

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

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Introduction

Phytoplankton communities are among the most important photosynthetic groups on Earth, being at the bottom of the marine food chain, and responsible for half the global primary production (Field *et al.*, 1998). Their contribution to ecosystem functions is only matched by their significance for more theoretical studies focusing on coexistence within a single trophic level. Indeed, phytoplankton communities are characterized by a surprisingly high biodiversity (up to hundreds of species within multiple genera and even classes in volumes as small as 10 mL), an observation which has led to the formulation of the so-called “paradox of the plankton” (Hutchinson, 1961). This term refers to the conflict between the observed diversity maintenance of species competing for similar resources in a seemingly homogeneous environment, and theoretical expectations of a few species outcompeting the others. Phytoplankton models for coexistence are now as diverse as their model organism (Record *et al.*, 2014). Proposed mechanisms to escape from competitive exclusion are based on the general literature on coexistence, which includes non-linear responses to the environment in a temporally fluctuating environment (Li & Chesson, 2016; Chesson, 2018), in a nonspatial setting, i.e. keeping the premise of a homogeneous environment. Such assumption needs to be challenged, as we know that spatialized models including a heterogeneous environment and/or non-mixed populations can lead to highly different outcomes from their nonspatial counterparts (Law *et al.*, 2003). This is even more relevant as field observations themselves have highlighted phytoplankton patchiness for more than a century (Bainbridge, 1957), from the macro- to the micro-scale (Leonard *et al.*, 2001; Doubell *et al.*, 2006; Font-Muñoz *et al.*, 2017).

Phytoplankton patchiness can at least be partly explained by the hydrodynamics of their environment (Martin, 2003): their size being mostly below the size of the smallest eddy (i.e., the Kolmogorov scale) in a typical environment such as the ocean, they are mostly embedded in viscous micro-structures at the individual level (Peters & Marrasé,

2000), but are still displaced by a common flow at the larger scale, due to turbulence. Viscosity decreases diffusivity, which can in turn generate an heterogeneous landscape by limiting movements and mixing. On the other end of the hydrodynamics spectrum, studies on the fluid mechanics of phytoplankton show that a turbulent flow, sometimes associated with other phenomena such as motility can encourage the formation of clusters (Reigada *et al.*, 2003; Durham *et al.*, 2013; Arrieta *et al.*, 2015; Breier *et al.*, 2018). Turbulence also affects phytoplankton organism interactions with their environment (Guasto *et al.*, 2012), by increasing nutrient consumption (Peters *et al.*, 2006) and encounter rates with either potential partners or predators (Kjørboe, 2018), therefore affecting organism growths: there can be an effect of the general movements of water on the ability of individuals to survive and reproduce, whether sexually or asexually (by fission).

This leads us to consider demography in the context of environmental variation created by hydrodynamics processes. Indeed, including simple processes such as reproduction and death in a spatial model can also create a patchy environment: individuals are born close to their parents, whereas mortality is a global phenomenon, which can lead to clusters of ‘family’ by itself (Young *et al.*, 2001). When hydrodynamics processes are considered, provided that the separation between parents and offsprings is not too fast to offset family aggregation, i.e. if turbulence and/or diffusion are not too high, including individual reproduction encourage a strong spatial structure by itself (Young *et al.*, 2001; Bouderbala *et al.*, 2018). Observed patchiness can therefore be reproduced in models taking into account basic mechanisms governing the life of phytoplankton organisms. This can have a strong impact if we consider the community level: intraspecific clustering itself is important as it increases the likelihood of a particle interacting with a conspecific as opposed to an heterospecific. Knowing that a high intra-to-interspecific interaction strength is associated with coexistence in models (Levine & HilleRisLambers, 2009; Barabás *et al.*, 2017) and often observed in the field (Adler *et al.*, 2018; Picoche & Barraquand, 2020), species-specific clustering might be key to diversity maintenance.

