

LINEAR STABILITY ANALYSIS FOR THE THERMOTACTIC MICROORGANISMS IN POROUS MEDIA

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Abstract. Thermotaxis or motion in the field of temperature gradient is a very common phenomenon and can be found in many events in nature, from biological ones to the migration of colloidal particles. In this paper, we suggest a deterministic model to describe the collective behavior of a microorganism population with a general form of stimuli gradient-based taxis in porous media. This population has the mass density slightly heavier than the water density and forms a suspension. The suspended cells are actively in motion with a thermotaxis behavior (temperature gradient follower). Based on an Eulerian framework, the model comprises basically the Darcy equation for the fluid motion in porous media, equation of cell conservation for the microorganism population and equation of conservation for the considered stimuli. To take into account the density effects, the Boussinesq's approximation will be used. Linear stability analysis shows that there are interesting effects of temperature on the bioconvection pattern of the thermotactic microorganisms.

Key words: Thermotaxis, gradient-based motion, linear stability, thermotactic bioconvection.

1. Introduction

One of the adaptive behavioral responses of living organisms in their environment is 'thermotaxis', by which they migrate toward a preferred temperature or away from the uncomfortable heat sources. Thermotaxis or motion in the field of temperature gradient is a very common phenomenon and can be found in many events in nature, from biological ones such as the motion of *Dictyostelium* slugs (Maree et al. [1]), self organized thermoregulation of honeybees (Watmough and Camazine [2]), *Caenorhabditis elegans* behaviors (Matsuoka et al. [3]), human and animal sperm (Bahat

and Eisenbach [4], Bahat et al. [5]), to the migration of colloidal particles (Golestanian [6]). Different models were suggested to mathematically describe the thermotactic behavior such as the model of Watmough and Camazine [2] with thermotaxis diffusion for thermoregulating bees, the model of Maree et al. [1] with the motion of the *D. discoideum* slugs, the hybrid cellular automata/partial differential equation of Savill and Hogeweg [7], etc. We can also cite here the works of Matsuoka et al. [3] with a simple Monte-Carlo model of simulation for *C. elegans* behavior, the model for thermophilic and cryophilic tendencies of worms suggested by Ito et al. [8], and a simple biased random walk model of the *C. elegans* population behavior of Nakazato and Mochizuki [9], which reflects the results of individual movement assays. Their results assert the importance of the steepness of the thermal gradient that may change the migration behavior drastically in experiments on thermotaxis. However, none of the models has mentioned the feedback convection which can be generated by the collective behavior of thermotactic microorganisms. In this paper, we investigate this aspect in porous media. The mathematical model we suggest is a coupled system of partial differential equations wherein the thermotaxis is described under the form of temperature gradient following term. The linear stability analysis will be used to define the onset of the thermotactic patterns, known under the name *thermotactic bioconvection*. Related to the bioconvection patterns in porous medium, Kuznetsov [10, 11] and Nguyen-Quang et al. [12] summarized most of works on different aspects (stability analysis and numerical simulation) of bioconvection in porous medium. The results in this paper will highlight the study of critical thresholds for *thermotactic bioconvection* in porous medium as well as provide insight into several fundamental processes under the

gradient-based motion and give direction for our future research involving thermotaxis, chemotaxis and prey-taxis behavior of microorganism populations.

2. Mathematical formulation

2.1. Dimensional governing equations

For the conceptual model of bioconvection in a porous medium, the governing equations for unsteady flow in a porous medium are obtained by volume averaging the equations of Pedley et al. [13] according to the theory of Whitaker [14]. The replacement of the Laplacian viscous terms with the Darcian terms describing viscous resistance in a porous medium is the basic concept of this approach (Nguyen-Quang et al. [12, 15, 16]). The validity of Darcy's law in the porous medium bioconvection model is therefore assumed similar to that in a natural convection model in a layer being heated from below. We consider a two-dimensional horizontal porous layer of thickness H' containing an initially uniform concentration N' of thermotactic microorganisms. The upper and lower boundaries of the layer are impermeable and subjected to constant temperatures. The porous medium is assumed isotropic with a permeability K as shown in Fig. 1.

