Analysis and simulations of bulk-surface reaction-diffusion systems

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ABSTRACT

In this brief exposition, we present a bulk-surface reaction-diffusion system on a stationary volume, whereby the bulk-reaction-diffusion system is coupled to the surface-reaction-diffusion system through mixed Robin-type boundary conditions which can be thought of as another form of nonlinear reaction-kinetics between bulk and surface molecular species in the context of cell and developmental biology or populations, in the context of ecology. We then derive bulk-surface diffusion-driven instability conditions, a generalisation of the classical necessary conditions for Turing diffusion-driven instability. Based on these conditions, we predict under what conditions on the bulk- and surface-diffusion coefficients does the bulk- or surface- or both bulk-surface- reaction-diffusion systems give rise to pattern formation. Theoretical predictions are then validated and confirmed by the use of the bulk-surface finite element method with piece-wise bilinear basis functions for space-discretisation and a fractional-step θ-scheme for time-discretisation.

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1. INTRODUCTION

Bulk-surface partial differential equations (BS-PDEs) coupling physical processes taking place inside a domain (referred to as the *bulk* domain) to physical processes occurring on the boundary of the domain (referred to as the *surface* domain) through mixed Robin-type boundary conditions are emerging as natural candidates to model pattern formation in developmental bio- logy [22, 29, 31, 32] and the spatiotemporal organisation of molecular species in cellular and molecular biology [6, 7]. In material science, for example, bulk-surface PDEs are widely applied to modelling surfactants [], thin films [15], polymer [37], nematic liquid crystals [4] and more recently, electrodeposition in batteries [8]. More recently, bulk-surface reaction-diffusion equations (BS-RDEs) have been coupled with continuum mechanics to model single cell migration with applications in cell biology [19, 28, 17].

Analytical techniques for the analysis of BS-PDEs include linear stability analysis [32, 22, 25, 34] and weakly nonlinear analysis [35, 30]. Linear stability analysis establishes the necessary and sufficient conditions for, say, diffusion-driven instability (DDI) (a generalisation of the Turing DDI) to occur, whereby a uniform steady state that is stable in the absence of planar and surface diffusion is driven unstable when planar and surface diffusion are introduced []. Weakly nonlinear analysis goes beyond linear stability analysis by looking at the stability analysis of space-dependent, time-independent solutions of the BS-PDE model to establish under what conditions other instabilities (such as Hopf, transcritical, pitch, etc) will occur within the system [35].

To validate analytical findings from linear and weakly nonlinear analysis, due to the complex nature BS-PDEs, novel numerical methods have been and continue to be developed. The most popular numerical methods for BS-PDEs include (but are not limited to) : the bulk-surface finite element method (and its variations) [24, 2, 10] ; the bulk-surface virtual element method [14, 13, 11, 12] ; cut-finite element methods [18, 5] ; ALE formulation for bulk-surface finite elements [21], the closet-point methods [27, 20] and finite difference methods applied to diffuse-interface formulations [16, 36, 1].

2. BULK-SURFACE REACTION-DIFFUSION SYSTEMS ON STATIONARY VOLUMES

Let $\Omega \in \mathbb{R}^d (d = 2,3)$ be a simply well-connected compact *bulk* domain in the d-dimensional Euclidean space and let $\Gamma := \partial\Omega \in \mathbb{R}^{d-1}$ be its smooth enclosing boundary, denoted as the *surface* domain.

Let $u(x,t) = (u_1(x,t), u_2(x,t), \cdots, u_p(x,t),)^T$, a vector of p-unknown species or populations react and diffusion in the bulk domain Ω and $v(x,t) = (v_1(x,t), v_2(x,t), \ldots, vq(x,t),)^T$ a vector of p-unknown species or populations react and

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diffusion in the surface boundary Γ. The bulk and surface species obey the following bulk-surface reaction-diffusion model [22, 14, 13]

$$\begin{cases} \frac{\partial u_i}{\partial t} = d_i^{\Omega}\Delta u_i + f_i(u_1,u_2,\cdots,u_p,x,t), & \text{for } x\in\Omega,\ t\in I=(0,T_f],\ T_f>0,\\ -d_i^{\Omega}(n\cdot\nabla u_i) = h_i(u_1,u_2,\cdots,u_p,v_1,v_2,\cdots,v_q,x,t), & \text{for } x\in\Gamma,\ t\in I,\\ \frac{\partial v_j}{\partial t} + d_i^{\Omega}(n\cdot\nabla u_i) = d_j^{\Gamma}\Delta_{\Gamma} v_j + g_j(v_1,v_2,\cdots,v_q,x,t), & \text{for } x\in\Gamma,\ t\in I,\\ u_i(x,0) = u_i^0(x), & \text{for } x\in\Omega,\ t=0,\\ v_j(x,0) = v_j^0(x), & \text{for } x\in\Gamma,\ t=0, \end{cases} \tag{1}$$

