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Step, dip, and bell-shape traveling waves in a $(2 + 1)$ -chemotaxis model with traction and long-range diffusion

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Abstract

In this paper, a new $(2 + 1)$ -dimensional chemotaxis model is introduced, the focus being the understanding of influences of cooperative mechanisms from traction forces, long-range diffusion to chemotaxis on the dynamical characteristics of waves and their transport. Applying the F-expansion method, three families of new traveling wave solutions of bacterial density and chemoattractant concentration are constructed, including step, dip, and bell-shape wave profiles. The dependence of the conditions of existence of our solutions with respect to the model parameters is fully clarified. We found that traction and long-range diffusion slow down the waves and entail the transport of a small number of particles. Surprisingly, the long-range diffusion increases the thickness of the wave but does not alter its magnitude. Amongst families of solutions constructed, dip waves travel faster may be used to explain fast coordination amongst particles. As they support the transport of large amounts of cells, step waves could explain the transport of particles in high dense media. Intensive numerical simulations corroborate with a pretty much accuracy our theoretical analysis, confirming the robustness of our predictions. Traction, long-range diffusion and chemotaxis deeply affect the wave dynamics, they must be taken into account for a better understanding of chemotaxis systems.

Keywords: Bacterial/cellular collective motion; chemotaxis; traction; long-range diffusion; advection; two-dimensional traveling waves; wave velocity

1 Introduction

Studies on the dispersal of active particles have shed light on different mechanisms associated with their response when placed under various mechanical and/or chemical conditions. An example of active particles is given by a distribution of bacteria in a uniform flow whose collective motion allows them to spread and colonize outward regions. Depending on their sensitivity and acquaintance with the local environment composition, such a collective motion has been characterized qualitatively and quantitatively [1-14].

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When placed in chemical fields with attractive properties, ciliated particles for example synchronize their flagella's rotation, the resulting quasi-linear run allows them to efficiently reach the core of higher chemical concentrations. Such a collective behavior termed chemotaxis has been widely studied since the pioneering work of Adler [1]. Besides the importance of chemotaxis in the cellular realm where it plays a major role in fertilization [2-4], intercellular communication [5,6], wound repair [2,3], and pattern formation [3,7], it has also been reported in animal and insect ecology [4], large scale collective behavior [1,8-14] and synchronization processes [5,8]. Though the literature is well furnished when it comes to chemotaxis, the various issues associated with a combination of chemical and mechanical constraints cells might feature in their natural habitats has just recently started receiving attention [10,12-22]. It is known that the latter interactions may lead to interesting holistic dynamical behaviors that to the best of our knowledge remain to be fully understood.

The collective dynamic entailed by chemotaxis indicates that bacteria are social entities and are therefore prone to communicate with one another. In some extreme cases, communication is made possible through chemoattractant production. The latter is responsible for the attraction of other distant entities. This phenomenon significantly different from chemotaxis at the molecular level can be termed auto-chemotaxis and was recently observed through lenses of experimental settings [5]. Though the authors were not able to provide full and satisfying explanations of its specific contribution at the local level, they showed that it has the potential of biasing the primary chemotactic signal at the onset of bacterial motion. Depending on the strength of the bias, cells rearrange themselves and exhibit a different moving pattern. Independently, a theoretical approach to the question was addressed to demonstrate that auto-chemotaxis is a factor of instability [15,16], while friction and proliferation in the system have stabilizing effects. Such an antagonism is at the onset of pattern selection with a well-defined wave number [15]. On the other side, the fact that cells can become attractive by producing their own chemoattractant implies that in a given population, certain cells are more chemotactic than others, therefore may exert distant actions like traction forces. In cancer invasion for example, those distant actions allow cancerous melanocytic cells to escape tumorous regions and undergo metastasis [17]. In the dynamic of micro-swimmers assembly, distant traction forces were also reported. This means that the existence of traction forces might be a common feature in reactive systems, especially for higher active particles densities [16].

