Populations dynamics in turbulence

I. INTRODUCTION

In nature, organisms are rarely distributed uniformly or at random, they form instead some sort of spatial patterns. This is due to various causes, environment inhomogeneities, externally induced drift, population competition for nutrients, or predation that result in spatially patchy structures or gradients. This spatial variance in the environment creates diversity in communities of organisms, as well as in the variety of the observed biological and ecological events. These observations are at the base of modern population dynamics research and of the discipline called spatial ecology [1]. The classic experiment of microbiology is the bacterial growth in a Petri dish: Depending on the nutrient concentration, an intriguing diversity of growth patterns have been observed. Of course, most bacteria do not live in Petri dishes, but rather in inhomogeneous environments characterized by, e.g., spatially varying growth rates and/or diffusion constants. Often, as in the soil after a rain storm, bacterial diffusion and growth are accompanied by convective drift in an aqueous medium in the presence of disorder. Therefore, the fluid environment in which these colonies live most of their time is an inhomogeneous and unsteady flow. Another example is marine plankton, which is made of small organisms (*zooplankton*) and algae (*phytoplankton*) incessantely transported by ocean turbulent currents. Turbulence indeed is a common phenomena in nature and provides an effective mixing and transport mechanism in fluid media, in water as well in air. It is well know however that the statistical properties of turbulence are non-trivial because of strong fluctuations in space and time. While turbulence acts as a very efficient mixing mechanism for passive quantities - like for instance an inert dye - the interplay between population dynamics and turbulent transport may lead to formation of persistent patches; in analogy with quantum physics one can talk about localization effect [2]. It has been observed that localization events of a population may in uence significantly the fixation of a gene mutation at the edge of a growing population (a phenomenon known as *gene surfing* [3]). The studies of population dynamics in presence of convecting drift or turbulence have been limited so far to simple cases; steady ow in a prescribed geometry, [4, 5], or a random vortices model in a two-dimensional space [6], or even one-dimensional shell-models of turbulence [2]. More refined investigations, accounting for the exact behavior of turbulent flows are clearly needed. I propose to investigate the quantitative effect of turbulence on the population dynamics by means of theoretical (statistical) and computational tools. To achieve this objective I will conduct state-of-the-art, high resolution, direct numerical simulations of turbulent flows coupled to models describing popula-

tions evolution. Populations will be mainly modeled in terms of a local concentration field. Note that particle-like models also exist. Typically they feature mutually interacting particles mimicking predator-prey dynamics which move according to brownian diffusion and a large-scale drift velocity. This latter type of modeling may be useful when the number of certain individuals considered is very limited as for instance when studying the fixation of a random mutation (see [7] for a discussion on the importance of fluctuations and a comparison between field approach vs. particle approach). On the fluid modeling side, the clear advantage of using direct numerical simulations, is that the fluid velocity field is at all scales and the statistical properties of turbulence are faithfully captured. I would like to remark that the phenomenology of turbulence is very dierent in two dimensions as compared to three dimensions, furthermore non isotropy and inhomogeneity can also affect significantly the *localization* effect. This opens a wide physical landscape to be explored. Some continuous models of population dynamics, based on the reaction-diffusion equation, have also relevance for the description of advancing fronts of several autocatalytic chemical reactions, for combustion or for the Belousov- Zhabotinski reaction paradigmatic in non-equilibrium thermodynamics. Multi-population models are also used to describe blood clotting process [8], in this domain the unsteady drift produced by turbulent motion may have indeed a significant impact. The equations which are used to mimic the dynamics of populations or chemicals have their basis in statistical physics, thus this study is multidisciplinary in its character and aims at bringing together the areas of fluid-dynamics turbulence, computational physics, statistical physics, with biology and chemistry that are essential ingredients for better modeling and understanding natural phenomena. In the following I will give a more detailed description of the subjects under scrutiny focusing on the mathematical formulation of the problem and on the open physical/biological questions. I have partitioned this investigation project in three main sections, from Sec. II to IV. Technical details on the numerical methods are provided in section V, while section VI is dedicated to the logistics: hosting laboratory and collaborations.

