

The impact of diffusion and stirring on the dynamics of interacting populations

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Abstract

We investigate the combined effects of diffusion and stirring on the dynamics of interacting populations which have spatial structure. Specifically we consider the marine phytoplankton and zooplankton populations, and model them as an excitable medium. The results are applicable to other biological and chemical systems. Under certain conditions the combination of diffusion and stirring is found to enhance the excitability, and hence population growth of the system. Diffusion is found to play an important role: too much and initial perturbations are smoothed away, too little and insufficient mixing takes place before the reaction is over. A key time-scale is the mix-down time, the time it takes for the spatial scale of a population to be reduced to that of a diffusively controlled filament. If the mix-down time is short compared to the reaction time-scale, then excitation of the system is suppressed. For intermediate values of the mix-down time the peak population can attain values many times that of a population without spatial structure. We highlight the importance of the spatial scale of the initial disturbance to the system.

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1. Introduction

Many biological populations, and chemical reactive systems, exhibit time evolving spatial structure, which is induced by a combination of reaction and diffusion (Winfree, 1972; Field and Burger, 1985; Murray, 1993; Hofer et al., 1995) or by fluid stirring (Edouard et al., 1996; Abraham, 1998). A particular class of systems is excitable media (Murray, 1993; Dawson et al., 2000) in which relatively small perturbations can trigger large excursions in phase space. Reaction with diffusion can support traveling reactive wave fronts (Murray, 1993) while reaction with stirring can promote filamentation and global excitation (Neufeld, 2001; Neufeld et al., 2002a). Here we consider the combined effects of

diffusion and chaotic mixing on the gross characteristics of an excitable reactive system. A natural question to ask is under what conditions will spatial structure impact upon the global dynamics of a population (or chemical constituent).

A number of recent studies have investigated the formation of spatial patterns in excitable media in the presence of stirring by a fluid flow, and in particular the impact on plankton dynamics (the primary motivation here). These include Neufeld (2001), Neufeld et al. (2002b), Hernandez-Garcia et al. (2003), Scheuring et al. (2003) and Hernandez-Garcia and Lopez (2004). In all these studies the presence of diffusion is necessary for mixing to take place, but typically the coefficient of diffusion is set to a small value under the assumption that there is a high Péclet number limit. Here we show that the level of diffusion is critical to the behavior of the system and that a key parameter is the mix-down time, i.e. the time it takes to stir an initial patch of tracer down

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to a scale where mixing takes place. This puts limits on the size of the initial patch.

2. Model

We will model the population dynamics of interacting species by a reaction–advection–diffusion equation. Thus, the time evolution of the state vector \mathbf{E} stirred by a given velocity field \mathbf{u} is governed by

$$\frac{\partial \mathbf{E}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{E} = \mathbf{f}(\mathbf{E}) + \kappa \nabla^2 \mathbf{E}, \quad (1)$$

where \mathbf{f} denotes the reaction terms and κ is the diffusivity. Here we consider a two-dimensional velocity field and a two-dimensional state vector

$$\mathbf{E} = \begin{bmatrix} P \\ Z \end{bmatrix}. \quad (2)$$

The interaction terms are taken to be

$$\mathbf{f} = \beta \begin{bmatrix} P(1 - P) - \alpha \left(\frac{ZP^2}{v^2 + P^2} \right) \\ \gamma \alpha \left(\frac{ZP^2}{v^2 + P^2} \right) - \omega h(Z) \end{bmatrix}. \quad (3)$$

The model is that of Truscott and Brindley (1994), which is known to exhibit excitable behavior with P acting as the “fast” growing population (or tracer) and Z the “slow” population. This model has been applied to ocean plankton populations (hence the notation, with P and Z representing phytoplankton and zooplankton population densities, respectively) (Truscott and Brindley, 1994; Matthews and Brindley, 1997; Brentnall et al., 2003). The dynamics of the system depend on the specification of the sink (mortality) term h . Here we consider a linear sink term, with $h = Z$. The system is known to be excitable if $\gamma \ll 1$ and $v < 1/\sqrt{27}$. Fig. 1 shows the nullclines (curves in P, Z space on which the time rate of change of P and Z is zero, respectively) and those regions of phase space where a given initial condition leads to excitable behavior. (The parameter values are the same as those used in Brentnall et al., 2003, i.e. $\alpha = 2.33, v = 0.053, \gamma = 0.05$ and $\omega = 0.04$.) We will call this system C1. System C1 has a single stable equilibrium point at $(P, Z) = (0.038, 0.046)$. For large enough displacements from this stable point (reduced Z and/or increased P) the system will undergo large changes in P and Z (i.e. the system temporarily enters an excited state before slowly returning to the stable point, in analogy to the ‘spring bloom’ in the ocean). Such a displacement may be brought about by a localized (in time) increase in the mortality rate of the predator Z or a sudden increase in the growth rate of P through an injection of nutrients. The factors that may