Apart from inter-species communication mechanisms, cells are also involved in hydrodynamic interactions which ensure an active transport of diffusive and non-active components over long distances. In aqueous media, swimming patterns of cells that consist of pulling, pushing, gliding, scrawling, imply that cells interactions with fluids constituents may lead to a variety of spatio-temporal patterns. Experimental and theoretical evidence showed that bacteria are collectively transported through wavy structures like solitary pulses [18-20,24-30]. Furthermore, other experimental findings suggest that hydrodynamic interactions coupled to the chemoattractant concentration gradient may guide traveling bands of bacteria at a constant speed [18-20]. Therefore the inclusion of advection rate while modeling chemotactic behaviors is expected to substantially improve our knowledge of the system. Mathematical modeling in this view requires to couple the Keller-Segel chemotaxis model to Navier-Stokes equations [16,21-23]. Another simple and realistic approach consists at collecting contributions emanating from stresses and traction cells exert upon each other in addition to the uniform flow coming from the background field within which cells are immersed in. In fact, recent evidences demonstrate that the collective motion of cells in a fluid generates flows mediated by the hydrodynamics interactions in between them [10,22,23]. It is therefore natural to wonder how both chemotaxis and traction forces contribute to producing structures like traveling waves observed from the Keller-Segel formulation for chemotaxis [24]. The latter model initially introduced to describe slime mold showed drawbacks and later experimental findings suggest that the issues may be circumvented when cells create their own chemoattractant gradient [25]. This implies that the collective motion of cells modifies the average flow of the medium, which in turn affects cellular response. In this way, cells' response to an excitatory source ceases to be proportional to the concentration gradient of the excitation. Another way of looking at the problem consists at considering the nonlocal character of bacterial response [3,26,31] which is responsible for the nucleation of long-range diffusion. In this work, we

introduce a mathematical model that extends the existing ones, with the aim to fill in the above-mentioned gaps. To this end, we consider a chemotactic system where long and short-range diffusions, chemotaxis, traction forces, cellular proliferation, and uniform advection are accounted for; dynamical behaviors of new traveling waves shall be investigated.

The rest of the manuscript is organized as follows. In Sec. II we derive the model and construct its analytical solutions. Secondly, we evaluate the effects of key parameters of the system on the proposed solutions and then make some predictions on the dynamical behavior of the system. In Sec. III, numerical simulations are performed to ascertain our predictions. Some biological implications, are discussed. Section IV concludes the paper.

2 Main results and discussions

2.1 The model

In this description of collective behavior, we are interested in a bacterial population in a two-dimensional frame, immersed in a fluid experiencing a uniform flow. Besides the chemotactic velocity and the medium flow rate, the bulk bacterial motion also has a drift-velocity contribution emanating from the stress cells exert upon each other. Recent studies show that many energy sources simultaneously influence cells motion [30], but in the present paper, we consider the case where bacteria are in presence of only one chemoattractant source. The timescale is large enough such that cells undergo proliferation, the nonlocal response ensures long-distance communications, and the cellular protrusion is also accounted for. The resulting model is an extended set of coupled partial differential equations that reads [3,24,28-31]

$$\frac{\partial n}{\partial t} + \vec{\nabla} \cdot (n\vec{\delta}) = D_1 \nabla^2 n - D_2 \nabla^4 n - \chi_0 \vec{\nabla} \cdot (n\vec{\nabla} c) + rn(\sigma - n), \quad (1a)$$

$$\frac{\partial c}{\partial t} + \vec{\nabla} \cdot (c\vec{\delta}) = D_3 \nabla^2 c + \frac{k_0 n}{k_1 + k_2 n^2} - \beta nc. \quad (1b)$$

