# Methods

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### Model

We use the model developed by Shoemaker & Melbourne (2016); Wisnoski et al. (2019), and previous findings in Picoche & Barraquand (2019a,b).

We consider two steps in the discrete-time model: species first grow following a Beverton-Holt model for the coastal and oceanic cells, while seeds are only subject to a small mortality. Then, we take into account exchanges between the coast and the open-ocean, and between the water column and the benthos.

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

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

with growth rate defined according to Scranton & Vasseur (2016) (eq. 3).

$$r_{i}(T) = a_{r}(\tau_{0})e^{E_{r}\frac{(T-\tau_{0})}{kT\tau_{0}}}f_{i}(T)$$
where  $f_{i}(T) = \begin{cases} e^{-|T-T_{i}^{opt}|^{3}/b_{i}}, & T \leq T_{i}^{opt} \\ e^{-5|T-T_{i}^{opt}|^{3}/b_{i}}, & T > T_{i}^{opt} \end{cases}$ 
and  $b_{i}$  is defined by numerically solving 
$$\int r_{i}(\tau)d\tau = A$$
 (3)

Parameters and state variables definitions are given in Table 1.

Value (unit)	in the benthos (b) NA (Number of cells)	NA (K)	NA	$(K^3)$	293 (K) / 20 (°C)	$386(\frac{kg}{kg \times vear})^1$	0.467 (eV)	$8.6173324.10^{-5} (\text{eV.K}^{-1})$	(NA)	288 (K)	298 (K)	Adapted from Picoche & Barraquand (2019b)	$\mathcal{N}(\mu, \sigma), \mu = 0.0, \sigma = 0.01$ ; adapted from Picoche & Barraquand (2019b)	1.5	$\approx 10^{-4}/10^{-5}$ Values from on McQuoid et al. (2002)	$30\beta(0.55, 1.25)$ from values given in Passow (1991)	$s=s'_i$	$0.64 \mathrm{d}^{-1} \mathrm{from \; Plus} \;et al. \;(2009)$	$[0.1,0.01,0.001] * 0.5 * s_i$ (abitrary)
Name	Abundances of species i at time t in the coast (c) or ocean (o) water column, or in the benthos $(b)$	temperature	growth rate of species $i$	Normalization constant for the thermal decay rate	Reference temperature	Growth rate at reference temperature	Activation energy	Boltzmann's constant	Fraction of the maximum rate achieved for the $i^{th}$ species	Minimum thermal optimum	Maximum thermal optimum	Optimal temperature for species i	interaction strength of species j on i	conversion coefficient from coastal to oceanic interactions	seed mortality of species i	sinking rate of species i in a coastal environment	sinking rate of species $i$ in an oceanic environment	exchange rate between ocean and coast	germination + resuspension rate of species i
Param	$N_{t,i,c/o/b}$	L	$r_i(T)$	$b_i$	70	$a_r( au_0)$	$E_r$	k	$f_i(T)$	$T_{\min}$	$T_{\rm max}$	$T_i^{opt}$	$\alpha_{ij,c/o}$	$k_{c2o}$	$m_i$	$s_i$	$S_i'$	e	$\gamma_i$

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Table 1: Definition of variable states and parameters

#### Parameter definition

Interactions Interaction matrices are inspired by previous works on phytoplankton abundance time-series (Barraquand et al., 2018; Picoche & Barraquand, 2019b). The model used in these two papers is a multivariate autoregressive (MAR) model, that is a discrete-time linear model of the dynamics in which  $X_{t+1} = BX_t$  where  $X_t$  is the vector of log-abundances of the phytoplankton species and B is the interaction matrices. Based on Picoche & Barraquand (2019b),  $b_{ij,i\neq j} \sim \mathcal{N}(\mu,\sigma)$  with  $\mu$  and  $\sigma$  around 0.0 and 0.01. Centric diatoms, pennate diatoms and dinoflagellates can only interact with each other, i.e. the community matrix is modular. Self-regulation is computed as a function of vulnerability, with  $b_{ii} \sim -0.49b_{i.} - 0.37$ . Assuming that nutrients are rarer in the ocean than in the coast [ref],  $\alpha_{ij,c} << \alpha_{ij,o}$ , with a fixed coefficient k such that  $b_{ij,c} = k_{c2o}b_{ij,o}$ 

Certain et al.  $(2018)^2$  showed that MAR and Beverton-Holt interaction coefficients, respectively  $b_{ij}$  and  $\alpha_{ij}$ , could map once abundances at equilibrium  $N_i^*$  are defined.

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

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

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

We then sum on columns (on j).

$$\sum_{j} [b_{ij}(1 + f_A(i))] = -f_A(i)$$

$$\Leftrightarrow -f_A(i)(1 + \sum_{j} b_{ij}) = \sum_{j} b_{ij}$$

$$\Leftrightarrow f_A(i) = -\frac{\sum_{j} b_{ij}}{(1 + \sum_{j} b_{ij})}$$

$$\Leftrightarrow \alpha_{ij} = -\frac{1}{N_j^*} b_{ij} (1 - \frac{\sum_{j} b_{ij}}{1 + \sum_{j} b_{ij}})$$

$$\Leftrightarrow \alpha_{ij} = -\frac{1}{N_j^*} \frac{b_{ij}}{1 + \sum_{j} b_{ij}}$$

**Optimal temperature** To define each species growth rate according to daily temperature, species are defined according to their optimal temperature. In the toy model of Picoche & Barraquand (2019a), optimal temperatures followed a uniform law between 15 and 25°C. This does not seem realistic, especially if we look at the effect of temperature in Picoche & Barraquand (2019b). We can define two species preferring the cold (around 15°C), as we had Asterionellopsis and Skeletonema in our datasets, and the other preferring warmer temperatures (uniform law between 20 and 25°C).

