Statistics of population dynamics in turbulence

Prasad Perlekar\textsuperscript{1}, Roberto Benzi\textsuperscript{2}, David R. Nelson\textsuperscript{3}, Federico Toschi\textsuperscript{1,4}

\textsuperscript{1}Department of Physics and Department of Mathematics and Computer Science, Eindhoven University of Technology, Eindhoven 5600MB, The Netherlands.
\textsuperscript{2}Dipartimento di Fisica and INFN, Università “Tor Vergata”, Via della Ricerca Scientifica 1, I-00133 Roma, Italy.
\textsuperscript{3}Lyman Laboratory of Physics, Harvard University, Cambridge, Massachusetts 02138, USA.
\textsuperscript{4}CNR-IAC, Via dei Taurini 19, 00185 Rome, Italy.

E-mail: p.perlekar@tue.nl, f.toschi@tue.nl

Abstract. We study the statistical properties of population dynamics in 2d turbulent and compressible surface flows. We show that the compressible surface flow leads to a patchiness in the population density that resembles the patchiness of the Plankton population as observed from the satellite images of the ocean surface. The statistical properties of the population concentration are investigated and quantified for different growth rates, diffusivities and for different level of compressibility of the surface flow.

1. Introduction

The Fisher equation (Fisher (1937); Kolmogorov \textit{et al.} (1937)) is commonly used to describe the spreading of microorganisms on a hard agar plate with high nutrient concentration. It was shown that this equation can provide a good description of the spreading of microorganisms, such as bacteria, at low Reynolds number (Wakita \textit{et al.} (1994)). However many microorganisms, such as those living in the oceans, must find ways to thrive and prosper in high Reynolds number fluid environments. In presence of a turbulent advecting velocity field, $u(x, t)$, the Fisher equation reads:

$$\frac{\partial c}{\partial t} + \nabla \cdot (uc) = D\nabla^2 c + \mu c(1 - c),$$

where $c(x, t)$ is a continuous variable describing the concentration of micro-organisms, $D$ is the diffusion coefficient and $\mu$ is the growth rate. As an example one can consider eqn. (1) as a description for the density of the marine cyanobacterium Synechococcus (Moore \textit{et al.} (1995)) under conditions of abundant nutrients, i.e. such that $\mu \sim$ constant.

In Fig. 1 we show the localization of the population concentration field near the regions of transient but long-lived sinks of the turbulent flows for the case of small growth rate $\mu$ and non-zero compressibility, see Perlekar \textit{et al.} (2010) for further details. In the same small growth rate limit, the space-time averaged concentration (denoted in the following as the carrying capacity) becomes much smaller than its maximum value 1 (Benzi & Nelson (2009); Perlekar \textit{et al.} (2010)). Both these effects are relevant in biological applications (Murray (2005); Nelson & Shnerb (1998)).
Figure 1. Concentration field and the correlation between regions of high concentration and negative divergence. (Left panel) Pseudocolor plot of the concentration field. The dark green regions indicate high concentration \( c > 0.1 \) and the white regions indicate low values of the concentration. (Right panel) Pseudocolor plot of \( [c(x, t_0)/(0.1 + c(x, t_0)) \tanh(-\nabla \cdot u)] \). The dark red regions indicate negative divergence and large concentration, whereas black regions indicate positive divergence and large concentration. Plots are made at identical time \( t_0 \) (after the steady state has been reached) on a slice \( z = \text{const} \) obtained from our \( 512^2 \) numerical simulations of eqn. (1) for \( \mu \tau_\eta = 0.0045 \) and Schmidt number \( Sc = 5.12 \). Note that microorganisms cluster near regions of compression \( (\nabla \cdot u < 0) \), as is evident from the high density of red regions.

We assume that the micro-organism population concentration field \( c(x, t) \), whose dynamics is described by eqn. (1), is constrained onto a planar surface at a constant height in a three dimensional fully developed turbulent flow. This is a rough approximation for the photosynthetic micro-organisms that actively controlling their buoyancy can maintain a fixed depth below the surface of a turbulent field (Martin (2003)). The flow field in the two dimensional slice is effectively compressible (Boffetta et al. (2004)).