for $i = 1, 2, \cdots, p$ and $j = 1, 2, \cdots, q$, with $p \geq 1$ and $q \geq 1$. In the above, Δ and Δ_Γ denote the Laplace and Laplace-Beltrami operators respectively [9] ; d_i^{Ω}, $i = 1, 2, \cdots, p$, denote positive bulk-diffusion coefficients, and d_j^{Γ}, $j=1,2,\cdots,q$ denote positive surface diffusion coefficients. fi (u_1, u_2,..., u_p, x, t) represents reaction kinetics taking place on the bulk domain, g_j (v_1, v_2, ⋯, v_q, x, t) represents reaction kinetics taking place on the surface and h_i(u_1, u_2,, u_p, v_1, v_2, ⋯ v_q, x, t) denotes the coupling mixed Robin-type boundary conditions which can be thought of as the reaction kinetics between bulk and surface species [6, 7, 22, 14,13, 2, 10, 24].

Activator-depleted reaction kinetics

For illustrative purposes, we assume a two- component bulk-reaction-diffusion system and a two component surface-reaction-diffusion system with activator-depleted reaction kinetics in the bulk and surface domains, respectively and these are given by

$$f_1(u_1,u_2) = \gamma^{\Omega}\left(a - u_1 + u_1^2 u_2\right), \tag{2}$$

$$f_2(u_1,u_2) = \gamma^{\Omega}\left(b - u_1^2 u_2\right), \tag{3}$$

$$g_1(v_1,v_2) = \gamma^{\Gamma}\left(a - v_1 + v_1^2 v_2\right), \tag{4}$$

$$g_2(v_1,v_2) = \gamma^{\Gamma}\left(b - v_1^2 v_2\right), \tag{5}$$

where γ^{Ω} and γ^{Γ} are the scaling parameters in the bulk and on the surface, respectively.

Coupling boundary conditions and initial conditions

For analytical purposes, we assume linear mixed Robin-type boundary conditions defined by the following coupling reaction kinetics between bulk and surface species

$$h_1(u_1,u_2,v_1,v_2) = \gamma^{\Gamma}\left(\alpha_1 v_1 - \beta_1 u_1 - \kappa_1 u_2\right), \tag{6}$$

$$h_2(u_1,u_2,v_1,v_2) = \gamma^{\Gamma}\left(\alpha_2 v_2 - \beta_2 u_1 - \kappa_2 u_2\right), \tag{7}$$

where $\alpha 1$, $\alpha 2$, $\beta 1$, $\beta 2$, κ_1 and κ_2 are constant non-dimensionalised parameters.

2.1. Conditions for bulk-surface diffusion-driven instability

For a two-component bulk reaction-diffusion system and a two-component surface reaction- diffusion system with *activator-depleted* reaction-kinetics (2)-(5) (also known as the Schnaken- berg reaction kinetics) [33] endowed with linear coupling boundary conditions (6)-(7) [22, 32], the bulk-surface diffusion-driven instability conditions are given by the following theorem.

Theorem 1 *The necessary conditions for bulk-surface diffusion-driven instability under which a uniform steady state that is asymptotically stable in the absence of bulk and surface diffusion becomes unstable in the presence of bulk- and/or surface-diffusion are given by [22, 34]*

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$$f_{1u_1} + f_{2u_2} < 0, \quad (8)$$

$$g_{1v_1} + g_{2v_2} < 0, \quad (9)$$

$$f_{1u_1} f_{2u_2} - f_{1u_2} f_{2u_1} > 0, \quad (10)$$

$$g_{1v_1} g_{2v_2} - g_{1v_2} g_{2v_1} > 0, \quad (11)$$

$$\text{and } d^{\Omega} f_{1u_1} + f_{2u_2} > 0, \text{ and } \left(d^{\Omega} f_{1u_1} + f_{2u_2}\right)^2 - 4d^{\Omega}\left(f_{1u_1} f_{2u_2} - f_{1u_2} f_{2u_1}\right) > 0, \quad (12)$$

$$\text{and/or } d^{\Gamma} g_{1v_1} + g_{2v_2} > 0, \text{ and } \left(d^{\Gamma} g_{1v_1} + g_{2v_2}\right)^2 - 4d^{\Gamma}\left(g_{1v_1} g_{2v_2} - g_{1v_2} g_{2v_1}\right) > 0, \quad (13)$$

