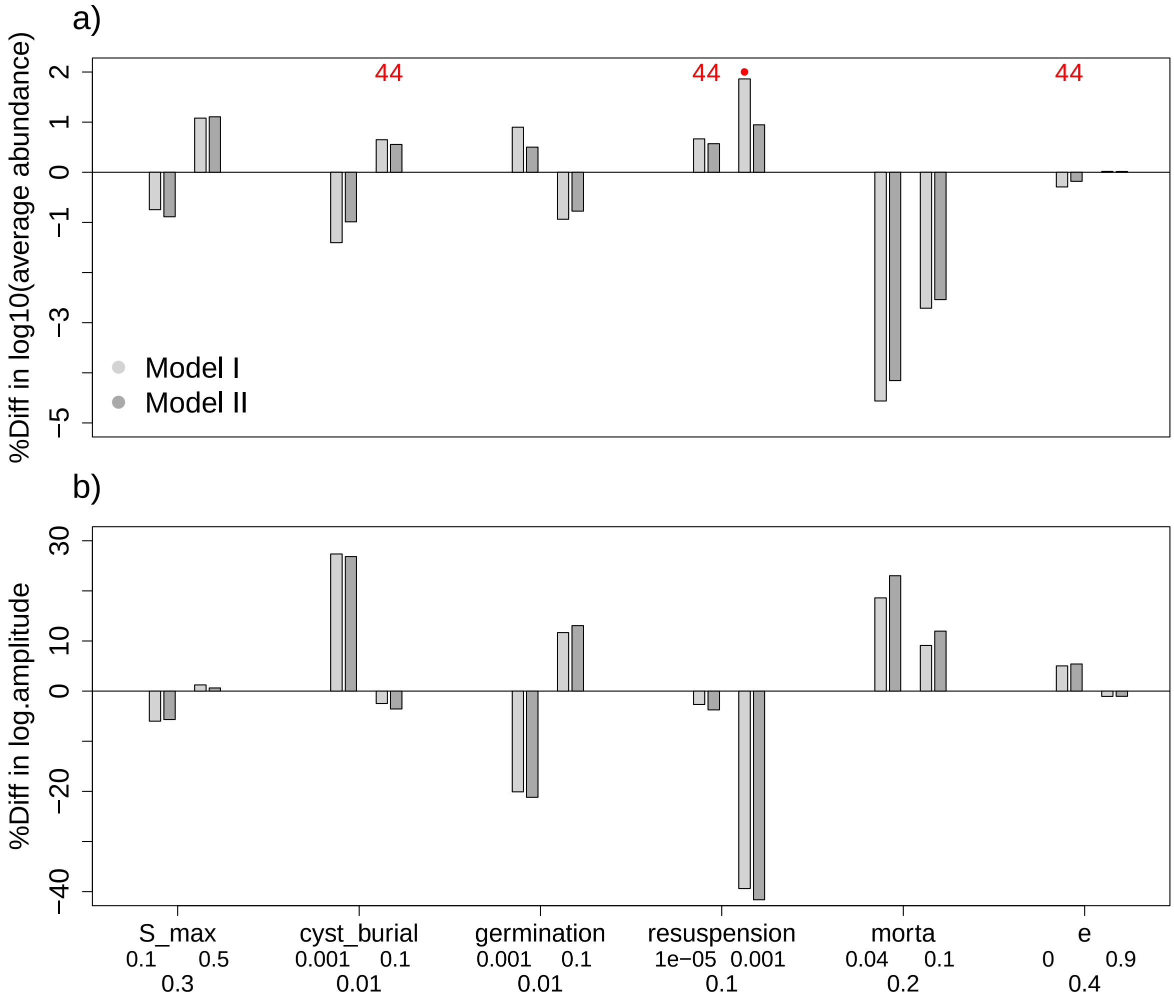

Figure 2: Sensitivity of the model to variation in parameters, measured as the difference between the reference simulation and the simulation with a change in parameter. The two metrics used were the average decimal log abundance (a) and the decimal logarithm of the ratio between maximum and minimum abundance (b) of the coastal phytoplanktonic community. Values used in the sensitivity analysis are in the second row of the x-axis while values used in the reference simulation are shown in the third row. Note that the reference value is not necessarily inside the range of values used in the sensitivity analysis (e.g. mortality rates in the sensitivity analysis are both below the value used in other simulations). Numbers in red are the final number of taxa and dots correspond to simulations in which at least one taxon reached 0 at one point but did not disappear.