We consider a turbulent advecting field \( u(x, t) \) described by the Navier-Stokes equations and we make time dimension-less by means of the Kolmogorov dissipative time-scale \( \tau_\eta \equiv (\nu/\epsilon)^{1/2} \) and space by means of the Kolmogorov length-scale \( \eta \equiv (\nu^3/\epsilon)^{1/4} \). As usual \( \epsilon \) denotes the mean rate of energy dissipation and \( \nu \) is the kinematic viscosity. The non-dimensional numbers characterizing the evolution of the scalar field \( c(x, t) \) are the Schmidt number, \( Sc \equiv \nu/D \), and the Damkohler number or the non-dimensional growth rate \( \mu \tau_\eta \).

We present a systematic study on the statistics of the population concentration in surface flows at varying the growth rate \( \mu \tau_\eta \), the Schmidt number \( Sc \), and the compressibility of the surface flow. The manuscript is organized as follows: In section 2 we detail the model and our numerical approach. Results for our investigation of the statistical properties of the concentration field are presented in section 3. Finally in section 4 conclusions are drawn.
2. Numerical method

To model the surface flow we performed a three dimensional direct numerical simulation (DNS) of homogeneous and isotropic turbulence using 512^3 collocation points in a cube of length \( L = 2\pi \). The Reynolds number based on the Taylor microscale (Frisch (1996)) was \( Re_\lambda = 180 \), the viscosity was \( \nu = 2.05 \cdot 10^{-3} \) and the total energy dissipation rate was \( \epsilon_{3D} \approx 1 \). For the integration of the Fisher equation we focused only on the time evolution of a particular 2d slab taken out of the full three dimensional velocity field; on this plane we evolved a concentration field \( c(x, t) \). A typical plot of the resulting 2d concentration field and of the same field when conditioned on the values of the local flow compressibility (taken at time \( t = 86 \), \( Re_\lambda = 180 \)) is shown in Fig. 1 (\( Sc = 5.12 \)). Similar to the Plankton population patterns observed on the surface of the oceans, the population concentration shows a remarkable degree of patchiness.

As already remarked, a 2d slice, \( \mathbf{u}(x, y) \equiv (u, v) \), from a three-dimensional incompressible homogeneous and isotropic turbulent velocity field \( \mathbf{u}_{3D}(x, y, z) = (u, v, w) \) is compressible. In the two-dimensional plane the compressibility of the 2d velocity field \( \mathbf{u} \) is defined as

\[
\kappa \equiv \frac{(\partial_x u + \partial_y v)^2}{(\partial_x u)^2 + (\partial_y v)^2 + (\partial_x v)^2 + (\partial_y u)^2},
\]

and \( \kappa = 0.16 \) for the original homogeneous and isotropic turbulent velocity field \( \mathbf{u} \). The limiting cases \( \kappa = 0 \) and \( \kappa = 1 \) correspond, respectively, to an incompressible and a potential flow. One can vary the compressibility of the 2d velocity field by decomposing \( \mathbf{u} \) into a compressible \( \mathbf{u}^c \) and an incompressible part \( \mathbf{u}' \). The incompressible part of the velocity field is obtained by taking the Fourier transform, \( \hat{\mathbf{u}} \), of the velocity field, \( \mathbf{u} \), and then applying to it the transverse projection operator \( \mathbb{P} = (\mathbb{I} - \mathbf{k}\mathbf{k}/k^2) \). Here \( \mathbf{k} \) denote the Fourier wave-vectors and \( \mathbb{I} \) is the identity tensor. One can obtain \( \mathbf{u}' \) by applying an inverse Fourier transform to \( \hat{\mathbf{u}} \). The compressible part of the velocity field is easily obtained as \( \mathbf{u}^c = \mathbf{u} - \mathbf{u}' \). With \( \mathbf{u}^c \) and \( \mathbf{u}' \) we can redefine the velocity field as \( \mathbf{u} \equiv \sqrt{2}[\mathbf{u}' \cos(\phi) + \mathbf{u}^c \sin(\phi)] \). The case of \( \phi = \pi/4 \) corresponds to the original 2d flow field. For \( \phi = 0 \) an incompressible flow is obtained and for \( \phi = \pi/2 \) we obtain a potential flow.