where the partial derivatives $\frac{\partial f_i}{\partial u_j}$ *and* $\frac{\partial g_i}{\partial v_j}$ *i=1,2 are all evaluated at the uniform steady state* $(u_1^*, u_2^*, v_1^*, v_2^*) = \left(a+b, \frac{b}{(a+b)^2}, a+b, \frac{b}{(a+b)^2}\right)$, *with non-dimensionalised a, b representing constant reaction kinetic parameters and* d^{Ω} *and* d^{Γ} *are the non-dimensionalised positive bulk- and surface-diffusion coefficients.*

Proof. The proof follows standard techniques for linear stability analysis whereby the bulk, sur- face and coupling boundary reaction kinetics possess a unique uniform steady state. The analysis is limited to the case of the ball where there is natural compatibility between the Laplace and Laplace-Beltrami operators. For the detailed derivation of the bulk-surface diffusion-driven in- stability, the interested reader is referred to the work by Rätz and Roger [32], Madzvamuse [22] and more recently by Villar-Sepúlveda et al., [35].

Some caveats

From the analytical results we state the following theoretical predictions which are confirmed through the use of numerical simulations.

1. It must be noted that $d^{\Omega} = d^{\Gamma} = 1$ are not admissible, since there is a contradiction bet ween the necessary conditions (8)-(9) and the first inequalities in (12)-(13), respectively.
2. Hence, the bulk and surface diffusion coefficients d^{Ω} and d^{Γ} must be different from one. In fact, it can be shown that the bulk- and surface-diffusion coefficients must be greater than one in order for bulk-surface diffusion-driven instability to occur (see the work by Madzvamuse et al. [26] for further details).
3. Hence, the bulk-surface reaction-diffusion system must obey the classical paradigm for pattern formation, that of *long-range inhibition, short-range activation*.
4. Taking $d^{\Omega} = d^{\Gamma} = 1$ ensures that the BS-RDEs (1) do not give rise to the formation of spatial structure. For this case, the uniform steady state is the only stable solution for the coupled system of BS-RDEs (1).
5. The above imply that taking $d^{\Omega} > 1$ and $d^{\Gamma} = 1$, the bulk-reaction-diffusion system has the potential to induce patterning in the bulk for appropriate diffusion-driven instability parameter values while the surface-reaction-diffusion system is not able to generate patterns.
6. Alternatively taking $d\Omega = 1$ and $d\Gamma > 1$, the bulk-reaction-diffusion system fails to in- duce patterning in the bulk while the surface-reaction-diffusion system has the potential to induce patterning on the surface
7. On the other hand, taking $d\Omega > 1$ and $d\Gamma > 1$ appropriately, then the coupled system of BS-RDEs exhibits patterning both in the bulk and on the surface.

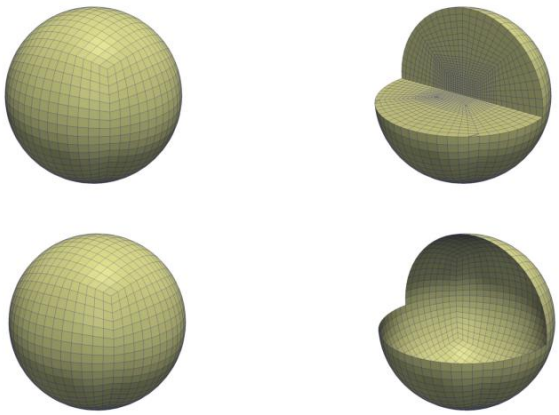


FIGURE 1: An example illustrating how the surface triangulation (bottom row) is naturally induced by the volume or bulk (top row) triangulation. Part of the domain has been cut away and shown on the right to reveal some internal mesh structure.

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3. THE BULK-SURFACE FINITE ELEMENT METHOD AND THE FRACTIONAL-STEP θ -SCHEME

3.1. Space discretisation: The bulk-surface finite element method with bilinear finite elements

Following the derivation of the weak variational form be seeking weak finite element solutions, we proceed to discretise the continuous weak variational formulation in space using piecewise bilinear finite elements with quadrilateral and hexahedral meshes. For finite element methods involving bulk and surface coupled dynamics, it is natural to define the surface triangulation as a collection of the faces of the elements of the bulk triangulation whose vertices lie on the surface [10, 22, 24]. The surface triangulation is therefore induced as the trace of the bulk triangulation. Under this approach, we use hexahedral meshes for the bulk geometries which induce quadrilateral meshes for the surface geometries. For further details on techniques for generating bulk and surface triangulations with adaptivity, the reader is referred to the work of Bangerth, Koster and others [3]. The space discretisation and assembly is carried out using the *deal.ii*, a *C* + + finite element software package [3]. For example for the case of the sphere, we illustrate a typical bulk and surface mesh in Figure 1.