However, spatial models of individuals at the microscale rarely include multiple species (Bouderbala *et al.*, 2018; Breier *et al.*, 2018), but it is clear that individual clustering can be enforced at the species level, as individuals of the same species share common parameters which rule their reaction to their environment. For example, experiments often relate a major trait of phytoplankton organisms, their size, to the viscosity of their environment (Guadayol *et al.*, 2021), reaction to turbulence (Barry *et al.*, 2015), or growth rates (Edwards *et al.*, 2012). On a more theoretical point of view, Barton *et al.* (2014) have already shown that coexistence between organisms of different sizes can be increased by the presence of turbulence. While taking diversity of organisms into account is the first step towards studying coexistence in spatial models, the lack of studies with multiple species can be explained by the computational cost of modeling many individuals, especially as very large numbers are required for phytoplankton organisms which can reach 10^6 individuals per liter, for many species. Numerical costs could be partially offset by favoring mathematical analyses of spatial models, which can predict spatial distributions in many scenarii.

Mathematical analyses of spatial models can quantify the degree of clustering in the environment by measuring

correlations between positions of pairs (or more) of particles (Illian *et al.*, 2008). A model of individuals randomly reproducing and moving in space, which is the type we have focused on here, is also called a spatial point process, for which a master equation can often be derived (Dieckmann & Law, 2000; Birch & Young, 2006) to describe the behaviour of the particles through time. The moment measures, which can be seen as the extension of moments of random variables, can also be used to compute the expected characteristics of the spatial distribution of individuals (Plank & Law, 2015). However, the moments of a process are mainly mathematical quantities which then need to be related to ecological processes (see, e.g., Bolker & Pacala, 1999, in which possible spatial strategies for population survival are identified), an endeavour often lacking in phytoplankton spatial models.

Here, we present the Brownian Bug Model (BBM), a 3D, individual-based model including turbulence and diffusion, as well as births and deaths, based on Young *et al.* (2001), with parameter values adapted to the physical properties of the environment and the organisms we study. We differentiate between organisms of different sizes and simulate multiple species within a single community. We are able to provide both numerical simulations and analytical formula to quantify the degree of intra- and interspecific clustering of organisms, which enables us to characterize the composition of their vicinity for different distances from a particle, and use this information to make informed guess about mechanisms supporting diversity within different communities of phytoplankton.

Material and methods

Brownian bug model

The Brownian Bug Model (BBM) describes the dynamics of particles going through demographic processes in a turbulent and viscous environment, in continuous space and time. It has been developed in its 2-dimension, monospecific version in Young *et al.* (2001), which we now extend to 3 dimensions and to S species having specific demographic and hydrodynamic properties.

In this model, we consider several populations of particles, each individual being characterized by its species i and its position $\mathbf{x}^T = (x\ y\ z)$. The population dynamics are modeled by a linear birth-death process with birth rate λ and death rate μ . Each particle independently follows a Brownian motion with diffusivity D , and is advected by a common stochastic flow modeling the turbulence with stretching parameter γ , meaning that the separation $s(t)$ between two points previously on top of each other follows $s(t) \propto e^{3\gamma t}$. We focus here on ecologically relevant quantities which can be extracted from this model, both analytically and numerically.

For numerical simulations, this model needs to be discretized. During each time step of duration τ , events unroll as follow:

1. demography: each particle can either reproduce with probability $p = \lambda\tau$ (forming a new particle of the same species i at the same position \mathbf{x}), die with probability $q = \mu\tau$, 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 Pierrehumbert map (Pierrehumbert, 1994), adapted in its 3D-version (Ngan & Vanneste, 2011).

$$\begin{cases} x(t + \tau) &= x(t + t') + U\tau/3 \cos(ky(t + t') + \phi(t)) \\ y(t + \tau) &= y(t + t') + U\tau/3 \cos(kz(t + t') + \theta(t)) \\ z(t + \tau) &= z(t + t') + U\tau/3 \cos(kx(t + \tau) + \psi(t)) \end{cases}$$

where U is the maximum 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 .

Particles are distributed in a cube of side L , with periodic boundary conditions.