In Eqs.(1), t is the time variable in seconds (s), $\vec{\nabla} = \left(\frac{\partial}{\partial x}, \frac{\partial}{\partial y} \right)^T$ is two-dimensional gradient, $\nabla^2 = \left(\frac{\partial^2}{\partial x^2}, \frac{\partial^2}{\partial y^2} \right)^T$, the two dimensional Laplacian. n is the cellular density, while c is the chemoattractant concentration. D_1 and D_3 , are short-range diffusions while D_2 stands for the long-range diffusion of bacteria. χ_0 represents the chemotaxis strength, r is the proliferation rate of cells, σ , the medium's carrying capacity. The term $\frac{k_0 n}{k_1 + k_2 n^2}$ describes the chemoattractant production. Numerical values of k_0, k_1, k_2 are not known to the best of our knowledge. β is the chemoattractant consumption's rate. $\vec{\delta} = (\delta_x, \delta_y)^T$ is the two dimensional bulk velocity field of the system. Recent studies of bacterial migration in a confined one-dimensional racetrack showed nucleation of strong flows emanating from cells closes to channel boundaries [14]. These flows were capable of swerving the bulk dynamic of cells placed far from channel walls. In this sense, the bulk velocity field in the system comprises an active part generated by the collective motion of cells and a passive part emanating from the perturbations of the medium within which cells are immersed. We propose a velocity field in the medium with the form

$$\vec{\delta} = \vec{\delta}_0 + \vec{\nabla} H(n, c), \quad \text{with} \quad \vec{\delta}_0 = \delta_{0x} \vec{e}_x + \delta_{0y} \vec{e}_y, \quad \text{and} \quad H(n, c) = \frac{\tau_0 n}{1 + \lambda n}. \quad (2)$$

δ_{0x} , and δ_{0y} are components of the uniform flow imposed by the medium within which cells and the chemoattractant are immersed. The function H takes into account the effects of traction forces generated by active particles present in the medium (here the bacterial cells). τ_0 is the maximum traction force ensuring a finite velocity at higher cellular density when the population increases in a quasi-dilute medium. λ measures the velocity decrease due to a higher density of cellular aggregation. In the thermodynamic

limit, this choice of H ensures that the velocity remains finite both at low and high densities. The current model diverges from the classical Keller-Segel models [3,24,29-31], since the chemotactic velocity drift, as well as wave profiles, remain bounded. This further sets the stepping stone to finding relevant physical solutions for the model under consideration. In that endeavor, we assume a quasi-dilute medium, corresponding to $\lambda \rightarrow 0$, meaning that hydrodynamic properties of bacteria are weak but non-null. Under this configuration, experimental studies revealed that one might still expect complicated patterns [7,32], and bacterial distribution per unit area may be very small but non-null. Hence, only a small amount of cells are expected to contribute to chemoattractant production, a situation entailing $\frac{k_2 n^2}{k_1} \ll 1$. Considering lower power series of the saturating term from Eq.(1b), and plugging Eq.(2) into Eqs.(1) yield the (2 + 1)-modified extended chemotaxis model

$$\frac{\partial n}{\partial t} + \vec{\nabla} \cdot (n \vec{\delta}_0) = D_1 \nabla^2 n - D_2 \nabla^4 n - \tau_0 \vec{\nabla} \cdot (n \vec{\nabla} n) - \chi_0 \vec{\nabla} \cdot (n \vec{\nabla} c) + rn(\sigma - n), \quad (3a)$$

$$\frac{\partial c}{\partial t} + \vec{\nabla} \cdot (c \vec{\delta}_0) = D_3 \nabla^2 c - \tau_0 \vec{\nabla} \cdot (c \vec{\nabla} n) + \beta_1 n - \beta_3 n^3 - \beta n c, \quad (3b)$$

$\beta_1 = \frac{k_0}{k_1}, \beta_3 = \frac{k_0 k_2}{k_1^2}$ are arbitrary real constants, and are also not known as the k'_j 's. Nevertheless, they will be chosen in accordance with biological relevance. β_1, β_3 are referred to as the new chemoattractant production rate parameters. More than a simple reaction-diffusion-advection process, the system of Eqs.(3) is dynamically interesting. It takes into consideration simple and nonlinear cross diffusions, in addition to incorporating two active transport mechanisms, namely chemotaxis and traction. Though traction has been the subject of intensive experimental studies [5,15,16,25], its contribution has not yet been mathematically formulated in chemotactic systems, to the best of our knowledge. The model Eqs.(3) indicates that taking into account traction forces enhances both cellular and chemical displacement towards one another. In this sense, Eqs.(3) can be used to explain a broad range of phenomena in systems made of composite materials. For example, it may describe the spreading behavior of two chemotactic subpopulations of bacteria moving toward each other with different velocities. Such a differential velocity may lead to rich phenomena like instabilities and new patterns formation just to name a few. We propose Eqs.(3) as a viable generalized chemotaxis model that incorporates several aspects of bacterial collective motion not discussed in previous models [3,15,28-31,33-42].

