

Working document

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

Introduction

The high biodiversity of plant communities has long been a subject of both experimental and theoretical ecologists. Both terrestrial plants and phytoplanktonic communities can present hundreds of species which seem to consume the same resources.

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).

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 theoreticians have proposed for a long time that the blooms may initiate after the resuspension and germination of seeds (Patrick 1948, Marcus and Boero 1998), it is unusual to see an explicit model of such process [[Note: not necessarily theoreticians, but they have done small review of the existence of spores and the possible benthic-pelagic coupling.]]. 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 and Ribeiro, 2018]. Neglecting explicit modeling of this life stage can modify the understanding we have of the dynamics of the populations [Nguyen et al., 2019].

Phytoplankton communities in coastal environments may benefit from seed banks even more than the oceanic communities, 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 and Ribeiro, 2018]

Param	Name	Value (unit)
$r_i(T)$	growth rate of species i	from Picoche and Barraquand [2019a]
T	temperature	
$\alpha_{ij,c/o}$	interaction strength of species j on i	$\mathcal{N}(\mu, \sigma)$, $\mu = 0.0$, $\sigma = 0.01$
m_i	seed mortality of species i	See McQuoid et al. [2002]
s_i	sinking rate of species i	See Kamykowski et al. [1992], Olenina et al. [2006]
e	exchange rate between ocean and coast	0.64
γ_i	germination + resuspension rate of species i	$[0.1, 0.01, 0.001] * 0.5 * s_i$

Table 1: Definition of main parameters in our model [[These are not the notations from Wisnoski et al., 2019]]

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 and Melbourne [2016], Wisnoski et al. [2019], and previous findings in Picoche and Barraquand [2019a,b], to examine the effect on coexistence and feedbacks from the different compartments (ocean, coastal water column and bottom).

Model

Let's consider two steps in the discrete-time model: species first grow following a Beverton-Holt model for the coastal and oceanic cells, while seeds only survive. Then, we take into account exchange with the open-ocean and with the benthic seeds.

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

$$\begin{cases} N_{t+1,i,c} &= N_{t+h,i,c}(1 - s_i - e) + \gamma_i N_{t+h,i,b} + e N_{t+h,i,o} \\ N_{t+1,i,o} &= N_{t+h,i,o}(1 - e) + e N_{t+h,i,c} \\ N_{t+1,i,b} &= N_{t+h,i,b}(1 - \gamma_i) + s_i N_{t+h,i,c} \end{cases}$$

Interactions For the interactions, we can have $\alpha_{ij,c} \ll \alpha_{ij,o}$ ¹ and $\alpha_{ii} \sim 10|\alpha_{ij}|$ and $\alpha_{ij} \sim \mathcal{N}(\mu, \sigma)$ with μ and σ from Picoche and Barraquand [2019b] (that is, very approximately, around 0.0 and 0.01² for the coast (and have a fixed conversion ratio k from coast to ocean, $\alpha_{ij,c} = k\alpha_{ij,o}$?). We could also use the formula for the 20-species example in the Granger-causality paper (based on a beta-distribution and much less facilitation).

Just a note regarding $\alpha_{...,c} \ll \alpha_{...,o}$: it's the other way around in Griffiths et al. [2015].

Growth rate

$$r_i(T) = a_r(T_0) e^{E_r \frac{(\tau - \tau_0)}{k\tau\tau_0}} f_i(T) \quad (1)$$

$$\text{where } f_i(T) = \begin{cases} e^{-|T - T_i^{opt}|^3/b_i}, & T \leq T_i^{opt} \\ e^{-5|T - T_i^{opt}|^3/b_i}, & T > T_i^{opt} \end{cases} \quad (2)$$

$$\text{and } b_i \text{ is defined by numerically solving } \int r_i(\tau) d\tau = A \quad (3)$$

We could also use a simpler Gaussian distribution for the growth rate, as in Wisnoski et al. [2019].

¹This must be true for competition, but what happens for apparent facilitation? Does it change sign? Does it just decrease?

²I know it is not the same model, I am just starting with some values here...

Optimal temperature If we use eq. 1 to model growth rate, we will need optimal temperature. Contrary to what was done in the toy model of Picoche and Barraquand [2019a], I do not think a uniform law is realistic. We can have the *Asterionellopsis*-lookalike and *Skeletonema* *costatum* at the lower end (which would differentiate it from *Chaetoceros*), around 15. Others can be between 20 and 25. Note that it's 5 degrees above the observed mean in the REPHY dataset, but it's also the domain of application of the model from Scranton and Vasseur [2016].