Scenarios

Two scenarios were designed to test the buffering effect of the cyst bank against disruption. In both cases, it consisted in removing the cyst bank by setting cyst mortality to 100% per day Without disturbing the system otherwise, this led to a decrease in taxon richness from 11 to 4 taxa at the end of the simulation. Taking into account the extinct taxa, the geometric mean abundance of the community was around 10^{-2} while it was around 10^{3} with a cyst bank. The average abundance of extant taxa only was around 30 without a cyst bank.

Biotic effects Our first hypothesis was that the absence of the cyst bank would cause the community to be more affected by higher competition. Counter-intuitively, our results (Fig. 3) showed that an increase in competition only had negative effect with model I and for high competition values (6 times the reference ones at least), shifting from 4 taxa to 3 taxa in the oceanic compartment of a community without cyst bank while it did not affect the richness of a community with a cyst bank. On the contrary, a decrease in competition (from a factor 0.5 and lower) or an increase in facilitation (starting from a factor 2 and higher) led to much smaller communities in model II, sometimes with a total competitive exclusion. Richness was lowest when competition was divided by 6 or when facilitation was multiplied by 8 in model II. The same pattern (richness stability with model I, sensitivity to a decrease in competition or an increase in facilitation with model II) was observed in a community with a cyst bank, but for larger disturbances. Competition indeed had to be at least divided by 6 or facilitation, to be multiplied by 7 for richness to decrease to 9 taxa.

The geometric mean abundance was also affected by such biotic changes. The order of magnitude of the average abundance without a cyst bank varied between a -1.4 and -2.8 with model I and between -1.3 and -3.3 with model II, while it was between 34.4 and 1.4 for model I and between 0.7 and 3.3 for model II with a cyst bank. It should be noted that model I was able to sustain much high abundances when competition was low, which can be related to the presence of a hard threshold on the amplifying effect of the interactions on the growth rate.

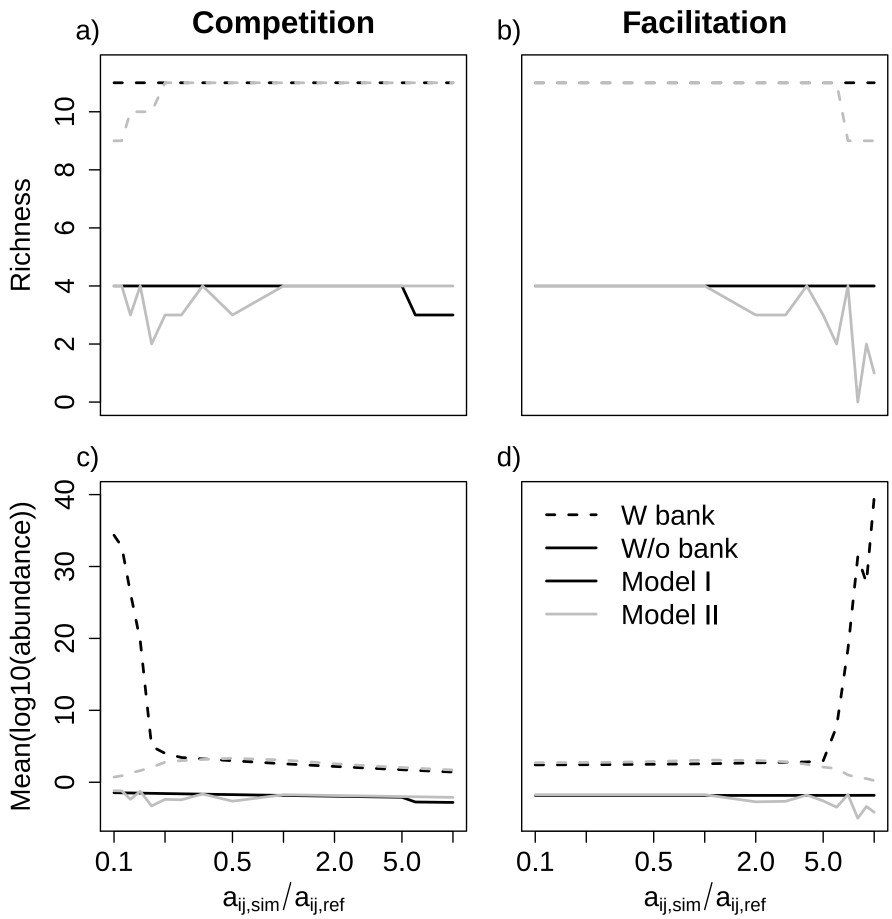

Figure 3: Variation in the total number of taxa still present in the ocean at the end of the simulation (richness) and the geometric mean abundance, including extinct taxa, with (dashed line) and without (solid line) a seed bank, as a function of the strength of competition and facilitation with a classical Beverton-Holt (black lines) or a saturating interaction (grey lines) formulation. The x-axis shows the factor by which each interaction was multiplied (note the logarithmic scale)

Taxa which disappear were always the same and were characterized by a lower minimum abundance, a higher amplitude and a small niche (Fig. 4). In contrast, their interactions were not qualitatively different from the other taxa.