Characterization of the spatial distribution

Let W be the observation window we are working on (here, the cube). The state of the system at time t can be described as a collection of S populations, where the population of species i is made of k_i particles randomly distributed in W , with positions $\mathbf{X}_i = [\mathbf{x}_{1,i}, \mathbf{x}_{2,i}, \dots, \mathbf{x}_{k_i,i}]$. It is a realization of the spatial point process deriving from a stochastic, spatialized individual-based model such as the Brownian Bug Model. One of the most common methods to describe a spatial point process is through its moments, that can be theoretically derived and allow us to check our simulations. Here, we also present the dominance index, on which we focus later on for its ecological relevance.

Moments

The first moment is the intensity of the process, or concentration of particles $C_i(t) = \frac{N_i(W)}{V(W)}$ where $N_i(W)$ is the number of particles of species i in the cube and $V(W) = L^3$ is the volume of the cube; it does not give any information regarding the spatial distribution, and possibly spatial correlation between particles.

The second moment, hereafter referred to as the pair correlation function $g(r, t)$, or pcf, can be thought of as the mean number of points at distance r of a particle. If we define $C_i(t)$ and $C_j(t)$ the concentrations of species i and j respectively, and $P_{ij}(r, t)$ 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 separated by distance r , we can write:

$$P_{ij}(r, t) = C_i(t)C_j(t)dV_1dV_2g_{ij}(r, t) \quad (1)$$

The pcf is commonly used to describe spatial point patterns (see formula for other standard processes in the Supplementary). In the Brownian Bug Model, we can show that the intraspecific pcf g_{ii} follows eq. 2 (see Appendices).

The system stabilizes in the presence of advection, but depends on time in its absence.

$$g_{ii}(r, t) = \begin{cases} 1 + \frac{\lambda}{4D\pi r C_i} \left\{ 1 - \operatorname{erf} \left(\frac{r}{\sqrt{8Dt}} \right) \right\} & \text{for } U = 0 \\ 1 + \frac{\lambda}{2\pi C_i} \left(\frac{\sqrt{\gamma} \arctan \left(\frac{\sqrt{\gamma} r}{\sqrt{2D}} \right)}{2^{3/2} D^{3/2}} + \frac{1}{2Dr} - \frac{\pi \sqrt{\gamma}}{2^{5/2} D^{3/2}} \right) & \forall U > 0 \end{cases} \quad (2)$$

As populations of different species do not directly interact, they constitute a random superposition of stationary point processes (Illian 2008) and $g_{ij}(r, t) = 1 \ \forall i \neq j, U$.

Related to the pair correlation function is the Ripley's K function, through equation eq. 3.

$$g(r) = \frac{K'(r)}{4\pi r^2} \quad (3)$$

The Ripley's K-function $K(r)$ is the average number of points surrounding a particle within a sphere of radius r (Illian *et al.*, 2008).

$$\forall r \geq 0, K(r) = \frac{1}{C} \mathbb{E} (N(b(o, r) \setminus \{o\})) \quad (4)$$

where C is the concentration of particles and $N(b(o, r) \setminus \{o\})$ is the number of points of the process N in the sphere of radius r centred on o , not counting o itself.

This definition can be extended to multivariate processes. $C_j K_{ij}(r)$ is the mean number of points of species j in a sphere of radius r centred on a point of species i .

$$\forall r \geq 0, K_{ij}(r) = \frac{1}{C_j} \mathbb{E}_i (N_j(b(o, r))) \quad (5)$$

where \mathbb{E}_i is the mean with respect to points of species i .

Thanks to eq. 3, we can show that:

$$K_{ii}(r, t) = \begin{cases} \frac{4}{3}\pi r^3 + \frac{\lambda}{C_i D} \left(\frac{r^2}{2} - \frac{1}{2} \operatorname{erf} \left(\frac{r}{\sqrt{8Dt}} \right) (r^2 - 4Dt) - \frac{\sqrt{2Dt} r}{\sqrt{\pi}} e^{-r^2/8Dt} \right) & \text{for } U = 0 \\ \frac{4}{3}\pi r^3 + \frac{2\lambda}{C_i} \left(\frac{r^2}{6D} + \frac{\sqrt{\gamma} r^3 \arctan(\frac{\sqrt{\gamma} r}{\sqrt{2D}})}{6\sqrt{2} D^{3/2}} + \frac{\log(\gamma \frac{r^2}{2D} + 1)}{6\gamma} - \frac{\sqrt{\gamma} \pi r^3}{12\sqrt{2} D \sqrt{D}} \right) & \forall U > 0 \end{cases} \quad (6)$$

For random superposition of stationary point processes, $K_{ij}(r, t) = \frac{4}{3}\pi r^3$.