give rise to perturbations to the system are further discussed in Section 4.

Experiments have been performed with a bistable system, system C2, with a quadratic sink term $h = Z^2$. The effects of diffusion and stirring on C2 are found to be broadly similar to those of C1 and will be only briefly reported in Section 3.4.

The stirring of the populations is done by a simple kinematic flow field which produces chaotic mixing. The flow field was introduced by Pierrehumbert (1994) and used by Neufeld (2001) and others in a context similar to that used here. The direction of a sinusoidal shear flow alternates such that it is directed along the x and y directions for the first and second half of the period, T . The components of the flow (u, v) in the (x, y) directions are

$$u = \frac{1}{T} \Theta \left(\frac{T}{2} - t \pmod{T} \right) \sin \left(\frac{2\pi y}{L} + \phi_i \right), \quad (4a)$$

$$v = \frac{1}{T} \Theta \left(t \pmod{T} - \frac{T}{2} \right) \sin \left(\frac{2\pi x}{L} + \phi_{i+1} \right), \quad (4b)$$

where Θ is the Heaviside step function and ϕ_i is a randomly distributed phase between $[0, 2\pi]$, set at each half-period, to avoid transport barriers in the flow. The Lyapunov exponent, λ , of the flow is related to the period, T , with $\lambda \simeq 1.1/T$.

The system is defined to be on a square domain of length L , which is periodic in both spatial dimensions (x, y) . We choose to scale the time-scale in Eq. (1) with the inverse of the maximum growth rate for P , namely β , and length with L . Solutions depend on two non-dimensional numbers, namely $D_a = \beta T$ (the Damköhler number, or ratio of the advection to growth time-scales) and $K_L = \kappa(2\pi)^2/\beta L^2$ (the ratio of growth to diffusion time-scales). Note the actual growth rate in Eq. (3) depends on the values of P and Z . We therefore define an effective growth rate, β' , where

$$\frac{\beta'}{\beta} = (1 - P) - \alpha \left(\frac{ZP}{v^2 + P^2} \right). \quad (5)$$

The system is initialized with P , a constant value of 0.045, and Z varying sinusoidally in both x and y with a wavenumber, k , amplitude equal to 0.02, and mean Z_0 . As Z_0 is decreased, a greater fraction of the initial state will be excitable. This fraction we denote as A_i . The equations are solved numerically by employing the positive definite advection scheme MPDATA; Smolarkiewicz and Margolin (1998).

3. Results

The question we ask is, under what conditions will fields that are initially heterogeneous become excited in the mean? Phase trajectories of the domain-averaged P