The Fisher equation is stepped forward using a second-order Adams-Bashforth scheme. The spatial derivatives in the diffusion operator are discretized using a central, second-order, finite-difference method. As the underlying flow field is compressible, sharp gradients can form in the concentration field during the time evolution. In order to capture these sharp fronts we use a Kurganov-Tadmor scheme for the advection of the scalar field by the velocity field (Kurganov & Tadmor (2000)). The discretized Fisher equation is

\[
\frac{c_{i,j}^{n+1} - c_{i,j}^n}{\delta t} = -A[u, c] + \frac{1}{2} \left( \frac{3.0[D[c^n] + R[c^n]] - (D[c^n] + R[c^n])}{\Delta^2} \right),
\]

\[
D[c^n] = \kappa \left[ c_{i+1,j}^n + c_{i-1,j}^n + c_{i,j+1}^n + c_{i,j-1}^n - 4c_{i,j}^n \right],
\]

\[
R[c^n] = \mu c_{i,j}^n(1 - c_{i,j}^n),
\]

Here \( i, j = 1, \ldots, N \) denote the grid points, \( \Delta \) is the spatial discretization, \( x = i\Delta \) and \( y = j\Delta \), the superscript \( n \) indicates the discretized time, \( \delta t \) is the time stepping, \( t = n\delta t, D \equiv \kappa \nabla^2 c \) denotes the diffusion term, and \( R \equiv \mu c(1 - c) \) is the reactive term in the Fisher equation. As described above, we discretize the advection term using Kurganov & Tadmor (2000). For the sake of brevity we will omit the superscript \( n \) in what follows.

\[
A[u, c] = \frac{A_{i,j+1/2} - A_{i,j-1/2}}{\Delta} + \frac{A_{i+1/2,j} - A_{i-1/2,j}}{\Delta},
\]
where \( A[u, c] \equiv \nabla \cdot (uc) \). Below we show the discretization of the first term on the rhs of Eqn. 6; the discretization of other advection terms is similar:

\[
A_{i,j+1/2} = \frac{c_{i,j+1/2}^+ - c_{i,j+1/2}^-}{2} - \frac{a_{i,j+1/2}^+(c_{i,j+1/2}^+ - c_{i,j+1/2}^-)}{2},
\]

where 
\[
c_{i,j+1/2}^\pm = c_{i,j+1} \mp \frac{\Delta}{2} (\partial_y c)_{i,j+1/2\pm 1/2},
\]

\[
a_{i,j+1/2} = |v_{i,j+1/2}|,
\]

\[
v_{i,j+1/2} = \frac{v_{i,j+1} + v_{i,j}}{2}.
\]

The derivative \((\partial_y c)_{i,j}\) is found using the minmod operator as

\[
(\partial_y c)_{i,j} = \text{minmod}\left(\frac{2c_{i,j} - c_{i,j-1}}{\Delta}, \frac{c_{i,j+1} - c_{i,j-1}}{2\Delta}, \frac{2c_{i,j+1} - c_{i,j}}{\Delta}\right),
\]

with

\[
\text{minmod}(a, b, c) \equiv \begin{cases} 
\max(a, b, c) & \text{if } a > 0, b > 0, c > 0 \\
\min(a, b, c) & \text{if } a < 0, b < 0, c < 0 \\
0 & \text{otherwise}
\end{cases}
\]

3. Results

A good indicator of the patchiness of the population concentration is the average concentration (or carrying capacity)

\[
Z(t) \equiv \frac{1}{L^2} \int c dx.
\] (7)

In the absence of a flow the steady state solution \(Z(t) = 1\) is obtained for the Fisher equation. In presence of compressible surface flows it was shown that the limits of very small \(\mu \to 0\) and very large \(\mu \to \infty\) growth rates are analytically understood (Perlekar et al., 2010; Benzi & Nelson, 2009). Using a series expansion for large \(\mu\), see Perlekar et al. (2010), it was shown that \(Z_{\mu \to \infty} \sim 1\) to leading order. For the \(\mu \to 0\) limit Perlekar et al. (2010); Benzi & Nelson (2009) used the equivalence between the Fisher equation at \(\mu = 0\) and the Fokker-Planck equation for a passive scalar in order to show that

\[
Z_{\mu \to 0} = \frac{1}{L^3/\langle P^2 \rangle},
\] (8)

where \(P\) is the probability distribution function of the concentration for \(\mu = 0\).

The effect of the compressibility is to confine the population concentration in small patchy regions (see Fig. 1). This leads to an increased competition in smaller environments where the population is confined. A larger diffusivity can strongly help under these conditions to explore a larger living space. In realistic settings, as in the case of Plankton in oceans, this increase in diffusivity can be attained by improved swimming capabilities. We now investigate the role of diffusivity on the population concentration by varying the Schmidt number \(Sc\) for fixed values of the compressibility \(\kappa\) and of the non-dimensional growth rate \(\mu\). In the following we use \(\kappa = 0.16\) and \(\mu\tau_0 = 0.076\). The plot in Fig. 2 shows the snapshots of the concentration fields at the same time and under the same flow conditions but for different values of \(Sc\). We find that the filamentary structures becomes broader at decreasing \(Sc\).

