Interaction and growth

February 6, 2020

Starting Point

When necessary, environmental variable values or examples of genera are taken from the Auger station of the REPHY dataset, as it balances the most common and numerous diatom species and the longest time series.

Growth rates

Phytoplanktonic growth rates are highly variable, in situ or in experimental conditions. For ten strains in one genus only, and in the same experimental conditions, Balzano *et al.* (2011) have been able to detect growth rates between 0.5 and 1.25 day⁻¹, which corresponds more generally to the values found in the literature (between 0.2 and 1.78 for diatoms, 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 accommodate realistic, seasonal environment.

In order to alleviate this obstacle, equations deriving growth rates from temperatures are useful. The equation from Scranton & Vasseur (2016)s can be considered but their range of application is between 15°C and 25°C whereas the minimum temperature in Auger is 3°C, with a mean value around 15°C. This leads to unrealistically small growth rates.

Another, more general formulation, is the one by Bissinger *et al.* (2008), itself based on a previous work by Eppley (1972). The relationship between temperature and growth rate, evaluated on a large database¹, is then $r(T) = 0.81e^{0.0631T}$, with T in °C. This represents the daily growth rate with 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.²

Interaction matrix

Interaction matrices are inspired by previous works on phytoplankton abundance time-series (Barraquand et al., 2018; Picoche & Barraquand, 2019). 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 $(2019)^3$, random values can be taken as $b_{ij,i\neq j} \sim \mathcal{N}(\mu,\sigma)$ with μ and σ 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 $b_{ii} \sim -0.49b_{i.} - 0.37$. However, we can also directly use the interaction matrix from Auger. Assuming that nutrients are rarer in the ocean than in the coast, competition in the ocean is considered higher than along the coast, and $\alpha_{ij,c} << \alpha_{ij,o}$, with a fixed coefficient k such that $b_{ij,c} = k_{c2o}b_{ij,o}$.

Certain et al. $(2018)^4$ showed that MAR and Beverton-Holt interaction coefficients, respectively b_{ij} and α_{ij} , could map once abundances at equilibrium N_i^* are defined.

¹1,501 data points from several studies

²It should however be noted that, contrary to the values obtained with the SV equations, the Bissinger formulation does not lead to real blooms (that is, a very large range of abundance values, covering up to 6 orders of magnitude, between winter and spring).

³However, strong variability between sites and calibration on biweekly data (so, we should actually use $\mathbf{B}^{\frac{1}{15}}$ but this leads to complex numbers and right now, I'm not sure what to do with that).

⁴Corrected in the Appendices of Picoche & Barraquand (2019)

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

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

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

We then sum on columns (on j).

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

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

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

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

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

This gives an exact correspondence between α_{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 su an additional calibrations of parameter could lead to more realistic simulations. Followin their example, we use quadratic programming (Bazaraa *et al.*, 2013), applied to interaction matrices and growth rates⁵.

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 $\mathbf{G}\mathbf{x} >= \mathbf{h}$.

Here, $\mathbf{C} = \mathbf{I}$, $\mathbf{d} = [\operatorname{vec}(\mathbf{A}^T) \mathbf{r}']$ where \mathbf{A} is the interaction matrix, $\mathbf{r}' = -(\mathbf{e}^{\mathbf{r}} - \mathbf{1})$ 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 vectore 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).

References

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.

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.

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.

⁵Actually, Maynard et al. 2019 uses a Least Square Inverse Problem solver, with a package (limSolve::lsei) that also offers quadratic programming

- 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.
- 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.
- Eppley, R. (1972). Temperature and phytoplankton growth in the sea. 70.
- Maynard, D.S., Wootton, J.T., ServÃjn, C.A. & Allesina, S. (2019). Reconciling empirical interactions and species coexistence. *Ecology Letters*, 22, 1028–1037.
- Picoche, C. & Barraquand, F. (2019). Strong self-regulation and widespread facilitative interactions between genera of phytoplankton. preprint, bioRxiv.
- Scranton, K. & Vasseur, D.A. (2016). Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. *Theoretical Ecology*, 9, 353–363.