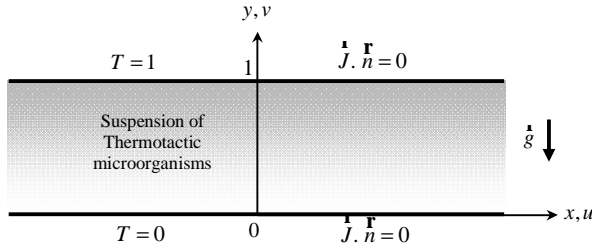


Fig. 1. Physical description of the problem

The following hypotheses are also assumed in order to ensure that the thermotactic behavior is not disturbed: (1) the porous matrix does not absorb microorganisms, (2) the pore sizes are significantly larger than the microbial cell sizes and the microorganism suspension is dilute; therefore, the change of permeability of the porous matrix due to cell deposition is negligible, (3) the possible local vorticity generated by flow through the pores does not affect the ability of microorganisms to reorient themselves; (4) the mortality and the multiplication of microorganism cells are neglected, in other words, the cells are assumed not to die or grow; the number of cells is therefore constant. We assume that all physical properties of the fluid are constant except the density in the buoyancy term of the Boussinesq's approximation. It is also assumed that the suspension of microorganisms is incompressible.

The governing equations are therefore:

$$\nabla' \cdot \mathbf{V}' = 0 \quad (1)$$

$$\frac{m}{K} \mathbf{V}' = -\nabla' P' + r \mathbf{g} \quad (2)$$

$$(rC)_p \frac{\partial T'}{\partial t'} + (rC)_f \nabla' \cdot (T' \mathbf{V}') = \nabla' \cdot (k_p \nabla' T') \quad (3)$$

$$e \frac{\partial N'}{\partial t'} + \nabla' \cdot (N' \mathbf{V}') = -\nabla' \cdot (N' \mathbf{V}'_c - D_c \nabla' N') \quad (4)$$

where $\mathbf{V}'(u', v')$ is the fluid velocity, P' the pressure, \mathbf{V}'_c the average cell swimming velocity due to thermotaxis and \mathbf{g} the acceleration of gravity.

The thermotaxis velocity is defined as follows.

$$\mathbf{V}'_c = W'_0 \frac{\nabla' T'}{|\nabla' T'|} \quad (5)$$

- Where W'_0 is a constant standing for the capacity of thermotactic motion of microorganisms (with the dimension $m^2 s^{-1} K^{-1}$), that actually is the diffusivity of microorganisms per 1 temperature degree.
- $\nabla' T'$ is the thermal gradient exerted on the considered system (K/m).

If we introduce the dimensionless velocity of thermotactic microorganisms Pe (Peclet number), we will have:

$$Pe = \frac{H'}{D_c} W'_0 = \frac{1}{D_c} W'_0 \Delta T' \quad (6)$$

We can notice that the system of governing equations is quite similar to the one of gravitactic bioconvection with double-diffusion treated by Nguyen-Quang et al. [16] except for the swimming velocity term Pe . This would be a base of discussion of our results in the next part.

We would remind herein the swimming velocity of microorganisms in the case of gravitaxis, which is $\mathbf{V}'_c = (0, V_c)$ with V_c is upward gravitactic swimming speed (m/s) (Nguyen-Quang et al. [16]).

In the thermotactic behavior, this swimming velocity would be assumed as $\mathbf{V}'_c = W'_0 \frac{\nabla' T'}{|\nabla' T'|}$ with an amplitude (swimming speed) defined as follows

$$W_0 = \frac{W'_0}{H'} \Delta T' \quad (m/s) \quad (7)$$

In the above equations $(rC)_f$ and $(rC)_p$ are respectively the heat capacity of fluid and of saturated porous medium. Also, e is the porosity of the porous medium and K the permeability of the porous medium. The fluid containing microorganisms is assumed to satisfy the Boussinesq's approximation. The density variation with temperature and concentration is described by the state equation:

$$r = r_f [1 - b_T (T' - T'_0) + b_N (N' - N'_0)] \quad (8)$$

where r_f is the fluid density at temperature $T' = T'_0$ and concentration $N' = N'_0$ and b_T and b_N are the

thermal and concentration expansion coefficients, respectively.

