Size-dependent clustering in phytoplankton communities in a 3D environment

Coralie Picoche[1,2,*] & Frédéric Barraquand[1,2]

[1]Institute of Mathematics of Bordeaux, University of Bordeaux and CNRS, Talence, France [2]Integrative and Theoretical Ecology, LabEx COTE, University of Bordeaux, Pessac, France

Introduction

Material and methods

Brownian bug model

The Brownian Bug Model (BBM) describes particles going through demographic processes (replication and death) in a turbulent and viscous environment. It has been developed in its 2-dimension, monospecific version in Young *et al.* (2001), which we now extend to 3 dimensions and to multiple species having different demographic and hydrodynamics behaviours. The Brownian Bug Model is a discrete-time, individual-based model where each particle is characterized by its species i and its position $\mathbf{x}^T = (x\,y\,z)$. During each time step of duration τ, events unroll as follow:

1. demography: each particle can either reproduce with probability p (forming a new particle of the sames species i at the same position $\mathbf{x}$), die with probability q, or remain unchanged with probability 1-p-q.
2. diffusion: each particle moves to a new position $\mathbf{x}(t+t') = \mathbf{x}(t) + \delta\mathbf{x}(t)$ where each element of $\delta\mathbf{x}(t)$ follows a Gaussian distribution $\mathcal{N}(0,\Delta)$ with $D = \frac{\Delta^2}{2\tau}$ the diffusivity.
3. turbulence: each particle is displaced by a turbulent flow, following the Pierrrehumbert map (Pierrehumbert, 1994), adapted in its 3D-version (Ngan & Vanneste, 2011).

$$\begin{cases} x(t+\tau) &= x(t+t') + U\tau/2\cos\left(ky(t+t') + \phi(t)\right) \\ y(t+\tau) &= y(t+t') + U\tau/2\cos\left(kz(t+t') + \theta(t)\right) \\ z(t+\tau) &= z(t+t') + U\tau/2\cos\left(kx(t+\tau) + \psi(t)\right) \end{cases}$$

where $U\tau/2$ determines the final velocity of the particle, $k = 2\pi/L_s$ is the wavenumber for the flow at the length scale L_s (see below) and $\phi(t)$, $\theta(t)$, $\psi(t)$ are random phases uniformly distributed between 0 and 2π.

Parameter values

We model two types of organisms: diatoms (focusing on the microphytoplanktonic size fraction, i.e. between 20 and 200 μm) and nanophytoplankton-size particles (defined by a diameter between 2 and 20 μm). These two groups are characterized by high-diffusivity and slow-growth particles vs. low-diffusivity and fast-growth particles, respectively. Particles are displaced by a turbulent fluid whose velocity defines the time scale of the whole model: we give here the reasoning behind parameter values, keeping in mind that our model can only be semi-quantitative. Main parameter definitions and values are given in Table 1.

Advection

We first consider the advection process, due to the turbulence of the environment. We only consider the Batchelor-Kolmogorov regime, i.e. the Reynolds number $Re \approx 1$ and two particles previously at the same position are separated by a distance lower than k^{-1}.

$$Re = \frac{V}{k\nu} \approx 1$$

where $\nu = 10^{-6}$ m^2/s is the kinematic viscosity for water. Here, we consider the smallest wavenumber corresponding to the largest length scale (Kolmogorov scale), i.e. $k = 2\pi/L_s$, with $L_s \approx 1$ cm in the ocean (Barton *et al.*, 2014).

$$\begin{aligned} 1 &\approx \frac{VL_s}{2\pi\nu} \\ U &\approx \frac{2\pi\nu}{L_s} \end{aligned}$$

This means that U=6.3×10^{-4} m.s^{-1}=5.4×10^3 cm.d^{-1}. Using $U\tau/2 = 0.5$ cm as in Young *et al.* (2001), we would have $\tau = 2 \times 10^{-4}$d= 16s.

Diffusion

If we use the Stokes-Einstein equations (Einstein, 1905, cited from Dusenbery, 2009), diffusivity can be computed according to the formula:

$$D = \sqrt{\frac{RT}{N_A}\frac{1}{6\pi\eta a}} \qquad (1)$$

where $R = 8.314$J.K^{-1}.mol^{-1} is the molar gas constant, $T = 293K$ is the temperature, $N_A = 6.0225 \times 10^{23}$ is Avogadro's number, $\eta = 10^{-3}$m^{-1}.kg.s^{-1} is the viscosity of water and a is the radius of the organism considered.