II. SINGLE POPULATION DYNAMICS AND REACTION-DIFFUSION-ADVECTION EQUATION

The Fisher-Kolmogorov-Petrovsky-Piskunov (F-KPP) equation [9, 10] is one of the most fundamental models in mathematical biology and ecology. It describes a population concentration $c(x, t)$ that evolves under the combined effects of spatial diffusion, advection, local logistic

growth and saturation. The F-KPP equation reads

$$\partial_t c + \nabla \cdot (\mathbf{u}c) = \kappa \nabla^2 c + sc(1 - c_\infty) \qquad (1)$$

with diffusion coefficient κ, fluid velocity $\mathbf{u}$; the difference between the linear birth and death rates is s, while c_∞ represents the saturation level for the population density, also called carrying capacity. The term $-sc^2/c_\infty$ models some self-limiting process, roughly proportional to the number of pairs of individuals at a given position in space. Logistic dynamics - linear growth and quadratic saturation - is the mean-field description of a variety of microscopic processes. One of its first application, by Fisher in 1937 [9], was in genetics. He introduced it, without the advection term, as a model for the spread of a dominant gene with selective fitness advantage s trough a population with maximal density c_∞. Fisher and Kolmogorov and coworkers showed that if initially some part of the habitat is not occupied, $c(x, 0) = 0$, then the population will propagate into this part with the constant velocity $v_f = \sqrt{s\kappa}$, hence there is a *travelling wave* solution of the form $c(\mathbf{x} - \mathbf{v}_f t)$. Clearly for the same initial condition, but in presence of constant advection $\|\mathbf{u}\| = U$, the population front spreads at a speed which is the sum of the the so called Fisher velocity and the drift, $\mathbf{v}_f + \mathbf{u}$. In case of an upwind migration front this defines a threshold condition for the expansion of the population $s\kappa > U$ in an unbounded domain. The interplay between drift and diffusivity - eventually space dependent - and also boundary conditions for c, makes the survival/extinction problem extremely rich. And of course the model greatly increases in complexity when the drift velocity $\mathbf{u}$ results from a chaotic dynamics. What should one expect in the fully turbulent state? The studies of the last decade have focused on a simplified version of this problem: the diffusion-advection equation of a passive scalar quantity in a turbulent incompressible velocity field [11]. The scalar field is said passive because neither back-reacts on the velocity field nor contains the logistic growth/saturation term: the equation is linear in the scalar field and therefore much simpler than F-KPP. Analytical treatment of this problem have been made possible through a simplification of the turbulent flow field, proposed by R. Kraichnan. Instead of using a truly turbulent field one can assume to have a delta-correlated in time Gaussian random field with some prescribed two-point spatial correlation function. The Kraichnan ensemble of velocities allows an exact analysis of the statistical properties of the scalar field and a deep insight into subtle features of the advection, like intermittency and anomalous scaling [12]. These corpus of works demonstrated that scalars in turbulence can produce sharp fronts which mark the edge of plateau regions, where a very efficient mixing takes place. However, the small-scale statistics of scalar fluctuations is dominated by the signature of sharp front-like events. Scalar jumps across the fronts are of the order of $c_{rms} = \sqrt{\langle c^2 \rangle}$, i.e., comparable to the largest values of the field itself. Furthermore, the minimal width of the fronts reduces with the dissipation scale,

pointing to their quasi-discontinuous nature. If the probability of having such c_{rms} jumps across a separation r goes as r^{ζ_s} then phenomenological arguments (multifractal modeling [12]) suggest a saturation of the structure functions, $\langle (c(\mathbf{x} + \mathbf{r}; t) - c(\mathbf{x}; t))^n \rangle \sim r^{\zeta_n} \to r^{\zeta_s}$, in the limit $n \to \infty$ [13]. These results were con