Dominance index

The dominance index D_i is presented in Wiegand *et al.* (2007). Let $M_i(r)$ be the average number of individuals within a circle of radius r around an individual of species i , which can also be written with Ripley's K function as $M_i(r) = C_i K_i(r)$. $M_{ii}(r)$ corresponds to the conspecific neighbourhood and $M_{io}(r)$ corresponds to individuals of all other species. We can then define D_i with eq. 7.

$$\begin{aligned}
D_i(r) &= \frac{M_{ii}(r)}{M_{ii}(r) + M_{io}(r)} \\
&= \frac{C_i K_{ii}(r)}{\sum_{j=1}^S C_j K_{ij}(r)}
\end{aligned} \tag{7}$$

When individuals of the same species i tends to cluster, $D_i(r)$ tends to 1 while it tends to the proportion of individuals of species i in the whole community when the distribution is uniform.

Using eq. 6 and 7, we can find a theoretical formula for the dominance index (shown below in the presence of advection, eq. 8).

$$D_i(r, t) = \frac{C_i \left[\frac{4}{3} \pi r^3 + \frac{\lambda}{3C_i D} \left(r^2 + \frac{\sqrt{\gamma} r^3 \arctan(\sqrt{\frac{\gamma}{2D}} r) + \frac{D \log(\gamma \frac{r^2}{2D} + 1)}{\gamma} - \frac{\sqrt{\gamma} \pi r^3}{2\sqrt{2D}} \right) \right]}{\sum_{j=1}^S C_j \frac{4}{3} \pi r^3 + \frac{\lambda}{3D} \left(r^2 + \frac{\sqrt{\gamma} r^3 \arctan(\sqrt{\frac{\gamma}{2D}} r) + \frac{D \log(\gamma \frac{r^2}{2D} + 1)}{\gamma} - \frac{\sqrt{\gamma} \pi r^3}{2\sqrt{2D}} \right)} \tag{8}$$

Parameters

We model two types of organisms: microphytoplankton (defined by a diameter between 20 and 200 μm , here 50 μm) and nanophytoplankton (defined by a diameter between 2 and 20 μm , here 3 μm). These two groups are characterized respectively by a low diffusivity, slow growth and lower concentration vs. high diffusivity, fast growth and higher concentration. Particles are displaced by a turbulent fluid whose velocity defines the time scale of the discretized 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 space size is below the size of the smallest eddy, but above the smallest scale of fluctuations in nutrient concentrations. The defining scale of the environment therefore corresponds to a Reynolds number $Re \approx 1$.

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

where $\nu = 10^{-6} \text{ m}^2/\text{s}$ is the kinematic viscosity for water. The smallest wavenumber k corresponds to the largest length scale L_s (Kolmogorov scale), i.e. $k = 2\pi/L_s$, with $L_s \approx 1 \text{ cm}$ 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 $U=6.3 \times 10^{-4} \text{ m.s}^{-1}=5.4 \times 10^3 \text{ cm.d}^{-1}$. Using $U\tau/3 = 0.5 \text{ cm}$ as in Young *et al.* (2001), we would have $\tau = 2.8 \times 10^{-4} \text{ d} = 24 \text{ s}$. When $U\tau/2 = 0.0$, i.e. the environment is only diffusive, we keep the same value for τ .