3.2 Time-discretisation: The fractional-step θ-scheme

Since the space-discretisation following the use of bilinear finite elements results in second order convergence of the semi-discrete finite element weak formulation, we proceed to develop a second order implicit time-stepping scheme. For this, we adopt the *fractional-step θ-scheme*

(FSTS) as outline in [23, 24]. This method is second order accurate in time when choosing $\theta = 1-1/\sqrt{2}$ and it was shown to be the quickest in a selection of tested methods in a previous investigation [23]. Since the FSTS is an implicit scheme, nonlinearities are treated either using the Newton-Raphson method or the Picard iteration method [23, 24]. For details on the convergence, stability and performance of the FSTS, the interested reader is referred to see the work by Madzvamuse and Chung [23, 24].

a	b	d	$\alpha 1$	$\alpha 2$	$\beta 1$	$\beta 2$	$\kappa 1$	$\kappa 2$
0.1	0.9	100	5/12	5	5/12	0	0	5

TABLE 1 – Parameter values for the coupled system of bulk-surface reaction-diffusion equations (1) with activator-depleted reaction kinetics (2)-(5).

equilibrium state is given by $(u*, v*, r*, s*) = (1, 0.9, 1, 0.9)$. We stop the simulations when the L_2-norm of the difference of the numerical solutions between two successive timesteps reaches some tolerance

$$\frac{||u_{i_h}^{n+1} - u_{i_h}^{n}||}{\tau} := \frac{1}{\tau}\Big(\int_{\Omega}(u_{i_h}^{n+1} - u_{i_h}^{n})^2\Big)^{\frac{1}{2}} \leq 10^2\varepsilon, \quad n > 0, \tag{14}$$

where ε is the tolerance used for the matrix solver. Similar quantities are defined for the other variables. It must be note that these quantities are related to the time-derivative of the solution and therefore should become smaller as the solution does not change much in time and converges. Numerical simulations of the coupled system of BS-RDEs on a sphere of radius one are exhibited in Figures 2-4. In all the simulations we fix the scaling parameter $\gamma^{\Omega} = \gamma^{\Gamma} = 500$ and vary the diffusion coefficients. The numbers of degrees of freedom for the sphere were 59042/3076
(bulk/surface), for the cube 71874/12292 and for the ellipsoid 59042/3076. The timestep chosen in each case was $\tau = 10^{-3}$.

In Figure 2 we illustrate the ability of the bulk-reaction-diffusion system to give rise to bulk-diffusion-driven instability both in the bulk and on the surface even though the surface-reaction- diffusion system is not able to give rise to pattern formation. This is due to role of the mixed Robin-type boundary conditions which play the role of reaction-kinetics of bulk and surface species. The sphere is cut open to exhibit three-dimensional spots and stripe tubes forming in the bulk, which induce stripe patterns on the surface.

Now, reversing the pattern formation mechanism, we select diffusion parameter values such that the bulk-reaction-diffusion system is not able to give to pattern formation, only the surface- reaction-diffusion system is allowed to fullfil surface-diffusion-driven instability conditions. In Figure 3 we illustrate the pattern formation process when the bulk-and surface-reaction-diffusion system is coupled in this manner. The surface-reaction-diffusion system gives rise to spot pat- terns on the surface, while the bulk-reaction-diffusion system is only able to generate patterns in a small region close to the surface. This region can be thought of a the epidermis, which is

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reminiscent of pattern formation in nature. The pattern formation mechanism is consistent with theoretical predictions outlined in Section 2.1.

We conclude our simulations by choosing bulk- and surface-diffusion coefficients such that the full bulk- and surface-reaction-diffusion system gives rise to pattern formation both in the bulk and on the surface. The pattern formation process is shown in Figure 4 where spots and stripe patterns are formed on the surface and in the bulk, respectively. Again, the results are consistent with theoretical predictions.