The boundary conditions applied on the walls of the layer are

$$v' = T' - T'_0 = \mathbf{J}' \cdot \mathbf{n} = 0 \quad \text{at } y' = 0 \quad (9a)$$

$$v' = T' - T'_0 - \Delta T' = \mathbf{J}' \cdot \mathbf{n} = 0 \quad \text{at } y' = H' \quad (9b)$$

where

$$\mathbf{J}' = N'(\mathbf{V}' + \mathbf{V}'_c) - D_c \nabla' N' \quad (9c)$$

2.2. Scaling of the governing system of equations

The system of governing equations is normalized by using scaling length by H' , velocity by D_c/H' and time by $(rC)_p H'^2 / [(rC)_f D_c]$. Also, we introduce the reduced temperature $T = (T' - T'_0) / \Delta T'$ and the reduced concentration $N = (N' - N'_0) / \Delta N'$. Using these scales, Eqs (1)-(4) can be transformed in terms of the stream function Ψ to the following dimensionless form:

$$\nabla^2 \Psi = Ra_N \frac{\partial N}{\partial x} - Le Ra_T \frac{\partial T}{\partial x} \quad (10a)$$

$$\frac{\partial T}{\partial t} + \frac{\partial \Psi}{\partial y} \frac{\partial T}{\partial x} - \frac{\partial \Psi}{\partial x} \frac{\partial T}{\partial y} = Le \nabla^2 T \quad (10b)$$

$$f \frac{\partial N}{\partial t} + \left(\frac{\partial \Psi}{\partial y} + Pe \frac{\partial T}{\partial x} \right) \frac{\partial N}{\partial x} + \left(-\frac{\partial \Psi}{\partial x} + Pe \frac{\partial T}{\partial y} \right) \frac{\partial N}{\partial y} = \nabla^2 N - Pe N \nabla^2 T \quad (10c)$$

where, in order to satisfy the continuity equation, the stream function Ψ is defined such that $u = \partial \Psi / \partial y$, $v = -\partial \Psi / \partial x$. $Pe = W_0 \Delta T' / D_c$ is the Peclet number, $Ra_N = g b_N \Delta N' H' K / n D_c$ is the bioconvection Rayleigh number, $Ra_T = g b_T \Delta T' H' K / n a_p$ is the thermal Rayleigh number, $Le = a_p / D_c$ the Lewis number and $f = e (rC)_f / (rC)_p$ the normalized porosity.

The corresponding boundary conditions are

$$\Psi = T = \frac{\partial N}{\partial y} - Pe N - \frac{Pe}{e^{Pe} - 1} \frac{\partial T}{\partial y} = 0 \quad \text{at } y = 0 \quad (10d)$$

$$\Psi = T - 1 = \frac{\partial N}{\partial y} - Pe N - \frac{Pe}{e^{Pe} - 1} \frac{\partial T}{\partial y} = 0 \quad \text{at } y = 1 \quad (10e)$$

When the fluid is motionless ($\Psi_B = 0$), the system of equations with boundary conditions (10a,b,c,d,e) yield the following temperature and concentration profiles :

$$T_B = y \quad (\text{linear profile}) \quad (11a)$$

and

$$N_B = \frac{e^{Pe y}}{e^{Pe} - 1} \quad (\text{exponential profile}) \quad (11b)$$

3. Linear stability analysis and numerical procedure for resolution

We perform the linear stability analysis to study the onset of diffusion convection caused by thermotactic microorganisms and by thermal effects. The results are presented as stability diagrams showing the critical Rayleigh number Ra_N vary with the wave number k , and as a function of thermal critical Rayleigh number Ra_T . These critical Rayleigh numbers represent for the onset of spatial-temporal pattern predicted by linear stability, focusing on the predicted impacts of thermal stratification on microorganisms hydrodynamic processes. Hydrodynamic processes, or flow regimes, are represented by the streamlines traced from the stream function. This dimensionless stream function denotes the path of a fluid particle. In our analysis, streamlines reveal the path of thermotactic cells or/and temperature trajectories in a flow field where temperature and microorganisms interact.

The stability to small perturbations from the quiescent state (Ψ_B, T_B, N_B) is introduced by rewriting the governing equations using $y = \Psi - \Psi_B$, $q = T - T_B$ and $h = N - N_B$. As usual, the disturbance solution is assumed to have the following functional form:

$$\left. \begin{aligned} y(t, x, y) &= \mathcal{Y}(y) e^{pt+ikx} \\ q(t, x, y) &= \mathcal{Q}(y) e^{pt+ikx} \\ h(t, x, y) &= \mathcal{H}(y) e^{pt+ikx} \end{aligned} \right\} \quad (12)$$

where $\mathcal{Y}(y)$, $\mathcal{Q}(y)$ and $\mathcal{H}(y)$ describe the vertical perturbation profiles and $p = p_r + iw$ is the complex growth rate of the perturbation. In the above equation $k = p / l$ is the real wave number, l the wavelength, p_r the grow rate of instability and w the frequency of instability.