Using $D = \frac{\Delta^2}{2\tau}$,

$$\begin{aligned} \Delta &= \sqrt{2\tau D} \\ \Leftrightarrow \Delta &= \sqrt{\frac{RT}{N_A}\frac{\tau}{3\pi\eta a}} \end{aligned}$$

We consider $a_n = 1.5\mu$m for nanophytoplankton and $a_d = 25\mu$ m for diatoms, which allows us to compute Δ_n and Δ_d.

Ecological processes

For both diatoms and nanophytoplankton organisms, $p = \lambda\tau$ with λ the growth rate and τ the duration of a timestep. We study the community at equilibrium, i.e. $p = q$. We use a diatom doubling rate of 1d^{-1} (Bissinger *et al.*, 2008) and consider the fastest-growing nanophytoplankton particles, corresponding to a diameter of 3 μm (Bec *et al.*, 2008), for which the doubling rate is between 2 and 3 d^{-1} (set to 2.5 d^{-1} here).

Parameter	Definition	Value
p_d, q_d	Probability of reproducing/dying for diatom particles	$2\,10^{-4}$
p_n, q_n	Probability of reproducing/dying for nanophytoplankton particles	$5\,10^{-4}$
$U\tau/2$	Stretching parameter proxy	0.5 cm
Δ_d	Diffusion parameter for diatoms	5×10^{-5} cm
Δ_n	Diffusion parameter for nanophytoplankton particles	2×10^{-4} cm

Table 1: Definitions and values of the main parameters used in the 3D Brownian Bug Model, assuming the duration of a time step τ is 16 seconds.

Metrics

Aggregation can be quantified by different spatial biodiversity indices (Rajala & Illian, 2012); we focus here on the pair correlation function and the dominance indices. The computation of both indices was checked on known distributions (Poisson and Thomas processes) before being applied to the Brownian Bug Model simulations (see Supplementary Material).

Pair correlation function

The pair correlation function (pcf, also written $g(r)$) is a measurement of particle aggregation. It can either be computed for a single species (monospecific pair correlation function, $g_{ii}(r)$ for species i) or between species (multispecific pair correlation function, $g_{ij}(r)$ for species i and j, with $i \neq j$). Let's define C_i and C_j the concentrations of species i and j respectively, and $P_{ij}(r)$ the probability of finding a particle of species i in the sphere dV_1 and a particle of species j in the sphere dV_2 where the centers of dV_1 and dV_2 are serated by distance r.

$$P_{ij}(r) = C_i C_j dV_1 dV_2 g_{ij}(r)$$

When $g_{ij}(r) > 1$, particles are aggregated, and they are segregated when $g_{ij}(r) < 1$.

Computation of the pcf was heavily based on the function `pcf3est` in spatstat 2.2-0 (Baddeley *et al.*, 2015), slightly modified to also compute cross-specific pcf.

Dominance index

The dominance index is presented in Wiegand *et al.* (2007). Let $M_{i\bullet}(r)$ be the average number of individuals within a circle of radius r around an individual of species i. $M_{ii}(r)$ corresponds to the conspecific neighbourhood and $M_{io}(r)$ corresponds to individuals of all other species. In this case,

$$d_i(r) = \frac{M_{ii}(r)}{M_{ii}(r) + M_{io}(r)}$$

In case of intraspecific clustering, $d_i(r)$ tends to 1 while it tends to $1/S$, with S the number of species, when the distribution of particles is uniform.

Scale of the study

As we examine particle clustering or segregation and their potential effects on interactions between species, we consider two main processes: direct interactions due to, e.g., competition for nutrients, auxotrophy or allotrophy, and emerging interactions due to predation.

Direct interactions due to a given chemical (whether a resource or a toxin) can only take place if the chemical concentration is relevant for the particle. We therefore need to define the volume around each particle in which microscale interactions can take place before the dilution effect of diffusion and turbulence take over. This volume will be called the phycosphere hereafter (Seymour *et al.*, 2009). Particles with different sizes have different ranges of effects. Based on a 3 μm diameter, the nanophytoplankton phycosphere radius should be around around 5 μm Seymour *et al.* (2009). The maximum distance between two particles of nanophytoplankton is therefore around 10 μm. This corresponds to range of meaningful values between 3×10^{-4} cm and 1×10^{-3} cm. We defined diatoms as 50 μm-diameter particles with a corresponding phycosphere of about 1200 μm (Seymour *et al.*, 2009), which means that we can consider radii between 5×10^{-3}cm and 2.4×10^{-1} cm.

Predators, on the contrary, are not likely to be as restricted as they have a larger detection range. We therefore also look at the overall distribution of species, between 10^{-4} and 1 cm, but should keep in mind that processes affecting diversity maintenance are not the same at different scales.