The advection parameter in continuous time, γ , is computed through simulations, based on $s(t) \propto e^{3\gamma t} \rightarrow 1/3 \ln(s(t)) = \gamma t$ with $s(t)$ the separation between pairs of particles before stabilization. γ is estimated as the slope of $1/3 \langle \ln(s(t)) \rangle = f(t)$ with $\langle \ln(s(t)) \rangle$ being the average separation between 800 pairs of particles. For $U\tau/3 = 0.5 \text{ cm}$, $\gamma = 1231 \text{ s}^{-1}$.

Diffusion

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

$$D = \frac{RT}{N_A} \frac{1}{6\pi\eta a} \quad (9)$$

where $R = 8.314 \text{ J.K}^{-1}.\text{mol}^{-1}$ is the molar gas constant, $T = 293 \text{ K}$ is the temperature, $N_A = 6.0225 \times 10^{23}$ is Avogadro's number, $\eta = 10^{-3} \text{ m}^{-1}.\text{kg.s}^{-1}$ is the dynamic 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 $a_n = 1.5 \text{ }\mu\text{m}$ for nanophytoplankton particles and $a_d = 25 \text{ }\mu\text{m}$ for microphytoplankton particles, which allows us to compute Δ_n and Δ_d (see Table 1).

Ecological processes

We study the community at equilibrium, with the birth rate equal to the death rate, i.e. $p = q$. We use a diatom doubling rate of 1 d^{-1} (Bissinger *et al.*, 2008) and consider the fastest-growing nanophytoplankton particles, corresponding to a diameter of $3 \text{ }\mu\text{m}$ (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	2.8×10^{-4}
p_n, q_n	Probability of reproducing/dying for nanophytoplankton particles	6.9×10^{-4}
$U\tau/3$	Stretching parameter proxy	$\{0, 0.5\}$ cm
Δ_d	Diffusion parameter for diatoms	6.4×10^{-5} cm
Δ_n	Diffusion parameter for nanophytoplankton particles	2.6×10^{-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 24 seconds.

Range of interaction

As we examine particle aggregation or segregation and their potential effects on interactions between species, we have to ascertain the volume around which a particle can be affected by the presence of other particles, or affect other particles. We only consider here interactions due to competition for nutrients, and therefore need to define a nutrient depletion volume. We approximate this volume as the sphere of radius r where $C(r) \leq 90\%C_\infty$ with C_∞ the background concentration of the nutrient (hereafter, the concentration boundary layer). The radius is maximized when the particle is in stagnant water (diffusion is the only hydrodynamics process). In this case, it corresponds to 10 times the radius of the particle (Jumars *et al.*, 1993; Karp-Boss *et al.*, 1996). We consider this maximum value as our baseline, keeping in mind that turbulence reduces the size of the concentration boundary layer and cause an increasing nutrient flux to the cell (Arnott *et al.*, 2021), but determination of the exact shape of the nutrient depletion volume in the presence of turbulence is too complex to be adressed here (Karp-Boss *et al.*, 1996).

We consider a volume of 1000 cm^3 for diatoms and 10 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 C/L for microphytoplankton, according to observations of field abundance distributions in Picoche & Barraquand, 2020, and multiplied by 10^2 for nanophytoplankton). All simulations are run for 1000 time steps of duration τ .

Results

NOTE: do we show the spatial distribution here or in the SI? There is nothing to comment in the Results, as they look pretty similar. This could go to SI, just for info, but that's it. I would rather put the Ripley's function fit here.