rmed by numerical calculations both via integration of the Kraichnan ensemble and with Navier-Stokes fully developed turbulence. Whether a similar approach can be extended - at least perturbatively - to a reacting system where a non-linearity is present is an open question and will be at the center of the investigation proposed here. From a phenomenological point of view, indeed, the patch formation for equation (1) is expected to be even more dramatic. Furthermore, a recent numerical study using a one-dimensional model of turbulence (GOY-shell model) coupled to F-KPP equation found quasi-localized solutions, i.e., solution localized in a statistical sense [2] (a phenomenon which reminds of the strong-localization - or Anderson localization - encountered in stochastic processes); those findings have been confirmed in a numerical study of populations dynamics in 2D compressible turbulent velocity field [14]. The question *whether the compressibility is essential for the formation of quasi-localized solutions*, however, remains open. The proposed study aims to a better understanding of the bacterial population dynamics in realistic situation of three-dimensional turbulent velocity fields described by the Navier-Stokes equations or alternatively to a two dimensional surface flow field (where some degree of compressibility may be included in a controlled way). A statistical characterization of this phenomenon will be performed in order to understand if and how the turbulent advection can lead to patchiness in a bacterial population with/without compressibility effects. Also it is of great interest to investigate the effect of different types of turbulent flows, for instance by relaxing either the condition of statistical isotropy, e.g., by introducing a mean shear, or the condition of homogeneity, by including walls around which boundary layers will develop. A special case of single-population dynamics is the condition of non-uniform carrying capacity, i.e. $c_\infty(x)$. In [15], for example, a model based on $c_\infty \neq const$ was studied for the case of phytoplancton in a turbulent 2-dimensional environment.

III. POPULATION DYNAMICS OF MULTIPLE SPECIES IN PRESENCE OF TURBULENCE

In most natural systems, such as in the ocean upper-layer ecosystem, the environment is inhabited by more than one biological species. Each species has its position in food chain: simplifying they are either predator or prey to other species. Marine plankton for instance has been modeled [6] by a three population system accounting for nutrients, phytoplancotn and zooplancton, although the fluid motion of the ocean was investigated via a synthetic two-dimensional flow field made by random eddies. To

understand the population dynamics of multiple species I will undertake the study of models similar to those proposed in [6]. The key step will be here to consider two population densities described by F-KPP equation with interaction terms of Lotka-Volterra type

$$\partial_t c_1 + \nabla \cdot (\mathbf{u} c_1) = \kappa \nabla^2 c_1 + s_1 c_1 (1 - c_\infty) - s_2 c_1 c_2 \quad (2)$$

$$\partial_t c_2 + \nabla \cdot (\mathbf{u} c_2) = \kappa \nabla^2 c_2 + s_2 c_2 (1 - c_\infty) - s_1 c_1 c_2 \quad (3)$$

When $s_2 \neq s_1$ the system describes the evolution of two populations in which a *mutant type* c_2 with selective fitness advantage (hence $s2 \gg s1$) has to compete with c_1, the typical form of the species (also called *wild type*). The respective ratios of the population doubling-times $1/s_1$ and $1/s_2$ with the turbulent eddy turnover time - which is a scale-dependent quantity $t_{eddy}(r) \sim r^{2/3}$ - are to be used as control parameters (analogous to the Damkhöler number in turbulent combustion [16]). One can expect that the effect of the turbulent stirring will produce population structures when all $t_{eddy}(r)$ are larger than the doubling-times, while homogenization will be produced in the opposite case. Let us stress again the similarity of a multi-component reaction-diffusion-advection system with models employed for chemical reactions, as for instance activator-inhibitor ones [17] widely used in pattern formation research.

IV. LIMITS OF POPULATIONS CONTINUOUS DESCRIPTION AND THE INDIVIDUAL/LAGRANGIAN POINT OF VIEW

The F-KPP equation can be thought as a mean-field description of a microscopic processes. It corresponds, in fact, to the Fokker-Plank equation for the evolution of probability density function of interacting brownian particles. It applies to the birth-coagulation process ($A \rightleftharpoons A + A$ at different rates in the two directions, the difference being proportional to the growth rate s) as well as to the chemical reaction scheme ($A + B \rightarrow A + A$, $A + B \rightarrow B + B$ with different specific rates). In order to derive F-KPP one has to neglect discreteness and fluctuations and spatial inhomogeneities (conditions which are all realized in the large particle number limit). Therefore, it comes with no surprise the fact that in several realistic situations characterized by a small number of individuals the continuous description of a population might fail. A paradigmatic example is genetics: in mutation-fixation studies a sample of where a mutation initially appears is typically constituted by a very small number of individuals, therefore fluctuations in the field can not be neglected. In some cases discretization effects may be taken into account in a continuous model introducing a threshold. For instance it has been suggested that the growth-rate can be modified as $s\,c \rightarrow s\,c\theta(c - \epsilon)$ where ϵ is a small parameter corresponding to the density of only one element of the population per unit volume and