We use our model near Re≈ 1 (Re, Reynolds number), i.e. we are working at a scale around 1 cm. The space in which particles are moving is made of several cubes of side 1 cm. We consider a volume of 1000 cm^3 for diatoms and 8 cm^3 for nanophytoplankton (volumes are adapted to balance realistic concentrations and computation time) with periodic boundary conditions. We run an idealized simulation with 3 species with an even abundance distribution of about 10^4 C/L for diatoms (Picoche & Barraquand, 2020) and 10^6 C/L for nanophytoplankton particles (Edwards, 2019). We then model a more realistic community with 10 species having a skewed abundance distribution (between 55 000 and 400 particles, according to observations of field abundance distributions in Picoche & Barraquand, 2020).

Results

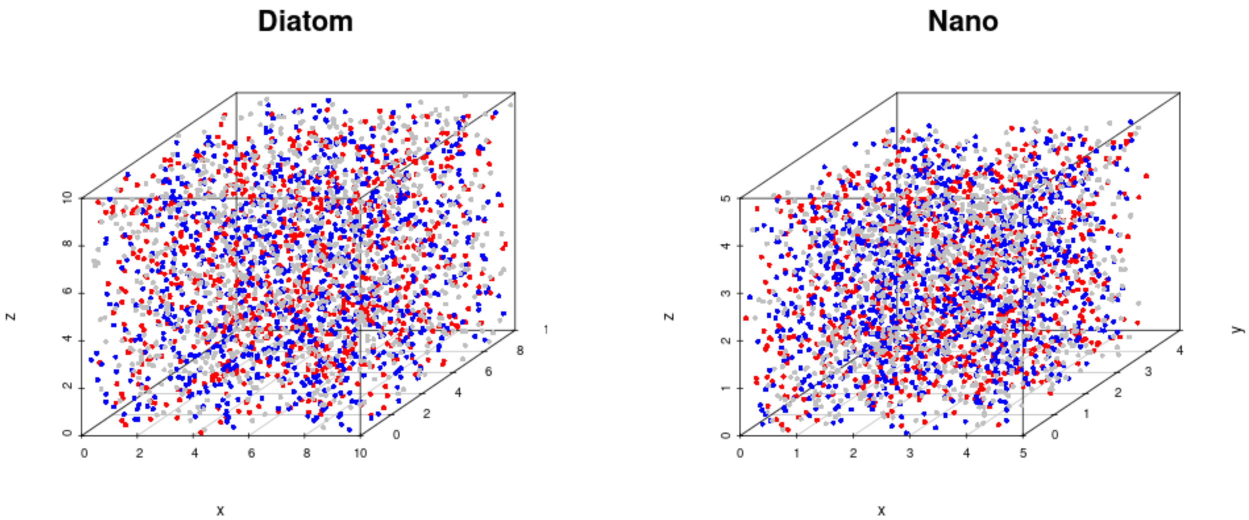

Figure 1: Example of distributions for diatoms and nanophytoplankton after 1000 time steps, starting with 1000 C/L and 10 000 C/L respectively.

We find that particles are strongly clustered, with only small differences between the dominance distributions of diatom and nanophytoplankton-particles (Fig. 2, pcf are shown in the SI).