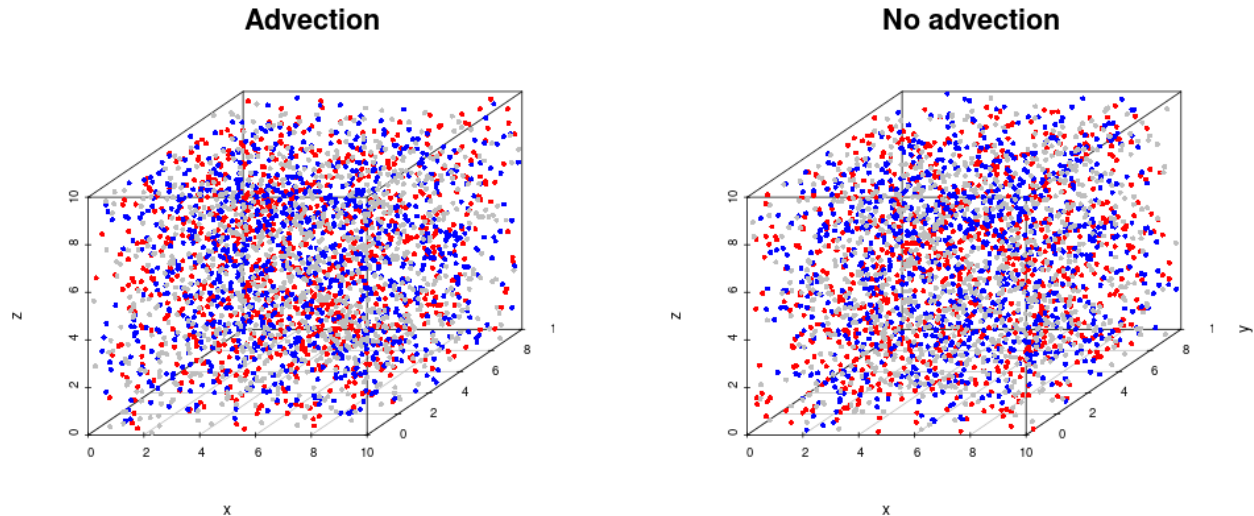


Figure 1: Spatial distributions of a 3-species community of microphytoplankton with and without advection with density $\lambda = 10 \text{ cm}^{-3}$ after 1000 time steps. Each color corresponds to a different species. For visualization purposes, only a 1000-point sample is shown.

Ripley's functions extracted from numerical simulations match theoretical formula (see Supplementary Information), which imply that simulated dominance indices also correspond to theoretical predictions.

Dominance indices all follow a similar pattern. The dominance index is close 1 for small radii: there is always a scale at which a particle is surrounded almost only by conspecifics. The index then decreases sharply to converge at large radii (close to 1cm) to the proportion of the focus species in the whole community, as it would for a uniform distribution. Patterns differ at intermediate ranges of distances between particles.

In the presence of advection, species tend to start mixing at lower radii than in the absence of advection: the dominance index starts decreasing for a radius at least ten times lower than when advection is absent. A quasi-uniform distribution is also reached for smaller radii than in the absence of advection. With and without turbulence, microphytoplankton starts mixing for distances larger than for nanophytoplankton.

In a 3-species community with the same initial abundances, microphytoplankton dominance indices are around 0.4-0.5 at a distance equal to 10 diameters of a particle, while it is around 0.9 for nanophytoplankton species when advection is present. When there is no turbulence, dominance indices are both close to 1 when the 10-diameter threshold is reached. Microphytoplankton organisms are as likely to share their depletion zone with conspecifics or heterospecifics, whereas nanophytoplankton have almost only conspecifics around them in this volume.