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]. If we take a tidal time-step, $e=0.64$ (we can also say that we have a daily time step, see notes below).

Seed mortality For mortality, we have maximum values in McQuoid et al. [2002]. Average values could be taken from Fig. 3 in this same paper(?).

Assuming, m is the probability of mortality, the life duration L follow the distribution $p(L > l) = e^{-mk}$. We have maximum values, we can arbitrarily choose that for these values $p(L > l_{max}) = 0.05$. In this, $m = -\frac{\ln(p(L > l_{max}))}{l_{max}}$. We then have values around 10^{-4} d⁻¹.

We also have mean survival. In this case, $m = \frac{1}{l_{mean}}$.

We also have values from Montresor et al. [2013], but they are much higher as they could only keep species for a little more than a year (which goes against Sanyal et al. 2018). This can be explained by the fact that spores were kept in dark and cold environments, not exactly what they could encounter in the field.

A fixed mortality could also be taken from Hinners et al. [2019] (0.0097 d⁻¹), but this seems very high compared to previous values.

Sinking rate Sinking rate can be an indicator of size. (so there will be two traits in this model: optimal temperature and size).

Taking the formula from Kamykowski et al. [1992], $s_i = -22.90 \frac{A_i}{V_i} + 7.50$ where A_i is the surface area and V_i is the volume, and s_i is the sinking-velocity in m.s⁻¹: we can divide it by the mean water depth. We can find values for surface and volume in Olenina et al. [2006]. This estimate was computed on narcotized dinoflagellates, so we don't need to take into account swimming velocities BUT they do not necessarily have the same compositions. NOTE: if we use this formula, we have rates well over 1. Something might be missing. Might be because of constant mixing. How to take that into account? NOTE BIS: This is because this formula compute sinking velocities. These are not sinking rates, even with a dimensional analysis. I am not even sure we can go from one to the other.

Values can be taken directly from Smayda and Bienfang [1983] for certain dinoflagellates.

Sinking can also be related to other events (for instance, overcrowding leading to reproduction as in Eilertsen and Wyatt [2000], but reasons behind reproduction are still not clear... Best is related to shrinking as in D'Alelio et al. [2010], but for now, we do not have an explicit representation of the size variation).

According to Passow [1991] (who measured actual sinking rate), rates can vary between 1 and 30% for the same species (*Chaetoceros* spp.), with the most usual values around 10%. However, this is based on two diatoms only (one ciliate has a sinking rate of 1%... but it's a ciliate, it can swim). What about a log-normal law centered on $\ln(10)$? NOTE: A lot of authors talk about sinking rate but present sinking velocity.

Germination/resuspension Germination and resuspension might be difficult to differentiate. 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), which is confirmed by the review by Agrawal [2009]. Photoperiodicity does not seem to have a strong effect, but see Eilertsen et al. [1995]. However, day light will be correlated, even slightly, with temperature anyway.

Even though we have no estimation of germination and resuspension rate, we can try several values. Germination can be 1%, 0.1%, 0.01%. Resuspension can be half sinking rate (maybe ?). Resuspension will not really matter with these low values of germination.

Species

The basis for the species we use can be Barraquand et al. [2018], Picoche and Barraquand [2019b] and Montresor et al. [2013] (who also tested if the species they observed were able to sporulate). Keeping in mind that we only have model diatoms, and not actual species, we can still try to model “look alike” groups.

We can have one small and one big *Chaetoceros* species.

One *Skeletonema* (whose functioning will be very similar to *Chaetoceros*) ?

One *Thalassiosira* ? (very low survival in the sediment)

A very big one, like *Rhizosolenia* (used *Gyrodinium aureolum*)

Pseudo-Nitzschia (no spore found in Montresor et al., 2013), *Nitzschia*, *Navicula* (as a replacement for *Asterionellopsis*, based on biovolume and the fact that it is a pennate diatom)

Two dinoflagellates: *Gymnodinium* and *Prorocentrum* (both present in Barraquand et al. 2018; and both having mortality values in McQuoid et al., 2002, one low, one high).

See temporary choice in param_plankton.ods for now.