θ is the Heaviside function. It has been shown that this may be critical to predict extinction/survival in regions - customarily called *deserts* - where the nutrients or the growth-rate are very low [7]. Other situations in which the discrete nature of a population may emerge is in connection with the fact that each elements has inertia and that such inertia can not be neglected when a population is swept by a flow. I would like to focus here on this latter aspect. Various studies [6, 19] modelled the dynamics of the plankton populations in ocean ignoring inertia and assuming, instead, that zooplancton and phytoplancton follow exactly the motion of water parcels. However, it is known that even tiny material particles do not follow the fluid flow but can accumulate in regions of space characterized by specific topological properties. As a consequence, particles with even a small mismatch in their material properties - size or density - can segregate in different ways [20]. This phenomenology may have significant effects, for instance, on the encounter-rate of preys and predators. The origin of particle concentration lies in the dissipative nature of the hydrodynamical forces acting on a particle in a flow. The simplest and most popular model [21] for particle evolution reads $\ddot{\mathbf{x}} = \beta \mathbf{a} + \tau^{-1}(\mathbf{u} - \dot{\mathbf{x}})$, where $\mathbf{u}$ and $\mathbf{a}$ are the values of the fluid velocity and acceleration at the particle position $\mathbf{x}$; β and τ are parameters linked to the mass density of the particle, its size and the viscosity of the fluid. It is easy to show that in the position-velocity phase-space this equation defines a dissipative dynamical system, therefore it may have an attractor [22]. A continuum description of particles can break down due to the formation of multiple-valued fields; it has been shown that this would happen even for particle Stokes response time τ of the order of the dissipative time scale of turbulence [23]. This condition may be realized for manifold zooplancton families (e.g. *Copepods* are typically 1-2 millimetres in size, the same order of the Kolmogorov scale on the ocean surface). Inertia can therefore provide a source of *effective compressibility* for organisms swept in an *incompressible* flow (such as zooplancton in the ocean). In this case it is more realistic to adopt a particle (Lagrangian) approach for the population dynamics while keeping a continuum (Eulerian) description for the advecting velocity field evolution.

V. NUMERICAL METHODS

Direct numerical simulations of Navier-Stokes equation in turbulent condition will be implemented via a pseudo-spectral algorithm in three- and two-dimensional rectangular domain with periodic (or wall in a further step) boundary conditions. As long as simple flow geometry are considered, spectral-methods remain nowadays the most accurate and effcient in computational fluid dynamics. The representation of the fluid velocity through a finite orthonormal basis of functions (Fourier basis or Chebyshev polynomials) guarantees exponentially fast convergence of the solution superior to any fi-

nite difference/volume/elements methods. Furthermore, for the calculations of spatial derivatives one can take advantage of the use of the fast Fourier transform (FFT) algorithm, which is typically highly-optimized on parallel super-computers. The same approach can be used for the numerical integration of Fisher-KPP equations, however extra care should be taken for the treatment of sharp gradients or discontinuities - shocks - appearing in the scalar field. The approximation of a discontinuous function with a finite series of continuous basis functions may lead to artificial fluctuations which do not reduce by increasing the order of the series but converge instead to a finite value (Gibbs phenomenon). There are several ways to construct a global approximation of non-smooth functions, for instance the Fourier basis can be extended by the addition of step Heaviside functions, or by using Padé-Fourier-like approximations. The method I am planning to use considers an *ad-hoc* local extra dissipation, as described in [24]. The global time-step size of the simulation will have to be adjusted by considering not only the shortest time scale of turbulence (the dissipative scale) or the standard Courant-Friedrisch-Lévy criterion, but also taking into account the shortest time characterizing the F-KPP equation, such as its diffusive time-scale and the doubling-time of bacterial growth.

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