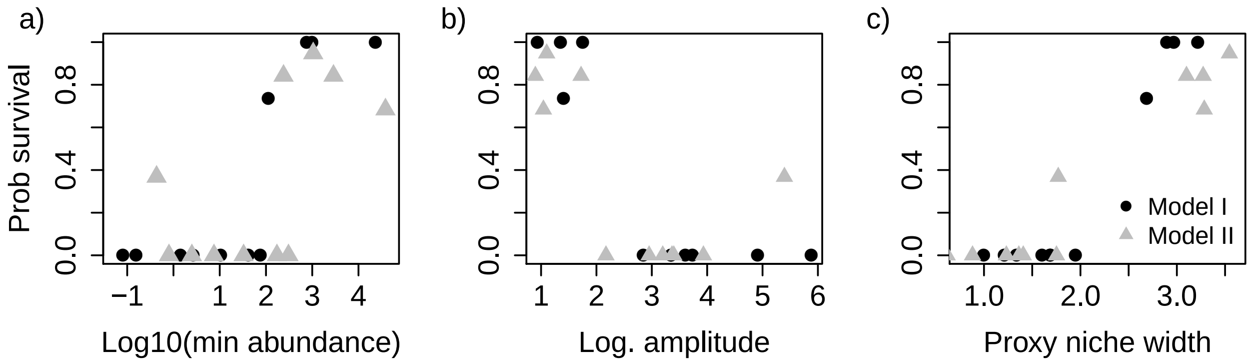

Figure 4: Probability of survival of taxa when competition increases, as a function of their dynamics characteristics (min abundance, logarithm of amplitude and niche width) in the reference parameter set .

Abiotic effects Our second hypothesis was that the absence of a cyst bank would reduce the ability of a community to buffer changes in the environment, here represented by variation in the temperature. As can be seen on Fig. 5, this was true for both models as the communities without a cyst bank could not maintain their richness with an increase in temperature above 2°, as opposed to communities with a cyst bank which could only be affected by a 7°C increase (scenario SSP5 8.5). In all cases however, the total abundances was not strongly affected. Indeed, the total abundance of a community is driven by a small number of cyst which do not disappear. High total abundances tend to correspond to the abundance of only one or two cysts. Model II consistenly led to higher abundances, as was already the case in the reference simulations.

The variance of the temperature did not affect richness nor total abundance of communities with and without a cyst bank.