Introducing (12) into (10a,b,c) and neglecting second higher-order nonlinear terms yields the following linear system:

$$(D^2 - k^2) \mathcal{Y} + i k Le Ra_T \mathcal{Q} - i k Ra_N \mathcal{H} = 0 \quad (13a)$$

$$Le (D^2 - k^2) \mathcal{Q} + i k DT_B \mathcal{Y} = p \mathcal{Q} \quad (13b)$$

$$(D^2 - k^2) \mathcal{H} - Pe DT_B D \mathcal{H} - Pe N_B (D^2 - k^2) \mathcal{Q} - Pe DN_B D \mathcal{Q} + i k DN_B \mathcal{Y} = p f \mathcal{H} \quad (13c)$$

The boundary conditions, corresponding to equations (10d,e) are:

$$\mathcal{Y} = \mathcal{Q} = D \mathcal{H} - Pe \mathcal{H} - \frac{Pe}{e^{Pe} - 1} D \mathcal{Q} = 0 \quad \text{at } y = 0, 1 \quad (14)$$

where $D = d / dy$.

The perturbed state equations (13a,b,c) with the boundary conditions (14) may be written in a compact matrix form as:

$$M_A(k)\mathbf{Y} = p M_B(k)\mathbf{Y} \quad (15)$$

where $\mathbf{Y} = [y, q, n]^T$ is a two-component vector of the perturbation and $M_A(k)$ and $M_B(k)$ are two linear differential operators that depend on the control parameters Ra_N, Ra_T, Le, Pe and f .

For the linear stability analysis, the set of equations (15) is solved using a discretization scheme by finite differences, which is one of the straightforward ways to deal with this kind of problem. The system is discretized by using fourth and second-order central difference schemes in the domain between $y=0$ and $y=1$. For n discretized points, the resulting discrete system has $3n$ eigenvalues that can be found by using a standard subroutine for eigenvalues such as EIGENC. The value of Ra_N for which the maximal growth rate p_r cancels is iteratively determined by Newton's method, holding wave number k, Ra_T, Le, Pe and f constant. The time needed for computational process to achieve a convergence remains quite reasonable however. The numerical procedure needs hence a discretisation number n greater than 100.

4. Results and discussion

4.1. The thresholds of thermotaxis patterns

In Fig. 2, we show a family of stability curves obtained with various Ra_N vs k when $Le=1$ and

$Pe = 0.5$. It divides the parameter space (Ra_N, k) into two regions: the region above the stability curve is unstable, while the one below is stable. For each value of Pe , we get one stability curve with a minimum at $Ra_N = Ra_c, k = kc$. This is referred to as the critical point for the onset of bioconvection caused by thermotaxis.

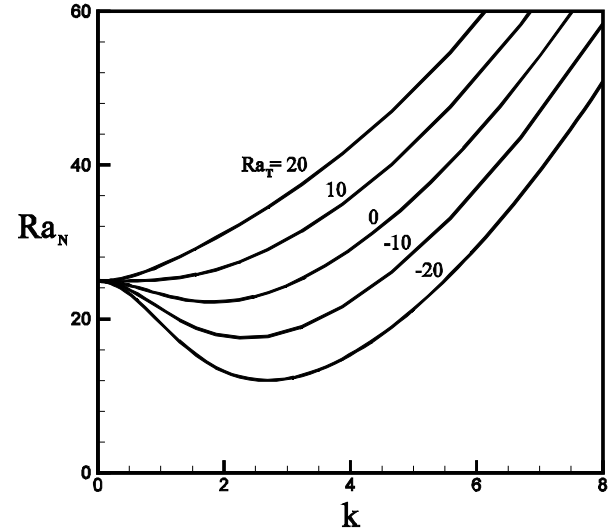


Fig. 2. Stability curves Ra_N vs k for different values of Ra_T when $Pe = 0.5, Le = 1$

Fig. 3 show the onset of the bioconvection patterning via iso-lines of stream function, concentration and temperature for the case of $Pe = 0.5, Le = 1$ when Ra_T adopted three different values 0, -5, and 5.