Results

References

- S. C. Agrawal. Factors affecting spore germination in algae - review. *Folia Microbiol*, 54(4):273–302, 2009.
- F. Barraquand, C. Picoche, D. Maurer, L. Carassou, and I. Aubry. Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127(12):1834–1852, 2018.
- C. E. Cáceres. Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proceedings of the National Academy of Sciences*, 94(17):9171–9175, 1997.
- Domenico D’Alelio, Maurizio Ribera d’Alcala, Laurent Dubroca, Diana Sarno, Adriana Zingone, and Marina Montresor. The time for sex: A biennial life cycle in a marine planktonic diatom. *Limnology and Oceanography*, 55(1):106, 2010.
- H.C. Eilertsen and T. Wyatt. Phytoplankton models and life history strategies. *South African Journal of Marine Science*, 22(1):323–337, 2000.
- Hc Eilertsen, S Sandberg, and H TÅžllefsen. Photoperiodic control of diatom spore growth; a theory to explain the onset of phytoplankton blooms. *Mar. Ecol. Prog. Ser.*, 116:303–307, 1995.
- M. Ellegaard and S. Ribeiro. The long-term persistence of phytoplankton resting stages in aquatic ‘seed banks’. *Biological Reviews*, 93(1):166–183, 2018.
- J.R. Griffiths, S. Hajdu, A.S. Downing, O. Hjerne, U. Larsson, and M. Winder. Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*, 125(8):1134–1143, 2015.
- J. Hinners, I. Hense, and A. Kremp. Modelling phytoplankton adaptation to global warming based on resurrection experiments. *Ecological Modelling*, 400:27–33, 2019.

- D Kamykowski, R E Reed, and G J Kirkpatrick. Comparison of sinking velocity, swimming velocity, rotation and path characteristics among six marine dinoflagellate species. *Marine Biology*, 113(2):319–328, 1992.
- M. R. McQuoid, A. Godhe, and K. Nordberg. Viability of phytoplankton resting stages in the sediments of a coastal Swedish fjord. *European Journal Phycology*, 37(2):191–201, 2002.
- M Montresor, C Di Prisco, D Sarno, F Margiotta, and A Zingone. Diversity and germination patterns of diatom resting stages at a coastal Mediterranean site. *Mar. Ecol. Prog. Ser.*, 484:79–95, 2013.
- V. Nguyen, Y. M. Buckley, R. Salguero-Gómez, and G. M. Wardle. Consequences of neglecting cryptic life stages from demographic models. *Ecological Modelling*, 408:108723, 2019.
- I. Olenina, S. Hajdu, L. Edler, A. Andersson, N. Wasmund, S. Busch, J. Göbel, S. Gromisz, S. Huseby, M. Huttunen, A. Jaanus, P. Kokkonen, I. Ledaine, and E. Niemkiewicz. Biovolumes and size-classes of phytoplankton in the Baltic Sea. *HELCOM Baltic Sea Environment Proceedings*, 106:144, 2006.
- U. Passow. Species-specific sedimentation and sinking velocities of diatoms. *Mar. Biol.*, 108(3):449–455, 1991.
- C. Picoche and F. Barraquand. How self-regulation, the storage effect, and their interaction contribute to coexistence in stochastic and seasonal environments. *Theoretical Ecology*, 2019a.
- C. Picoche and F. Barraquand. Strong self-regulation and widespread facilitative interactions between genera of phytoplankton. preprint, bioRxiv, 2019b.
- M. Plus, F. Dumas, J.-Y. Stanisière, and D. Maurer. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. *Continental Shelf Research*, 29(8):1008–1013, 2009.
- A. Sanyal, J. Larsson, F. van Wirdum, T. Andrén, M. Moros, M. Lönn, and E. Andrén. Not dead yet: Diatom resting spores can survive in nature for several millennia. preprint, bioRxiv, 2018.
- K. Scranton and D. A. Vasseur. Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. *Theoretical Ecology*, 9:353–363, 2016.
- L. G. Shoemaker and B. A. Melbourne. Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology*, 97(9):2436–2446, 2016.
- T. J Smayda. Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as “pelagic seed banks”. *Harmful Algae*, 1(1):95–112, 2002.
- T. J. Smayda and P. K. Bienfang. Suspension properties of various phyletic groups of phytoplankton and tintinnids in an oligotrophic, subtropical system. *Marine Ecology*, 4(4):289–300, 1983.
- N. I. Wisnoski, M. A. Leibold, and J. T. Lennon. Dormancy in metacommunities. *The American Naturalist*, 194(2):135–151, 2019.