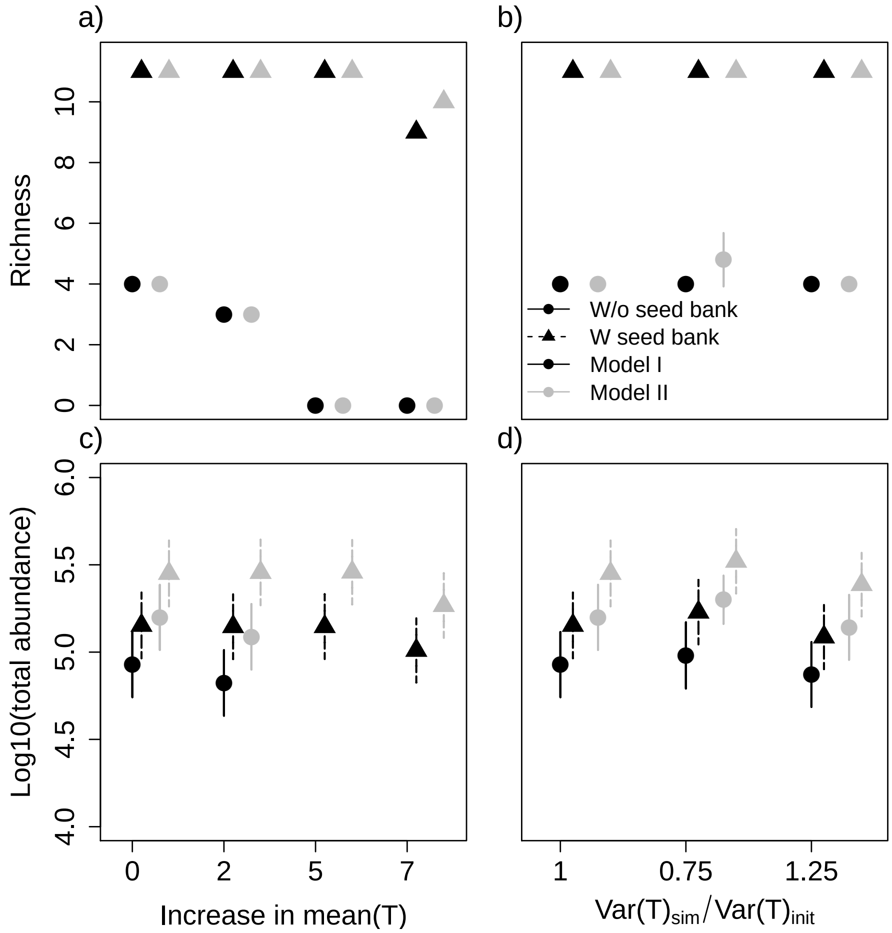

Figure 5: Variation in richness and total abundance with and without a cyst bank as a function of the mean and variance of the temperature with a classical Beverton-Holt (left) or a saturating interaction (right) formulation.

Discussion

Using a meta-community model which accounts for migrations between the ocean and the coast, as well as migrations between the top and the bottom of the coastal water column, we were able to show the way a specific life stage, the cyst, can maintain biodiversity in different marine compartments. With field-based parameters, we modeled the behaviour of phytoplanktonic communities with and without a cyst bank. Biodiversity decreased drastically in the absence of a storing compartment, as well as the total abundance of the community. Moreover, when faced with a biotic or abiotic perturbations, communities that could divert part of their population to a dormant stage were less prone to species loss and could maintain their biomass through the years. These results were consistent in the two interaction models, with and without saturating effects, that were compared.

The assessment of the cyst bank effect depends on the accuracy of the dynamics described in the model. Our model parameters were partly based on a specific field abundance dataset, which allowed us to approximate the biotic interactions between phytoplanktonic taxa and their phenology, and partly based on observations made at other study sites. The range of values found in the literature for certain parameters demonstrated both the variability of the environment and phytoplanktonic reactions, and the uncertainty one can have when measuring certain processes. Hydrodynamics features are highly site-dependent and sometimes poorly defined: cyst burial and resuspension, for instance, are functions of the shape of the coastal site and its interface with the ocean, as well as stochastic phenomena, such as gusts of wind, bioturbation or anthropogenic disturbances. On the other hand, taxon specificities such as shape, buoyancy regulation capacity or cyst formation rate can influence the rate of contribution to the seed bank (which could be approximated by the variation in sinking rate in our model). [[[Here maybe discuss what we have in the literature for hydrodynamics stuff]]] [[This would also be the place -as we are speaking of parameters uncertainty for some words on niches]]] Our model proved quite resilient to variations in these parameters, which makes our conclusions qualitatively reliable.

The capacity of a seed bank to buffer disadvantageous environments to maintain population over time is a staple in terrestrial plant literature [[refS]]. Both empirical [[ref]] and theoretical [[ref]] evidence show that investing part of the biomass of a population in stages that will spread their growth over periods longer than the usual life cycle of the organisms is a successful strategy to maintain over time. This is the basis of bet-hedging

[[See outline]]

[[Need to compare our values to Jewson *et al.* (1981) who took into account most of the phenomena we describe here and the cyst bank as well as the water column]]

References

Agrawal, S.C. (2009). Factors affecting spore germination in algae - review. *Folia Microbiologica*, 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.

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.

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.

Ellegaard, M. & Ribeiro, S. (2018). The long-term persistence of phytoplankton resting stages in aquatic s̀eed 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. *Fishery Bulletin*, 70, 1063–1085.

Hinners, J., Hense, I. & Kremp, A. (2019). Modelling phytoplankton adaptation to global warming based on resurrection experiments. *Ecological Modelling*, 400, 27–33.

Jewson, D.H., Rippey, B.H. & Gilmore, W.K. (1981). Loss rates from sedimentation, parasitism, and grazing during the growth, nutrient limitation, and dormancy of a diatom crop. *Limnology and Oceanography*, 26, 1045–1056.

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.

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. *Marine Biology*, 108, 449–455.

Patrick, R. (1948). Factors effecting the distribution of diatoms. *Botanical Review*, 14, 473–524.

Picoche, C. & Barraquand, F. (2020). Strong self-regulation and widespread facilitative interactions between genera of phytoplankton. preprint, bioRxiv.

Qian, J. & Akçay, E. (2020). The balance of interaction types determines the assembly and stability of ecological communities. *Nature Ecology & Evolution*, 4, 356–365.

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 naturefor 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.