Note that these temperature values are 5 degrees above the observed temperature mean in the REPHY dataset, but they are in the domain of application of the model from Scranton & Vasseur (2016).

This leads to growth rates between  $10^{-1}$  and  $10^{-8}$ . However, if we follow Reynolds (2006), such values should be vary between 0.7 and 1.8 (only considering Bacillariophyta), and may be calibrated on the surface/volume ratio instead of temperature.

**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 daily time-step and consider only the tide that takes place during the day, there is only one tide and then,  $e=0.64^3$ .

<sup>&</sup>lt;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>&</sup>lt;sup>2</sup>Corrected in the Appendices of Picoche & Barraquand (2019b)

<sup>&</sup>lt;sup>3</sup>We need to have very good arguments to take into account only one tide per day.

**Seed mortality 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 phytoplankon 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,  $m \propto 10^{-4} d^{-1}$ .

**Burying by deposition** Even when seeds can be resurrected, they are not accessible when they are below a certain depth. Deposition happens, which reduces the reachable stock of seeds<sup>4</sup>.

**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 for the others, around 1% for the others.

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  $s \sim \beta(0.55, 1.25) * 30$ .

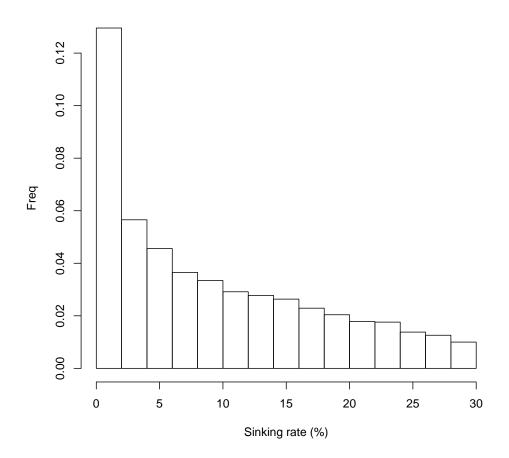


Figure 1: Possible distribution of sinking rates

<sup>&</sup>lt;sup>4</sup>No idea how to parameterize this. Arcachon tends to silt-up, by what rate? We also need to know the maximum depth of sediments which can resuspended through hydrodynamics. However, this might become a key parameter (much higher than mortality in the sediment).

We may have to force the values for species like Chaetoceros, Thalassiosira, to have higher sinking rates.

Germination/resuspension Germination and resuspension might be difficult to differentiate, they are defined by the same parameters ( $\gamma$  = resuspension\*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%. Resuspension is arbitrarily set as a function of sinking rate. Species that have the highest sinking rates have the lowest resuspension values, and conversely. We use only half of the resulting value (abritrary too). Contrary to what we previously thought, this value has a strong effect on the dynamics even though germination was supposed to be the most important.

Resuspension values vary from one publication to another: in Fransz & Verhagen (1985), resuspension rate of sediments is evaluated around  $5.10^{-5}$  day<sup>-1</sup> 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  $1.9.10^{-5}$  day<sup>-1</sup>, with a maximum sinking rate of 0.085 day<sup>-1</sup>. In Le Pape *et al.* (1999), resuspension rate of sediments and dead diatoms is 0.002 day<sup>-1</sup>.

Additional information regarding germination: 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). Photoperiodicity does not seem to have a strong effect according to this review (but see Eilertsen et al. (1995)). We could use a temperature threshold at 15°C, as we already take this temperature for the growth rate (Scranton & Vasseur, 2016).

### Species definition

The composition of the community is inspired by the most common species along the French coast (see time series in Picoche & Barraquand, 2019b), with a preference for species also present in McQuoid *et al.*  $(2002)^5$ .

- Chaetoceros (2 species) are one of the most common diatoms present along the French coast. We can define a small and big species among this genera, with potentially different sinking rates, related to their volume.
- Thalassiosira
- Skeletonema (also interesting because of a preference towards colder temperatures)
- Gyrosigma/Rhizosolenia (the idea behind is to have a very large species, maybe leading to higher sinking rate/lower growth rate?)
- Pseudo-Nitzschia and Nitzschia
- Asterionellopsis (also interesting because of a preference towards colder temperatures)
- Gymnodinium and Protoperidinium as two of the most common dinoflagellates

#### Intermediate results

Looking at species in isolation, we aim to obtain realistic abundances, that is of the same order of magnitude than observed abundances. Each compartment (ocean, coast, seed bank) contain  $10^6$  cells at the beginning of the simulation, which is run for 10000 time steps. Up to now, we focused on Chaetoceros species.

## References

Agrawal, S.C. (2009). Factors affecting spore germination in algae - review. Folia Microbiol, 54, 273–302.

Barraquand, F., Picoche, C., Maurer, D., Carassou, L. & Auby, I. (2018). Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127, 1834–1852.

Certain, G., Barraquand, F. & G, A. (2018). How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution*, 9, 1975–1995.

Eilertsen, H., Sandberg, S. & T, H. (1995). Photoperiodic control of diatom spore growth; a theory to explain the onset of phytoplankton blooms. *Mar. Ecol. Prog. Ser.*, 116, 303–307.

<sup>&</sup>lt;sup>5</sup>But if we finally ignore this paper as mortality in the sediment is too low, we might as well change this a bit

- 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.
- 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.
- 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.
- Passow, U. (1991). Species-specific sedimentation and sinking velocities of diatoms. Mar. Biol., 108, 449-455.
- Picoche, C. & Barraquand, F. (2019a). How self-regulation, the storage effect, and their interaction contribute to coexistence in stochastic and seasonal environments. *Theoretical Ecology*.
- Picoche, C. & Barraquand, F. (2019b). 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.
- 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.
- 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.