In a 10 species-community, XXX

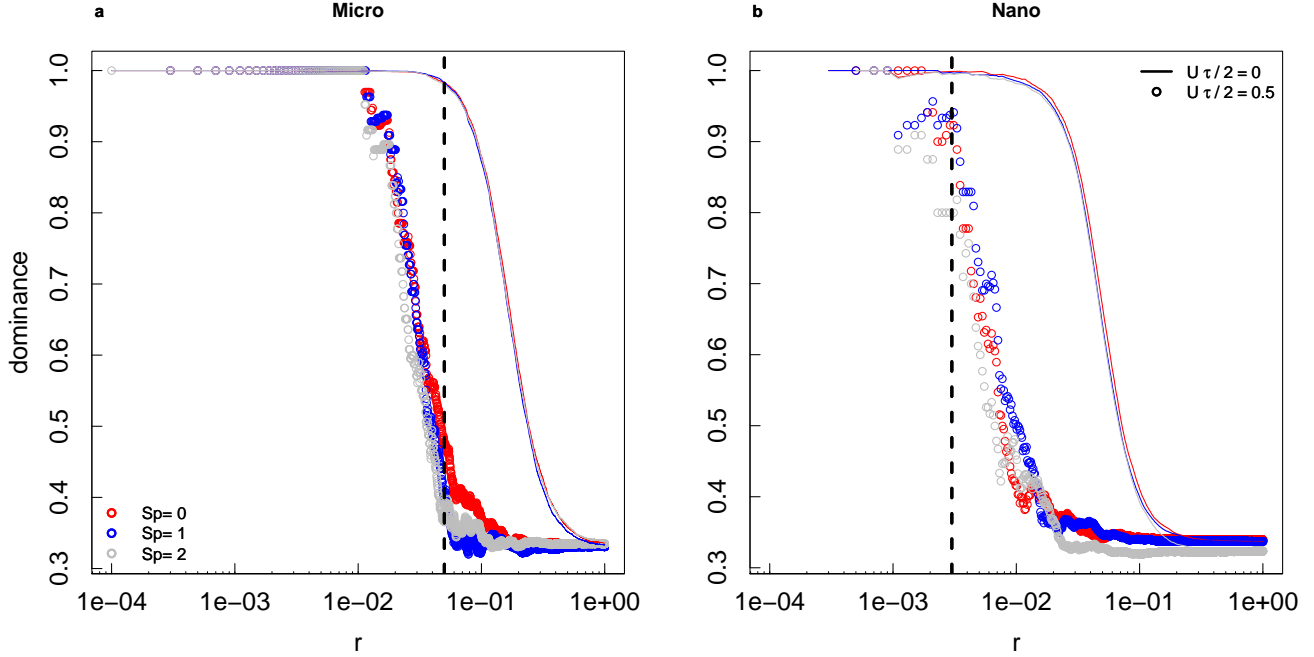


Figure 2: Dominance indices for microphytoplankton (a) and nanophytoplankton (b) in a 3-species community with even distributions after 1000 timesteps, with (circles) and without (lines) advection. Each color represents a different species. The black dashed line corresponds to the 10-diameter threshold considered as the maximum range for nutrient-based competition.

Fig3: Result for dominance index for 10 species

Discussion

We designed a stochastic, 3D, multispecific model of particles in a viscous and turbulent flow, and conducted both analytical and numerical analyses to quantify spatial correlations in particle distributions. We focused on the second moment of the spatial point process, or pair correlation function, for which numerical and theoretical analyses showed a good agreement. From the pcf and corresponding Ripley's function, we extracted the dominance index to quantify the degree of interspecific mixing. Comparing the behaviour of organisms of different sizes and demography, we showed that proximity between particles of different communities depends on the characteristics of the particles. While turbulence always lead to more mixing, microphytoplankton, larger cells with a lower diffusivity, encountered heterospecifics at larger distances from the particle than nanophytoplankton, but still within what we defined as a possible zone of nutrient depletion surrounding a particle.

Intraspecific clustering at small distances from a particle is a constant in our model. It shows a balance between diffusivity and turbulence, possibly speeding up the separation of particles, and growth rates, which increases their aggregation. The distance between particles is relevant, as each phytoplanktonic cell creates a zone of depletion around itself, where nutrient concentration is lower than the ambient concentration (Karp-Boss *et al.*, 1996): when