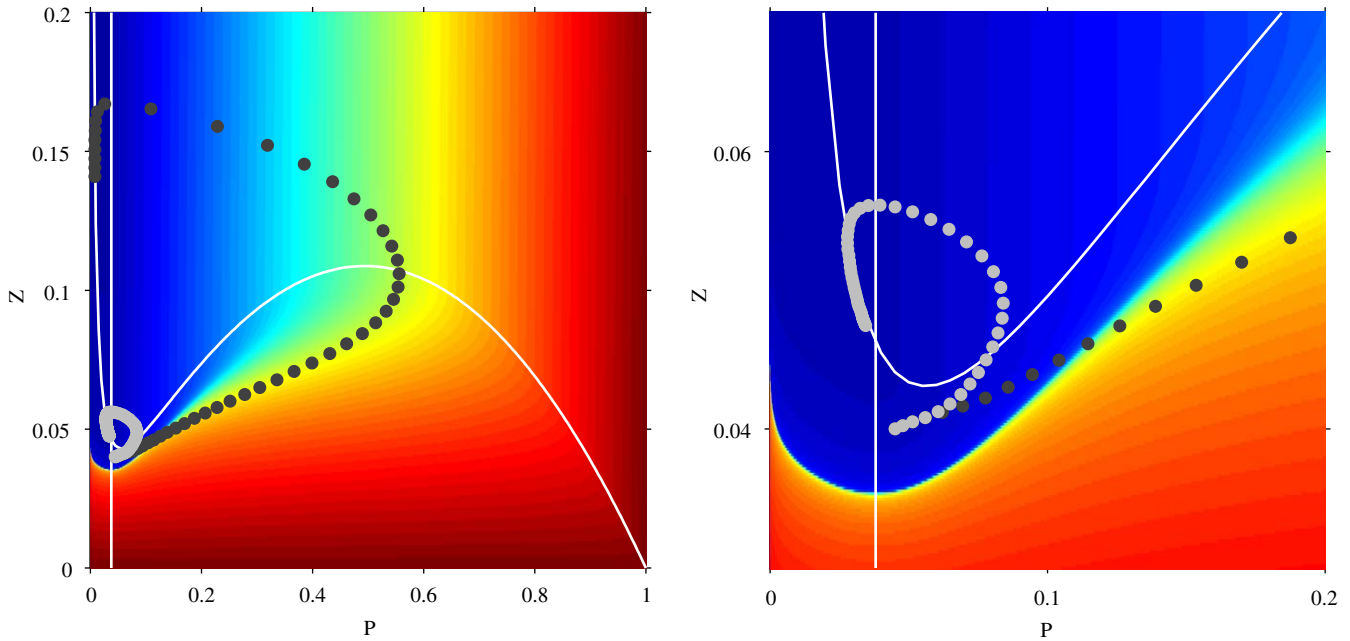


Fig. 1. Phase diagram for system C1 (the panel to the right is an enlarged portion of the panel to the left). White lines denote the P and Z nullclines. The color shading gives the maximum value of P for an initial value of (P, Z) with the darkest red shading corresponding to 1. The filled circles denote phase plane trajectories of the domain averaged (P, Z) with the same initial conditions at intervals of 0.86 time units ($D_a = 1.43$ and 2.15 for light and dark gray circles, respectively).

and Z for two cases with the same initial conditions are shown in Fig. 1, but one case becomes excited while the other does not. The details of these particular trajectories will be discussed below, but note that in both cases the domain-averaged initial values of (P, Z) lie outside the region of excitability.

3.1. Diffusion alone

First we consider the case with diffusion but no stirring ($1/T = 0$). The maximum value attained by the domain-averaged P and Z , P_{max} and Z_{max} , for varying A_i , with no stirring and $K_L = 5 \times 10^{-5}$, is shown in Figs. 2a and b, respectively, as open circles. For comparison, the well-mixed case, i.e. homogeneous initial Z with the same value of Z_0 , is shown as the dashed line. (We choose to use P_{max} and Z_{max} as a measure of the level of excitation of the system. Using other measures such as the change in total primary productivity would yield similar results.) Heterogeneity in the initial conditions produces increased reaction rates in the mean. Our reaction system can support waves of excitation that sweep across the domain and increase the area of the system that gets into an excited state. For instance, with $A_i = 0.25$ (and $K_L = 5 \times 10^{-5}$), P_{max} is increased by 50% over the case with no diffusion.

In the case of excitable media the excitation wave is “pushed” by the nonlinear dynamics of the system (cf. Murray, 1993). For the Fitz–Hugh–Nagumo (FHN)

model, an exact solution exists (under certain conditions) for the speed of the excitation wave, c_r (Neufeld, 2001). No analytic solution exists for the Truscott–Brindley (TB) model but, based on the FHN solution, we may expect the wave speed for the TB model to be expressed as

$$c_r \sim \sqrt{\beta^* \kappa}, \tag{6}$$

where β^* is an effective reaction rate taking into account the suppression caused by the grazing of the background Z population and the location of the threshold of excitability. Indeed, numerical experiments demonstrate that the speed of the reaction wave conforms to expression (6) when β^* is taken as the effective reaction rate β' at the excitability threshold. For the parameters considered here, this is approximately 15% of β .