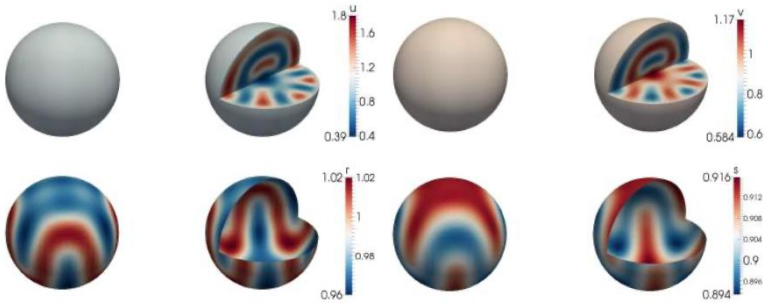


FIGURE 2 – Bulk-surface finite element solutions corresponding to the coupled BS-RDEs (1) with two-bulk and two-surface species with $d^{\Omega} = 10$ in the bulk, $d^{\Gamma} = 1$ on the surface and $\gamma^{\Omega} = \gamma^{\Gamma} = 500$. The bulk-reaction-diffusion system generates patterns everywhere in the interior bulk domain as well as on the surface, even though the surface-reaction-diffusion system is not able to produce patterns by itself.

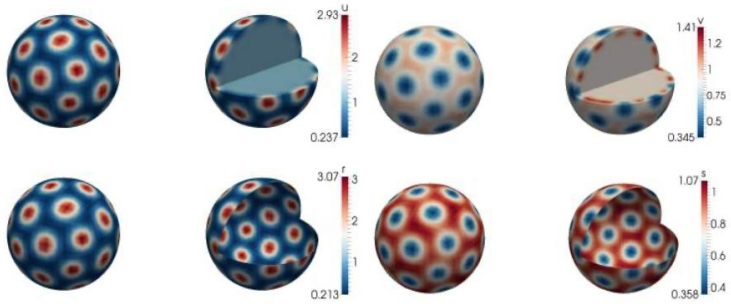


FIGURE 3 – Bulk-surface finite element solutions corresponding to the coupled BS-RDEs (1) with two-bulk and two-surface species with $d^{\Omega} = 1$ in the bulk, $d^{\Gamma} = 10$ on the surface and $\gamma^{\Omega} = \gamma^{\Gamma} = 500$. The bulk-surface reaction-diffusion system is generates patterns on the surface as well as in a small region next to the surface, but not everywhere in the bulk.

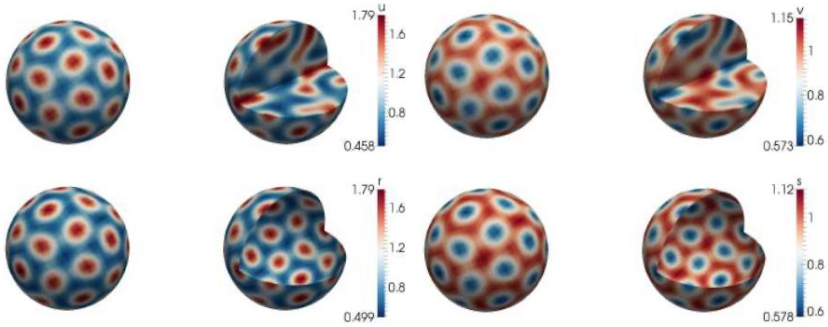


FIGURE 4 – Bulk-surface finite element solutions corresponding to the coupled BS-RDEs (1) with two-bulk and two-surface species with $d^{\Omega} = 10$ in the bulk, $d^{\Gamma} = 10$ on the surface and $\gamma^{\Omega} = \gamma^{\Gamma} = 500$. The bulk-surface reaction-diffusion system gives rise to pattern formation both in the bulk and on the surface in the form of stripes and spots.

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4. CONCLUSIONS

In this brief exposition, we have presented a bulk-surface reaction-diffusion model for pat- tern generation and have shown both theoretically and computationally its ability to give rise to patterns either on the surface and within a small region close to the boundary, with no patterns forming everywhere else in the bulk or when the bulk-reaction-diffusion system induces pattern everywhere both in the bulk and on the surface. In the absence of bulk-diffusion-driven instability in the interior, the surface reaction-diffusion system is able to generate patterns on the surface as well as in a small region inside the volume. This is biologically plausible, since patterns form on the skin as well as within the epidermis region adjacent to the skin surface. In the absence of surface-diffusion-driven instability on the surface, the bulk-reaction-diffusion system has the capability to induce patterns in the interior as well as on the surface. The computational results are based on the implementation of the bulk-surface finite element method for a coupled system of bulk-surface reaction-diffusion equations. The numerical method was used to validate and confirmed analytical theoretical results for pattern formation in the bulk and on the surface of stationary volumes.

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