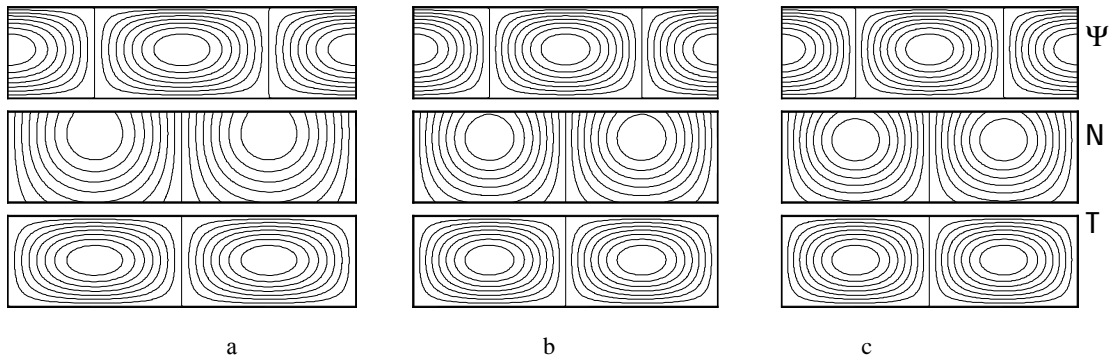


Fig. 3. Iso-lines of stream function (left), concentration (middle) and temperature (right) for the case of $Pe = 0.5, Le = 1$ when (a) $Ra_T = 5$, (b) $Ra_T = 0$, (c) $Ra_T = -5$

4.2. Effects of the thermotaxis speed

Fig. 4 shows the curves of Ra_N vs k in functions of Pe , for the case of $Ra_T = 0$ (i.e no double-diffusion effects) and $Le = 1$. We can see that when Pe varies, influences of mobility on the pattern are very significant. Precisely, when $Pe \rightarrow 0$, the

threshold of thermotactic bioconvection Ra_{NC} tends to the value of $4\pi^2$ while the critical wavenumber k_C tends to π . It is very interesting to observe that these thresholds correspond exactly to the thresholds of a porous layer heated from below with a constant temperature (Nield and Bejan [17]). To understand this important discovery, we have to recall that for

the case of $Pe \rightarrow 0$ in pure gravitactic bioconvection published in Nguyen-Quang et al. [15], the obtained thresholds are equivalent to a porous layer heated from below by a constant flux ($Ra_{NC} \rightarrow 12, k_C \rightarrow 0$).

From Fig.5, we also observed that there exists a critical value of Pe for the minimal value of Ra_{NC} . That critical Pe value is around 5.9 (where Ra_{NC} reached the minimum value shown in Fig. 5). The equivalent wavenumber k_C is not however the equivalent minimum value and we notice that k_C gets its minimum value when Pe is approaching closer to 1.03. In other words, the critical values of Ra_{NC} and of wavelength k_C do not happen in the same moment.

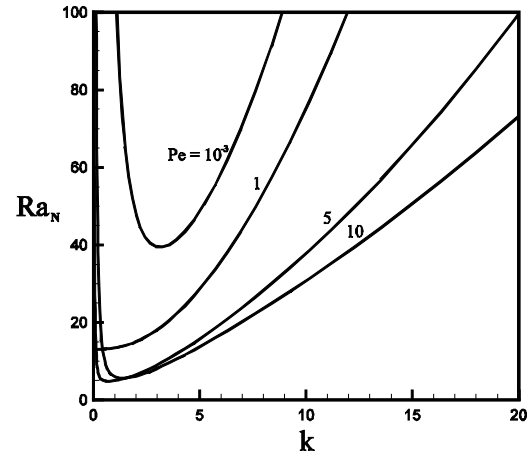
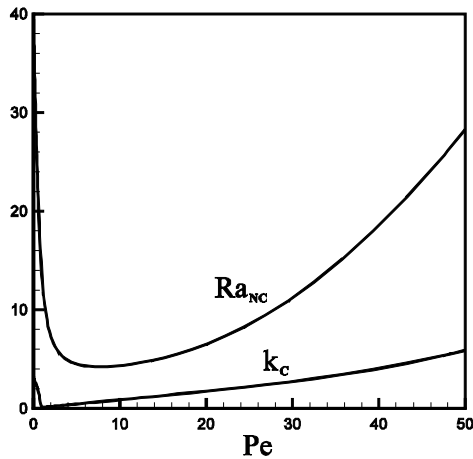