3.2. Stirring with diffusion

Stirring by fluid motions can either promote or suppress excitation of the fields depending on the value of D_a (Neufeld, 2001). Two phase trajectories for the domain averaged P and Z are shown in Figs. 1a and b for $D_a = 1.43$ and 2.15. For the higher value of D_a the system undergoes a global excitation, in the sense that elevated values of P are attained for (almost) all fluid elements. For the lower value of D_a (increased stirring rate) excitation is suppressed.

The behavior of the system also depends on the fraction of the system initially exceeding the excitability

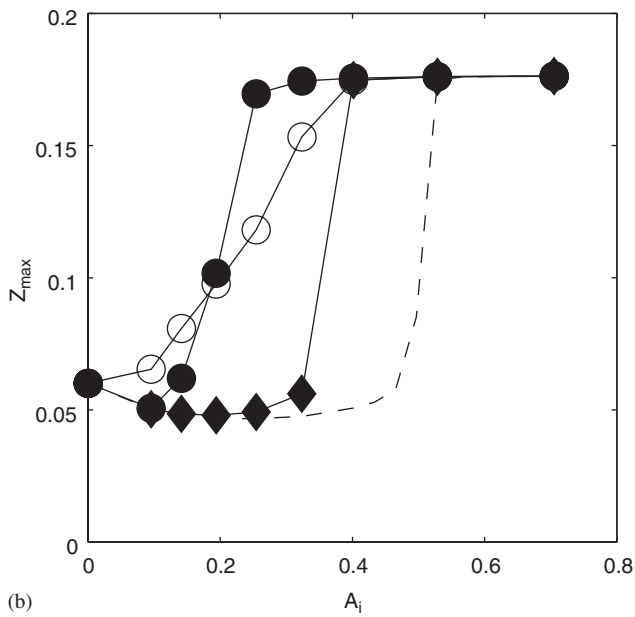
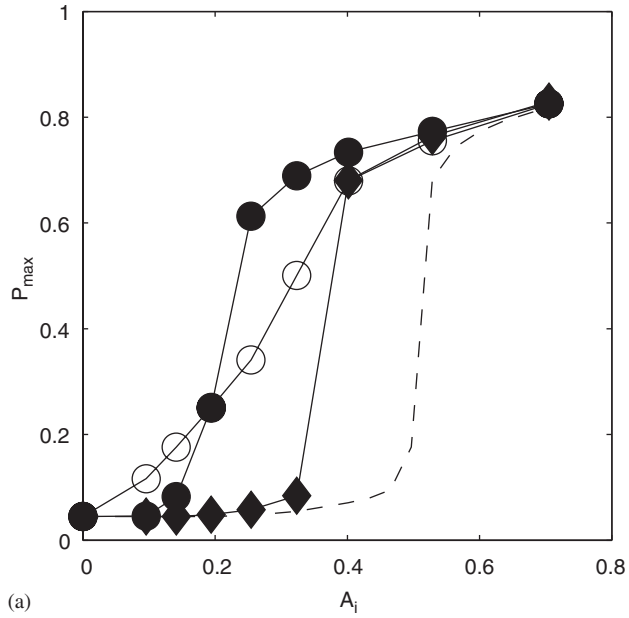


Fig. 2. (a) The maximum value attained by the domain average P , P_{max} , as a function of the fraction of tracer initially exceeding the excitability threshold, A_i , with no stirring (open circle), $D_a = 4.3$ (closed circles) and $D_a = 1.43$ (closed diamonds): $K_m = 0.001$ (see Eq. (9) for definition). The dashed line is the well-mixed case. (b) As (a) but for Z .

threshold, A_i , and the relative diffusion rate, K_L . Figs. 3a and b show P at $t = 21.5$ with two different values of A_i . The structure along $y = 0.5$ for both fields is shown in Figs. 4a and b, respectively. Stretching by the flow produces filamentary structures. For the lower value of A_i only a small fraction of the system exceeds the excitability threshold and the filaments are isolated. For the higher value of A_i merging filaments produce enhanced excitation.