The probability distribution function (PDF) of the population concentration [Fig. 3 (left panel)] shows that for larger \(Sc\) number higher values of the population concentration are attained. This is consistent with the picture that increasing \(Sc\) (or decreasing \(D\)) leads to an accumulation of the populations.
Figure 2. Snapshot of the concentration field for $Sc = 0.1$ (left, large $D$) and $Sc = 10$ (right, small $D$) taken at the same time and under the same flow conditions. The yellow regions indicate regions of high concentration ($c > 1$) whereas black regions indicate low concentrations.

Figure 3. (Left panel): The PDF of the population concentration for different values of $Sc$. For $Sc = 10$ an higher value for the maximum concentration is attained in comparison to $Sc = 0.1$. (Right panel) Plot of the carrying capacity, $Z$, versus the Schmidt number, $Sc$. In the plots the non-dimensional growth rate is $\mu \tau_\eta = 0.076$ and the compressibility $\kappa = 0.16$.

In Fig. 3 (right panel) we plot the carrying capacity $Z$ for different values of the diffusivity $D$. The carrying capacity decreases on increasing the diffusivity, this indicates an increase in the population patchiness.

Next we study the role of compressibility on the population patchiness and we show that the patchiness in the population occurs even for very small values of compressibility. As we vary the compressibility we keep the $Sc = 1$ fixed but systematically vary the growth rate. In Fig. 4 we present the PDF of the population concentration for different values of compressibility. For all values of $\kappa$, the largest growth rate $\mu \tau_\eta = 3.3$ has a PDF with peak around 1. This is consistent with the asymptotic prediction $c \sim 1$ for $\mu \to \infty$ (Perlekar et al., 2010). For a fixed $\mu \tau_\eta$ we find that the PDF of $c$ broadens on increasing the compressibility. For the smallest $\mu \tau_\eta = 0.076$, we
Figure 4. PDF of the concentration for different values of the non-dimensional growth rate $\mu \tau_\eta$ and compressibility $\kappa = 0.065$ (top left), $\kappa = 0.16$ (top right), $\kappa = 0.39$ (bottom left), and $\kappa = 1$ (bottom right). In all the four values of compressibility considered above, the maximum value of the concentration is always attained at $\mu \tau_\eta = 0.0076$. For $\mu \tau_\eta = 3.3$, the PDF of concentration peaks around unity at fixed compressibility.

find that the initial dip in the PDF becomes faster and the tails of the PDF decay slower on increasing the compressibility. To uncover the exact decay behavior of the tails for $\mu \tau_\eta = 0.076$, we require much better statistics than what is achieved in the present study.

In Fig. 5 we quantify the patchiness of the population concentration by measuring the carrying capacity with varying $\kappa$ and $\mu \tau_\eta$ at fixed $Sc = 1$. For fixed growth rate $\mu \tau_\eta$, $Z$ decreases at increasing the compressibility. For a fixed value of $\kappa$, the carrying capacity increases with increasing $\mu \tau_\eta$. For large value of the growth rate $Z \to 1$. Using Eqn. (8) we can also calculate the value of the carrying capacity in the limit $\mu \to 0$. Similar to Fig. 5 we observe that the carrying capacity decreases with an increase in the compressibility. Thus even for very small values of compressibility we observe a reduction in the carrying capacity and hence an increase in the patchiness of the population concentration.

4. Conclusions

We performed a systematic study of the patchiness of the population concentration in Fisher equation coupled with a turbulent surface flow. We showed that the patchiness in the population decreases with an increase in either the $Sc$ or the compressibility $\kappa$. Finally we showed that even in the limit of small compressibility we find a reduction in the carrying capacity and hence a patchy structure in the population.
Figure 5. Plot of the carrying capacity $Z$ versus non-dimensional growth rate $\mu \tau_\eta$ for different values of compressibility $\kappa$. For a fixed growth rate $\mu \tau_\eta$ the carrying capacity $Z$ decreases with an increase in the compressibility.

Figure 6. Limiting value of the carrying capacity $Z_{\mu \to 0}$ [Eqn. (8)] for different values of the compressibility.

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