Fig. 4. Ra_N vs k in functions of Pe for the case $Ra_T = 0$ and $Le = 1$

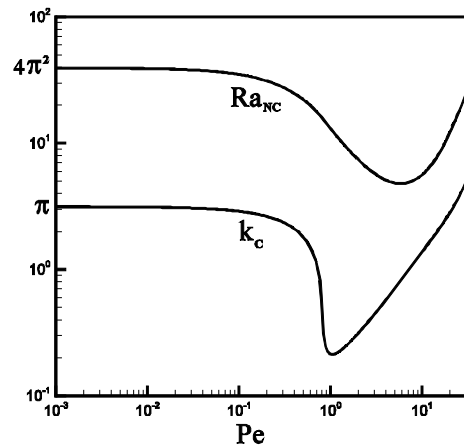


Fig. 5. Ra_{NC} and k_C vs Pe for the case $Ra_T = 0$ and $Le = 1$ (left: normal scale and right: log-scale)

4.3. Effects of the double-diffusion

Fig. 6 illustrates the curve Ra_{NC} vs Ra_T for the case of $Le = 1$ at different values of swimming speeds Pe (it is reminded that $Le = a_p / D_c$ is the ratio between thermal diffusivity and cell diffusivity). We notice that negative values of Ra_T (i.e. heating from below according to our temperature gradient context assumed in Fig. 1) destabilize the system, because the system becomes exactly the classical thermo-convection configuration heated from below by a constant temperature (Nield and Bejan [17]). From Fig. 6, it is observed that $Ra_{NC} = 0$ when $Ra_T = -4p^2$ (i.e. at the exact value of thermal threshold to decline the thermo-convection) with any value of Pe . In this case, convection patterning may happen and be governed by thermal effects.

When Lewis number Le varies, we obtain the curve of Ra_{NC} versus k_C for $Ra_T = 0$ and $Pe = 10$ (Fig. 7).

We recognized that contrarily to the gravitactic thermo-bioconvection (Nguyen-Quang et al. [16]) where the Lewis number Le did not have any effect when $Ra_T = 0$, here this ratio plays a very significant role in the quantification of Ra_{NC} . From Fig. 7, we can see that when $Ra_T = 0$, the larger Le , the higher Ra_{NC} and vice-versa. However, the critical wave number k_C changes only slightly with this ratio Le .

It is extremely interesting to underline that the thermotaxis linear stability analysis can lead to the case of *overstability* when $Le = 0.1$ (i.e the cell diffusivity is ten times greater than thermal diffusivity). Fig. 8 (left) gives us two critical thresholds of Ra_N versus the wavenumber with three different cases of Ra_T . This phenomenon can be explained by the fact that from equations (12), $p = p_r + iw$ was assumed as the complex growth rate of disturbances where p_r and w stand for the growth rate and the frequency of instability respectively.