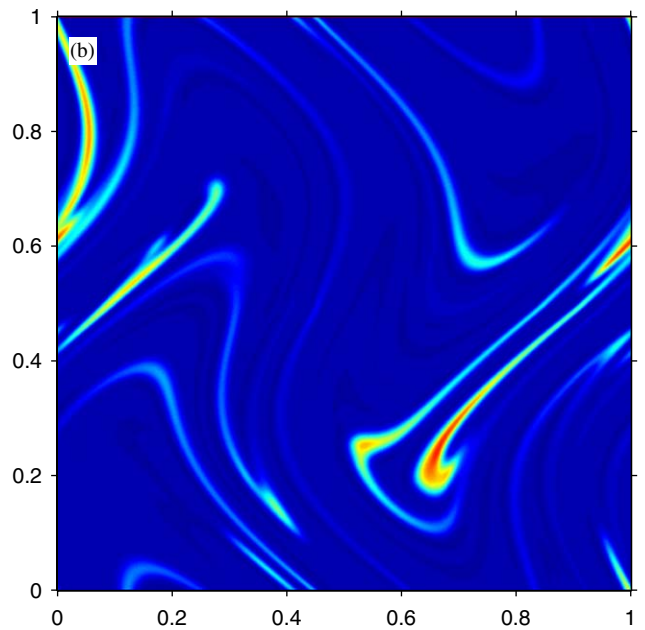
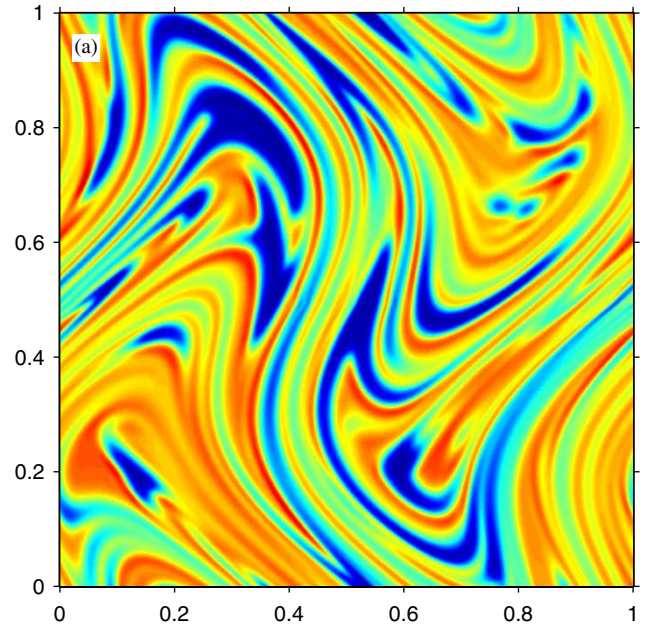


Fig. 3. Snapshot of the distribution of P for two different values of A_i , (a) $A_i = 0.25$ and (b) $A_i = 0.09$: $t = 21.5$, $D_a = 4.3$, $K_L = 5 \times 10^{-5}$.

The width, w_f , of a filament is governed by the balance between the straining of the flow, which is tending to thin the filament, and diffusion and excitation waves which are tending to broaden it. When the balance is between the straining flow and the speed of the excitation wave we expect

$$w_f \sim \frac{c_r}{\lambda} \sim \frac{\sqrt{\beta^* \kappa}}{\lambda} \quad (7)$$

(Neufeld, 2001; McLeod et al., 2002; Neufeld et al., 2002b; Hernandez-Garcia et al., 2003). Again, for the TB model we have no analytic solution, but we expect c_r

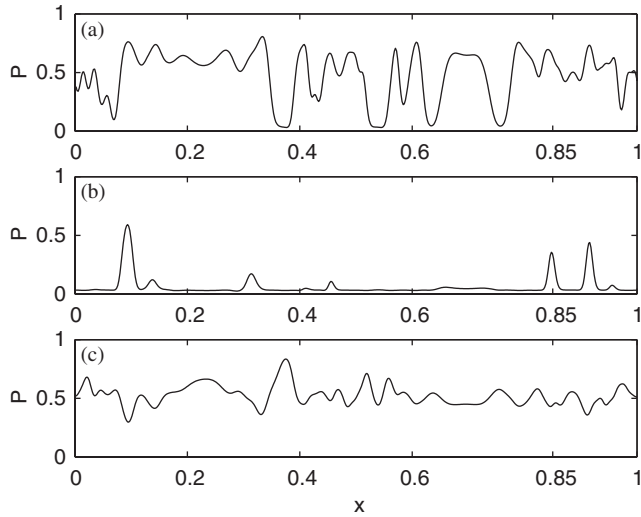


Fig. 4. Filamentary structure along $y = 0.5$ for the reactive tracers with (a) $A_i = 0.25$ and (b) $A_i = 0.09$ (from Fig. 3). (c) The same but for an inert tracer ($\beta = 0$) initialized with a concentration between 0 and 1.