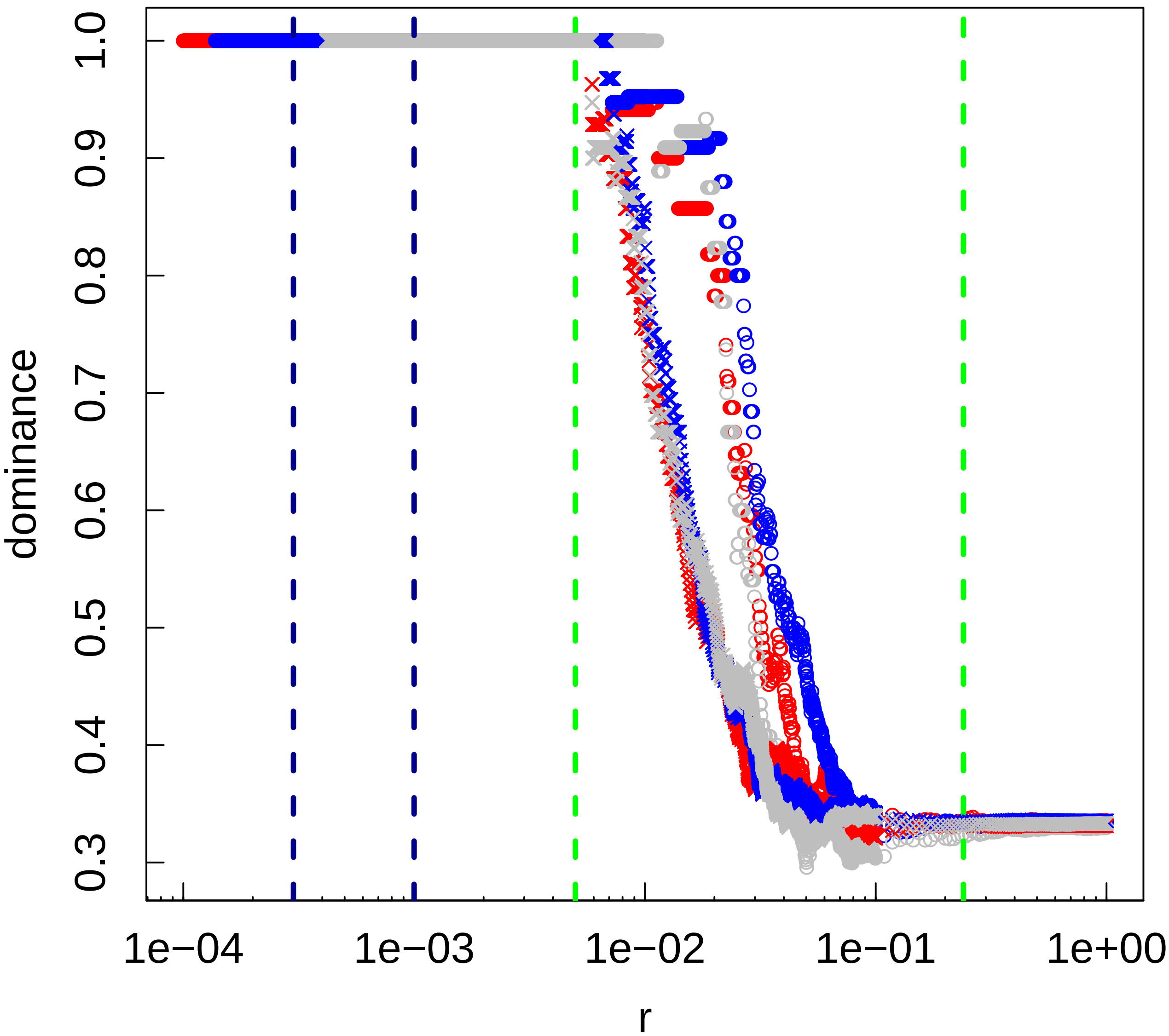

Figure 2: Dominance index for 3 species of diatoms (circles) and nanophytoplankton particles (crosses) with an even abundance distribution after 1000 time steps. Limits of interactions between particles for diatoms and nanophytoplankton are indicated by green (diatoms) and blue (nanophytoplankton) dashed lines.

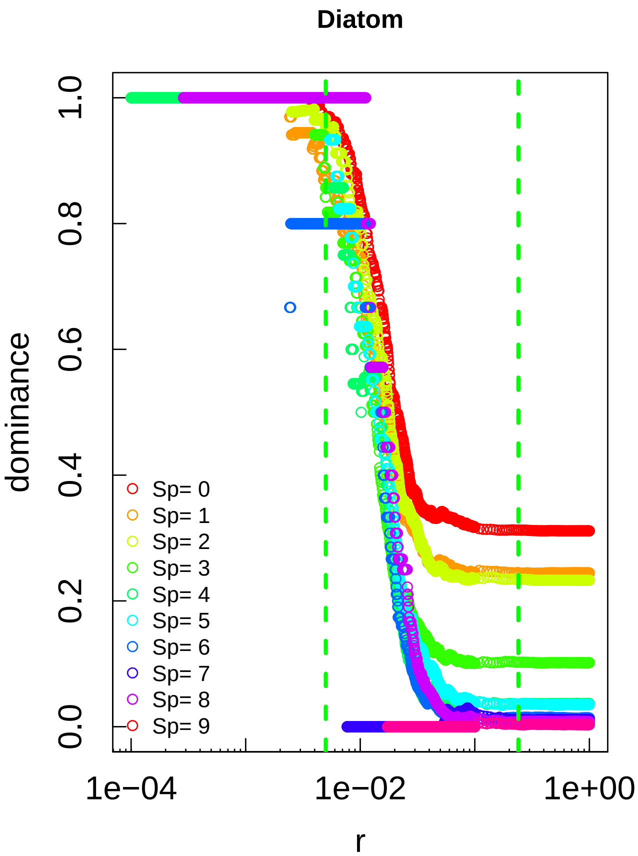

Figure 3: Dominance index for 10 species of diatoms (circles) and nanophytoplankton particles (crosses) with a skewed abundance distribution after 1000 time steps. Species are ordered by decreasing initial abundance in the legend. Limits of interactions between particles for diatoms and nanophytoplankton are indicated by green (diatoms) and blue (nanophytoplankton) dashed lines.

Discussion

References

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