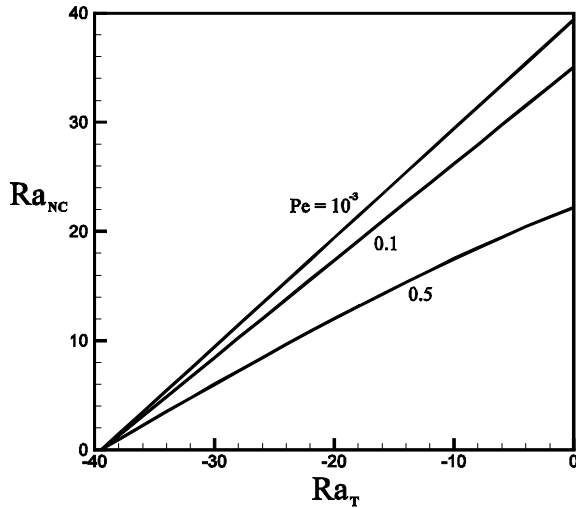


Fig. 6. Ra_{NC} vs Ra_T for $Le = 1$ at various Pe

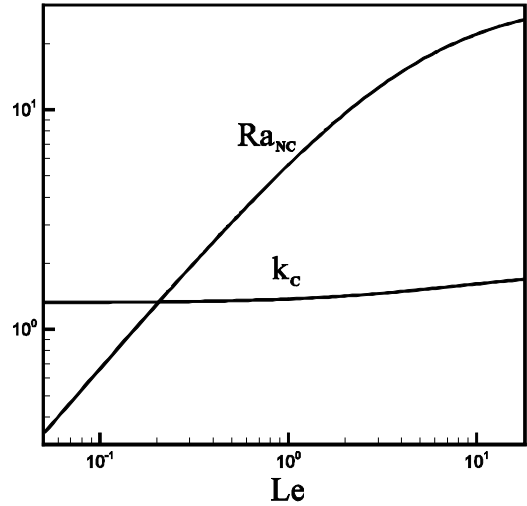


Fig. 7. Ra_{NC} and k_c vs Lewis number for $Ra_T = 0$ and $Pe = 10$

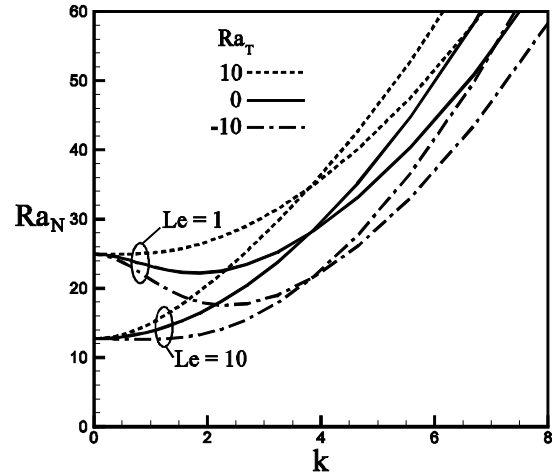
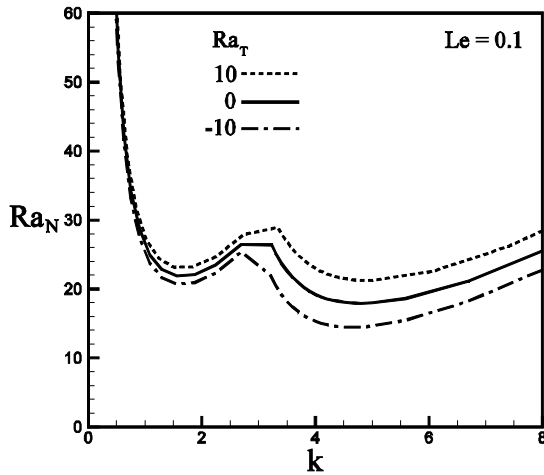


Fig. 8. Ra_N vs k in function of Ra_T , case of $Pe = 0.5$, with $Le = 0.1$ (left-Overstability) and $Le = 1$ and 10 (right)

By the theory of linear stability for natural convection, we knew that if p is real, the amplitude of the velocity is a monotonic function of time; and when the growth rate p is a complex quantity, the system will become overstable, equivalent to the exponential increase with time of velocity amplitude but this increase varies periodically (Kosmeider [18]). The results we obtained herein showed that calculated values of W are non zero (Table 1), meaning clearly that our growth rate p is a complex quantity, hence the overstability occurs (Fig. 8 left). When the cell diffusivity is equal or less than the thermal diffusivity ($Le = 1$ or 10 , Fig. 8 right), we will not have the overstability anymore.

Table 1

Variation of w versus k in the case of $Pe = 0.5$, $Ra_T = 0$ and $Le = 0.1$

k	Ra_N	W
1.56	21.90	3.56
2.69	26.45	3.46
3.23	26.38	0
4.80	17.92	0

4.4. Discussion on the case of $Ra_T = 0$

If we replace the expression (6) above $Pe = \frac{H'}{D_c} W_0 = \frac{1}{D_c} W_0' \Delta T'$ in the formula $Ra_T = \frac{g b_T \Delta T' H' K'}{n a}$,

we will get the thermal Rayleigh number in function of Peclet number Pe as follows.

$$Ra_T = \frac{g\beta_T H' K' D_c Pe}{\nu \alpha W_0} \quad (16)$$

Based on (16), we can discuss following different cases:

4.4.1. If $\Delta T' = 0$, it means that there is no thermal gradient, $Ra_T = 0$, then $Pe = 0$ (from (6)), and we will have no pattern nor thermotactic behaviors occurring. In this case, the system could be understood as having no thermal effects and hence no thermotactic patterns happening.

4.4.2. However, because we have already applied the Dirichlet condition for $T' = 1$ at the top and $T' = 0$ at the bottom, i.e. $\Delta T'$ cannot cancel out, hence there exists always a temperature gradient in the system. We also assumed previously that the capacity of thermotactic motion of microorganisms is W_0 (eq. 7). Therefore, Pe can tend to 0 when W_0 tends to 0 in the case of microorganism cells having a very weak thermotactic motion capacity or not having it anymore due to age or stress. This case of $Pe \rightarrow 0$ was previously discussed.