to be given by Eq. (6) and β^* to be given by the effective growth rate at the threshold of excitability. We also expect there to be a lower bound on w_f given by the inert tracer case, namely $w_f = \sqrt{\kappa/\lambda}$ (McLeod et al., 2002). The amplitude of filaments is enhanced if $\beta'/\lambda > 1$, and suppressed otherwise (Martin, 2000). For comparison, a cross-section of an inert tracer is shown in Fig. 4c. The inert tracer was initialized between 0 and 1 and placed in the same flow field as the reactive tracers shown in Figs. 4a and b. The amplitude of the filaments for the inert tracer is much reduced compared to the reactive tracer. However, there is little difference in the width of filaments. In the cases considered here there is little broadening of the filaments by reactive waves.

P_{max} and Z_{max} are shown in Figs. 2a and b, respectively, as a function of A_i for two values of D_a . We see an abrupt change from suppressed excitation (when P_{max} is close to the well-mixed value) to an excited state as A_i is increased. For $D_a = 4.3$, and lower values of A_i , the value of P_{max} is less than that with diffusion alone, while for values of A_i above the transition stirring enhances the excitability of the system. For $D_a = 1.43$ there is very little enhancement by stirring. For a given value of A_i there is a critical value of D_a above which global excitation takes place. The inverse of this critical value is shown in Fig. 5a as a function of A_i . A higher value of A_i requires larger stirring rates to suppress excitation.

3.3. Mix-down time

An important time-scale is the time, T_m , it takes to stir a patch initially of size L_p down to the filament size, w_f . This time-scale is sometimes referred to as the “mix-down time” (Thuburn and Tan, 1997; Hu and Pierre-

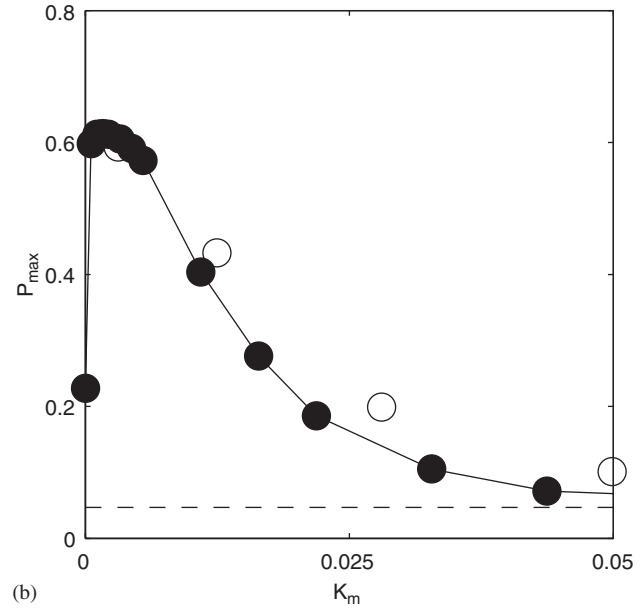
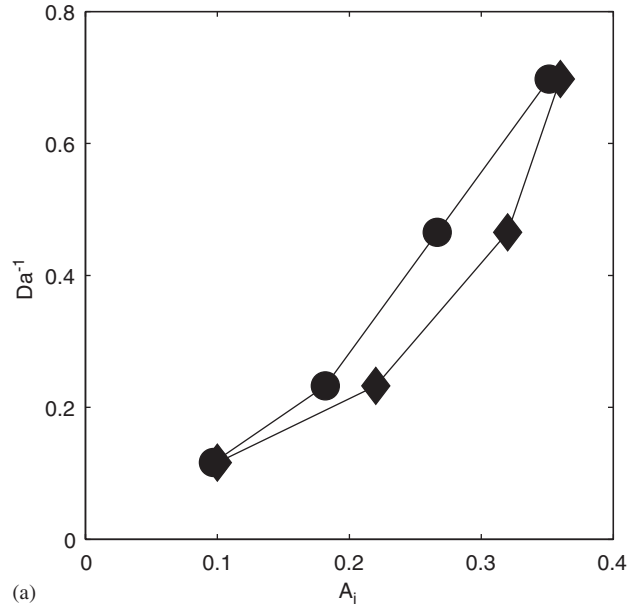