particles are close enough to decrease concentration of nutrients in their respective zones of depletion, competition for nutrients, often assumed to be the main direct interaction between primary producers, may happen. The equilibrium between mixing and clustering then affects the balance between intra- and interspecific interactions. The effects of such balance are size-dependent: intraspecific clusters are larger for microphytoplankton but particles still mix enough to have to share their depletion zone with heterospecifics. Nanophytoplankton organisms mainly share this space with conspecifics while microphytoplankton organisms can affect both conspecifics and heterospecifics. It should be noted that interaction via zone of depletion overlap has been debated, but usually in the context of a uniform distribution and/or with diffusion only (Hulburt, 1970). On the contrary, models of microscale spatial distribution show lower distances between particles than expected from a uniform distribution (Bouderbala *et al.*, 2018). While competition for nutrient is the most direct interaction between particles, indirect interactions can also affect phytoplankton growth. For instance, each particle is surrounded by a micro-environment called the phycosphere, where communities of bacteria exchange with the particle (Seymour *et al.*, 2017): we can assume that sharing such communities could impact, both positively and negatively, an organism. For a particle of microphytoplankton with a diameter of 50 μm , the phycosphere radius reaches 1200 μm (a zone where a particle may interact mostly with heterospecifics if its concentration is less than 50% of the sum of all concentrations), while it is nearly non-existent for particles below 3 μm . This tends to confirm that microphytoplankton organisms are much more likely to interact with heterospecifics than nanophytoplankton individuals, via exchanges of compounds necessary for their survival. However, larger cells are affected by additional phenomena: they are much more sensitive to increases in turbulence, which reduce the volumes of specific zones around them (Karp-Boss *et al.*, 1996) and augment nutrient uptakes. Here, both the phycosphere and the depletion zone sizes are computed with diffusion only in mind. It is possible that, if we determined adjusted depletion zone sizes, conspecifics would be as predominant for microphytoplankton as they are for nanophytoplankton. This is crucial for coexistence, as preferential interactions with conspecifics is a requirement for the maintenance of diverse particles (Barabás *et al.*, 2017): diversity may therefore be more dependent on the balance between diffusion and growth rates for nanophytoplankton, while turbulence might be key mechanism for microphytoplankton.

Our model focuses on size as the defining trait of the communities we consider. This is in line with many studies which take size as a major functional trait (Marañón, 2015), correlated with other capacities such as growth rate or nutrient affinities (Edwards *et al.*, 2012), or even average abundances (Agusti *et al.*, 1987). In this model, we focus on a single size per phytoplankton category, which defines both the diffusivity and the growth rate of the organisms. Smaller sizes lead to a higher diffusivity, i.e. less clustering, and a higher growth rate, i.e. more clustering, but they also have a smaller zone of depletion. In reality, phytoplankton size classes cover a much wider range (Boyce *et al.*, 2015), and organism diameters may vary greatly even within a single species. Taking into account this variability creates new mechanisms sustaining diversity: for example, size-based inertia in a chaotic flow creates size-specific aggregates, implying more conspecifics clusters (Benczik *et al.*, 2006). These results complement ours in the way

they highlight the relevance of turbulence at microscale to produce new spatial niches for particles of different sizes. We can assume that, in our model, introducing a size gradient for species within a single phytoplankton community would create more complex spatial distributions. At the same time, the conspecifics clustering observed at small scales seems to be quite unsensitive to variations in sizes (more than one order of magnitude between nanophytoplankton and microphytoplankton): there would still be probably, even slightly, more conspecifics than heterospecifics at scales relevant for interactions.

Here, interactions are only defined indirectly as we consider distances from a particle in which competition for nutrients may happen. However, particles interactions can be modeled a much more direct way. For instance, birth and death rates can be density-dependent: (Bouderbala *et al.*, 2019) shows that when density-dependence and attraction between motile particles are defined within a specific range of distances around a particle (the kernel of interaction) clusters of organisms emerge. Even in the absence of demographic processes, attraction between particles able to propulse themselves is sufficient to create dense clusters at the micro-scale in a turbulent environment - especially when length scales associated to interactions and turbulence are close (Breier *et al.*, 2018), or when species are colonial and actively create clusters by sticking together (Kiørboe *et al.*, 1990). This is common for microphytoplankton: our model should be considered a null model for independent cells, but can also highlight the importance of coloniality for larger cells to be able to be closer to conspecifics. Our model is therefore another step in the building of meso- or micro-scales models to describe phytoplankton distribution, with phenomena adapted to this scale, by introducing a multispecific community, with organisms defined by their traits (sizes, average concentrations in the environment). Introducing new traits and/or spatial heterogeneity in terms of environmental quality could constitute help to understand the observed patchiness of phytoplankton, and the way their diversity may be sustained by phenomena that cannot be considered with usual mean-field models.

References

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