When $Pe \neq 0$ and $\Delta T' \neq 0$, $Ra_T = 0$ could be understood as the following scenarios in the system according the equation (16).

a) **$Ra_T = 0$ when $D_c \rightarrow 0$:** The diffusion coefficient of microorganisms is very small. Depending on the species and taxis velocity, this coefficient varies very much. Le becomes much higher when $D_c \rightarrow 0$ ($Le = a_p / D_c$), and Ra_N can be much stronger. In this case, the pattern can be generated by Ra_N and Lewis effects;

b) **$Ra_T = 0$ when $K \rightarrow 0$:** When the porous medium permeability is so low such as in a rock structure (but the porous matrix is large enough for the movement of microorganisms passing through), the Ra_T can tend to 0. Bioconvection patterns may happen due to a temperature gradient and thermotactic motion capacity of cells existing in the system;

c) **$Ra_T = 0$ when $\beta_T \rightarrow 0$:** This case can happen when the coefficient of thermal expansion of the considered porous medium (ici c'est plutôt le coefficient du fluide non?) is zero. Because this coefficient describes how the size of the medium changes with a change in temperature, it would imply that the volume of isotropic porous medium does not change significantly under the temperature effects. The thermotactic patterns would happen under Ra_N effects, when $\Delta T \neq 0$ and $Ra_T \neq 0$, we will have definitely the case of thermotactic or thermophilic patterns. If we simulate the system of governing equations for the supercritical cases, we would observe a very interesting phenomenon: microorganisms will have a preferable place to move forward and to accumulate. This means

that the highest concentration zone of cells is not at the top (where $T = 1$) but somewhere in the lower level because microorganisms would show their behavior to a comfortable and preferable temperature to be growing up. Some very first step simulations (not presented here) of the system of equations and equivalent boundary conditions (10) can show that obtained results seem to fit with many experiences on the thermotactic behaviors of microorganisms. The profound simulations with high precision and accuracy are part of our future research.

6. Concluding remarks

In this paper, we used the linear stability analysis to predict the onset of thermotaxis patterns in porous media. Results obtained by linear stability analysis show that thermotactic behaviors may be analogous to the thermal convection heated from below by constant temperature when the Peclet number (capacity of thermotactic motion) is very weak (approaching 0) and there exists an important overstability state when the cell diffusivity is much greater than the thermal diffusivity.

In the system where temperature and cell motility by thermotaxis can both result in hydrodynamic patterns, we found strong interactions between thermal gradients and cell population via the spatial distribution of cells. Although this pioneering work still has to be developed and tested in natural systems, laboratory experiments with thermophilic species such as *Tetrahymena thermophila* (Shiurba et al. [19]) or *Caenorhabditis elegans* would confirm the results of our model.

The results reported here reveal a bio-physical coupling that results from the scale of individual behavior. They also suggest its importance to define the spatiotemporal pattern over larger ecological scales of porous medium. Further investigation will elucidate the robustness of this gradient-based taxis model and its importance in natural ecological systems such as the behavior of algal blooms.

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Nomenclature

D_c mass diffusivity of microorganisms
 g gravitational acceleration

H'	height of porous layer
k	wave number
k_p	thermal conductivity of the porous medium
K	permeability of the porous medium
Le	Lewis number, (a_p / D_c)
N	reduced concentration of microorganisms, $(N' - N'_0) / \Delta N'$
p	complex growth rate of the perturbation.
p_r	real grow rate of instability
P'	pressure
Pe	Peclet number, $(W_0 \Delta T' / D_c)$
Ra_N	bioconvection Rayleigh number, $g b_N \Delta N' H' K / n D_c$
Ra_T	thermal Rayleigh number, $g b_T \Delta T' H' K / n a_p$
t	dimensionless time, $t'(rC)_f D_c / [(rC)_p H'^2]$
T	dimensionless temperature, $(T' - T'_0) / \Delta T'$
u	dimensionless velocity in x direction, $(u' H' / D_c)$
v	dimensionless velocity in y direction, $(v' H' / D_c)$
\mathbf{V}'_c	average cell swimming velocity due to thermotaxis
W'_0	constant standing capacity of thermotactic motion of microorganisms
x	dimensionless coordinate axis, (x' / H')
y	dimensionless coordinate axis, (y' / H')

Greek symbols

a_p	thermal diffusivity
b_N	concentration expansion coefficient
b_T	thermal expansion coefficient
m	dynamic viscosity of fluid
n	kinematic viscosity of fluid
e	porosity of the porous medium
f	normalized porosity, $e (rC)_f / (rC)_p$
l	wavelength
r	density of fluid, kg / m^3
w	frequency of instability
Ψ	dimensionless stream function, Ψ' / a

Subscript

0	reference state
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Superscript

'	referring to dimensional variable
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