Fig. 5. (a) The critical value of the inverse Damköhler number for which excitability is suppressed as a function of A_i , for system C1 (closed circles). The critical inverse Damköhler number for which transition to an excited state is suppressed for system C2 (closed diamonds) is also shown. (b) P_{max} as a function of the non-dimensional diffusion coefficient K_m with $D_a = 4.3$: K_m varied by varying κ (closed circles) and the wavenumber of the initial distribution (open circles). The dashed line is the well-mixed case.

humbert, 2001). The straining flow produces an exponential reduction with time of the cross-patch scale, so that the mix-down time is given by

$$T_m = \frac{1}{\lambda} \ln \left(\frac{L_p}{w_f} \right). \tag{8}$$

For times longer than T_m , subsequent stretching and folding by the flow will cause filaments to merge and

mixing to take place. For times shorter than this little mixing will occur. If T_m is short compared to the time-scale for the growth of the population P , then mixing will have smeared out perturbations to the system before significant reaction has taken place. (The importance of the mixing time for pattern formation has been noted by Nugent et al. (2004) in their experimental study of a reaction–advection–diffusive system.)

Eq. (8) involves the filament width, which is controlled not only by stirring but also by diffusion. Diffusion, therefore, plays a crucial role in the system: too many and initial perturbations are smoothed away, too little and insufficient mixing takes place before the reaction is over. An appropriate scaling for the diffusion coefficient κ comes from the ratio w_f/L_p . We define

$$K_m = \frac{\kappa}{\lambda L_p^2}, \quad (9)$$

where L_p is the length scale of the region which initially exceeds the excitability threshold ($L_p \sim \sqrt{A_i}$). K_m is an inverse Péclet number based on the patch size.

P_{max} as a function of K_m is shown in Fig. 5b with $D_a = 4.3$ and $A_i = 0.25$. Note it is inappropriate to talk of a high Péclet number limit. The curve for P_{max} peaks at a value of $K_m \simeq 0.001$. For lower values of K_m the mix-down time is long compared to the reaction time. For large values of K_m significant mixing takes place before the reaction peaks.

Returning to the critical Damköhler number for excitability (Fig. 5a) we can now write this in terms of the mix-down time, T_m , relative to the inverse reaction rate. As A_i increases so does the maximum in the initial reaction rate, β_{max} (A_i is increased by reducing Z_0 , the mean value of the initial Z field, which, referring to Eq. (5), increases β'). For system C1, to a good approximation, we find the critical value for T_m is given by

$$\frac{1}{T_{mc}} = 0.54(\beta_{max} - \beta^*), \quad (10)$$

where, as before, β^* is the reaction rate at the threshold of excitation. For $D_a = 4.3$ and $A_i = 0.25$, this value of T_{mc} is equivalent to $K_m = 0.01$ (cf. Fig. 2d). For higher values of K_m (smaller T_m), P_{max} is much reduced.

But note there is an upper limit to the value of T_m for which a significant enhancement of population growth will occur. The growth and subsequent decay of the population occurs over a finite time. If T_m is too large, then the “bloom” will have taken place before mixing can have an impact (see Fig. 5b). Subsequent stirring will have little effect.

3.4. A bi-stable system

In order to assess the applicability of the above results to other reactive systems, experiments have been performed with a bi-stable system, by setting the sink term in

Eq. (3) to be quadratic, i.e. $h = Z^2$. By a suitable choice of parameters (the values used here are the same as those used in Brentnall et al. (2003)) the system, C2, now has two stable equilibria with relatively low and high values of P , respectively. Modest displacements from the low P state can cause the system to transition to the high P (excited) state. The effects of diffusion and stirring are found to be qualitatively similar to those for system C1, in terms of promoting or suppressing this transition to the excited state, for spatially varying initial conditions. The critical value of D_a^{-1} for the excitation to be suppressed is shown in Fig. 5a as a function of A_i . For system C2 the constant of proportionality in Eq. (10) is found to be 0.2 for A_i less than 0.25.

