Steps

$$1-\begin{cases} N_{t+h,i,c} &= \frac{e^{r_i(T)}N_{t,i,c}}{1+\sum_j \alpha_{ij}N_{t,j,c}} - lN_{t,i,c} \\ N_{t+h,i,o} &= \frac{e^{r_i(T)}N_{t,i,o}}{1+k_{c2o}\sum_j \alpha_{ij}N_{t,j,o}} - lN_{t,i,o} \\ N_{t+h,i,b} &= N_{t,i,b}(1-m-\zeta) \end{cases}$$

$$2-\begin{cases} N_{t+1,i,c} &= N_{t+h,i,c}(1-s_i-e)+\gamma N_{t+h,i,b}+eN_{t+h,i,o} \\ N_{t+1,i,o} &= N_{t+h,i,o}(1-s_i-e)+eN_{t+h,i,c} \\ N_{t+1,i,b} &= N_{t+h,i,b}(1-\gamma)+s_iN_{t+h,i,c} \end{cases}$$

Param	Name	Value (unit)
$N_{t,i,c/o/b}$	Abundances of species i at time t (coast, ocean, benthos)	NA (Number of cells)
T	temperature	NA (K)
r_i(T)	maximum growth rate of species i	NA
$\alpha_{ij,c/o}$	interaction strength of species j on i	Adapted from Picoche&Barraquand 2020
k_{c2o}	conversion coefficient from coastal to oceanic interactions	1.5 [arbitrary]
s_i	sinking rate of species i	$\{0.1; 0.3; 0.5\}\beta(0.55, 1.25)$
e	exchange rate between ocean and coast	{0.4 ; 0.6 ; 1}
l	loss of vegetative phytoplankton (predation, mortality...)	0.04
m	cyst mortality	$\approx 10^{-4}/10^{-5}$
ζ	cyst burial	{0.01 ; 0.1 ; 0.3}
γ	germination × resuspension rate of species	{0.1;0.01;0.001} * {10^{-5},0.1}

Table 1: Definition of main state variables and parameters of the model. Fixed values or distributions are estimated from the literature. When a set or a range of values is given, the sensitivity of the model related to changes in parametes has been assessed.

Saturating interactions

$$N_{t+h,i,c} = \frac{e^{r_i(T)}N_{t,i,c}}{1+\sum_j \alpha_{ij}N_{t,j,c}} - lN_{t,i,c}$$

There are both competitive (α_{ij}>0) and facilitative (α_{ij}<0) interactions, which means that the denominator $1+\sum_j \alpha_{ij}N_{t,j,c}$ can be very close to 0, or negative, thus leading to unrealistic growth rate values. Ignoring possible overyielding, we should have $\sum \alpha_{ij}N_{t,j,c} \geq 0$, as $e^{r_i(T)}$ is considered a maximum growth rate in ideal conditions.

For now, coefficients are directly adapted from the MAR model (exact equivalence).

We consider saturating interactions, for both competition and facilitation. I did not find direct formulations of such feature in a Beverton-Holt growth model. My only idea is loosely based on the Unique Interaction Model of Qian and Akçay (2020) who however use a continuous-time, linear model. I only added a saturating competition in addition to saturating facilitation:

$$N_{t+h,i,c} = \frac{e^{r_i(T)}N_{t,i,c}}{1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_{t,j,c}}{h_C+N_{t,j,c}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_{t,j,c}}{h_F+N_{t,j,c}}} - lN_{t,i,c}$$

where $\mathbb{C}$ and $\mathbb{F}$ are the sets of competitive and facilitative interactions.

Jacobian

We can try and start with a simplified version of the model, without the loss term.

$$N_{t+1,i} = \frac{e^{r_i}N_{t,i}}{1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_{t,j}}{h_C+N_{t,j}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_{t,j}}{h_F+N_{t,j}}}$$

Let's have $n_{t,i} = \log(N_t)$.

$$n_{t+1,i,c} = r_i + n_{t,i} - \log(1 + \sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_{t,j}}{h_C + N_{t,j}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_{t,j}}{h_F + N_{t,j}})$$

We assume that there is an equilibrium for $N_i = e^{n_i}$ (we just remove the time subscript) and we have $X_i = \log(1 + \sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_j}{h_C+N_j} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_j}{h_F+N_j})$. We want to compute $\frac{\partial X_i}{\partial n_i}$ and $\frac{\partial X_i}{\partial n_j}$.

$$\frac{\partial X_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i}\frac{\partial N_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i}e^{n_i}$$

Let's take it step by step: $X_i = \log(u(N_i))$ and $u(N_i) = 1 + \sum_j \frac{f_i(N_j)}{g_{\bullet}(N_j)}$ where $g_{\bullet}(N_j)$ can be either $h_C + N_j$ or $h_F + N_j$. The sum on j can be simplified by the derivation:

$$\frac{\partial u_i}{\partial N_j} = \partial\frac{\alpha_{ij}N_j}{h_{\bullet} + N_j}\frac{1}{\partial N_j} = \frac{a_{ij}(h_{\bullet} + N_j) - a_{ij}N_j}{(h_{\bullet} + N_j)2} = \frac{a_{ij}}{(h_{\bullet} + N_j)^2}$$

Therefore,

$$\frac{\partial X_i}{\partial n_j} = \frac{a_{ij}h_{\bullet}}{(h_{\bullet} + N_i)2}\frac{N_j}{\left(1 + \sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_j}{h_C+N_j} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_j}{h_F+N_j}\right)}$$

If we have b_{ij} the MAR coefficients:

$$\begin{cases} b_{ii} - 1 = & \frac{a_{ii}h_C}{(h_C+N_i)2}\frac{N_i}{\left(1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_j}{h_C+N_j}+\sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_j}{h_F+N_j}\right)} \\ b_{ij,i\neq j} = & \begin{cases} \frac{a_{ij}h_C}{(h_C+N_j)2}\frac{N_j}{\left(1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_j}{h_C+N_j}+\sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_j}{h_F+N_j}\right)} & \forall a_{ij}\in\mathbb{C} \\ \frac{a_{ij}h_F}{(h_F+N_j)2}\frac{N_j}{\left(1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_j}{h_C+N_j}+\sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_j}{h_F+N_j}\right)} & \forall a_{ij}\in\mathbb{F} \end{cases} \end{cases}$$