4. Discussion

The similarity of the behavior of the two systems considered, C1 and C2, with respect to the impact of the combined effects of diffusion and fluid stirring, suggests that the results may be applicable to a broad class of biological populations or reactive systems which exhibit excitable dynamics or that are bi-stable. A key measure of the combined effects of diffusion and stirring is the ratio of the mix-down time, T_m , to the inverse of the growth rate. Regard therefore needs to be given to the initial scale of the spatial variability of the system (and the processes controlling that scale) as well as the mixing and reaction processes. Diffusion is crucial for the mixing process. However, the right amount (relative to the reaction and stirring rates) is required to enhance the reaction. With strong diffusion properties are smeared out before significant reaction takes place, while with weak diffusion little mixing occurs before the reaction is over.

To illustrate the implications of the above findings we consider a particular situation, that for plankton in the ocean. A typical value of the strain rate by oceanic mesoscale eddies is $\lambda \sim 0.1 \text{ day}^{-1}$ (e.g. Abraham et al., 2000). (Mesoscale eddies are sometimes referred to as the weather systems of the ocean and are responsible for the lateral stirring of properties on scales of a few Tens of kilometers and less.) If we assume that spatial variations in the distribution of zooplankton, or injection of nutrients, have increased the effective growth rate of phytoplankton locally by 0.1 day^{-1} , then the critical mixing-down time given by Eq. (10) is $T_{mc} = 20$ days. If the actual mix-down time, T_m , is greater than this value we expect the fluid stirring to impact on the populations dynamics of the plankton. T_m is given by Eq. (8) and, therefore, with the above values the critical ratio of initial patch size to filament width, L_p/w_f , is approximately 7. Taking $\kappa = 1 \text{ m}^2 \text{ s}^{-1}$ for the background diffusivity (a rough estimate for the effect of unresolved turbulent scales $\lesssim 1 \text{ km}$, using

Okubo (1971)) then, from Eq. (7), $w_f = 1$ km. For stirring to be important we require initial patch sizes to be of the order of 7 km or more. Note that the critical value of L_p is a strong function of the strain rate. Increasing the stirring rate by a factor of two in the above example increases the critical initial patch size to ~ 40 km.

The above raises the question as to how the initial perturbation to the system is produced, something we will not explicitly consider here. Spatial variations in the full marine ecosystem may be brought by a number of factors and include spatial variability in the overwintering zooplankton and phytoplankton populations, the supply of nutrients to the euphotic zone through eddying and frontal activity, and the depth of mixing induced by the air/sea interactions (cf. Martin, 2003). The parameters of the model used here are constant in time and space and therefore the nullclines of the system are fixed. Assuming constant parameters is a reasonable first step to studying the impact of stirring and mixing and assumes that any temporal change is sufficiently rapid that the system is unable to track the change in stable equilibria points in P, Z space. However, many of the processes listed above will affect the growth and decay rates of the components of the system and therefore induce spatial and temporal variations in the parameters of our simple model. Matthews and Brindley (1997) have studied the impact of temporal variations in the parameters of the TB model and find a lower limit to the rate of increase of the phytoplankton growth rate for excitation of the system to occur. The study of the effects of temporal and spatial variability of the TB model parameters on the behavior of the system in the presence of fluid stirring is the next step the present authors will take.

In practice, the geometry of a flow may well be more complex than considered here. In particular, either transient or permanent barriers to tracer transport may exist (Ottino, 1989), which will impact on the population dynamics (cf. Bracco et al. (2000); Martin et al. (2002) for marine ecosystem examples). In addition, of course, the population dynamics of the ecosystem will be more complex. However, it is clear that heterogeneity in the distribution of a population impacts on the overall dynamics of the system and needs to be taken into account in developing models of such systems. The above highlights the need to determine the factors that control the spatial distribution of anomalies, or perturbations, to the distributions of populations as well as the impact of stirring and mixing.

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