2.2 Analytical solutions through the extended F-expansion method

To solve Eqs.(3), the traveling wave variable $\xi = kx + ly - \omega t$ is assumed, $\frac{1}{k}$ and $\frac{1}{l}$ being the wave widths along the x - and y - directions, respectively, ω the wave velocity taken in the laboratory frame. Eqs.(3) become

$$D_2 K^2 \frac{d^4 n}{d\xi^4} - D_1 K \frac{d^2 n}{d\xi^2} + \Omega_0 \frac{dn}{d\xi} + \chi_0 K \frac{d}{d\xi} \left(n \frac{dc}{d\xi} \right) + \tau_0 K \frac{d}{d\xi} \left(n \frac{dn}{d\xi} \right) - rn(\sigma - n) = 0, \quad (4a)$$

$$-D_3 K \frac{d^2 c}{d\xi^2} + \Omega_0 \frac{dc}{d\xi} + \tau_0 K \frac{d}{d\xi} \left(c \frac{dn}{d\xi} \right) - \beta_1 n + \beta n c + \beta_3 n^3 = 0, \quad (4b)$$

with

$$K = k^2 + l^2, \quad \text{and} \quad \Omega_0 = \delta_{0_x} k + \delta_{0_y} l - \omega.$$

Solutions of Eqs.(4) are sought for a chemoattractant concentration of the form

$$c(\xi) = G(n(\xi), \xi). \quad (5)$$

Inserting Eq.(5) into Eqs.(4) leads to the fourth order nonlinear ordinary differential equation

$$D_2 K^2 \frac{d^4 n}{d\xi^4} + \chi_0 \left(\frac{\Omega_0}{\chi_0 - \tau_0} \right)^2 + \left[\frac{\beta \chi_0 \Omega_0 \xi}{K(\chi_0 - \tau_0)^2} + \frac{\beta}{\tau_0} \frac{D_1(\chi_0 - \tau_0) + \tau_0 D_3}{\chi_0 - \tau_0} - r\sigma + \beta_1 \right] n + \left(r + \frac{\beta \tau_0}{\chi_0 - \tau_0} \right) n^2 - \beta_3 n^3 = 0, \quad (6)$$

provided that

$$c(\xi) = -\frac{\tau_0 n(\xi) + D_3}{\chi_0 - \tau_0} - \frac{\Omega_0 \chi_0 \xi}{K(\chi_0 - \tau_0)^2} - \frac{D_1}{\tau_0}. \quad (7)$$

We restrict ourselves to the case where $\omega = k\delta_{0_x} + l\delta_{0_y}$ to avoid nonphysical solutions that diverge at infinity. Such a choice is also consistent with recent numerical and theoretical results presented in [19,42,43] where the authors proved that the wave velocity in the Martiel-Golbeter chemotaxis model (for *Dictyostelium discoideum* dynamics) varies linearly with the imposed flow. On the other hand, Eq.(7) tells that variations of chemoattractant and bacterial waves are directly linked, hence corroborating results obtained in the analysis of chemotactic *Dictyostelium* colonies [40]. The same study showed that by increasing background level, the directed propagation can be suppressed, due to memory inactivation. In other words, cells can be swept or their direction propagation swerved, enforcing the conclusion that medium flow rate has the potential of favoring the rise of progressive or regressive waves. In the present study, the transition from forwards to backward propagation is attained when parameters are chosen such that the critical line $\frac{\delta_{0_x}}{\delta_{0_y}} = \frac{-l}{\sqrt{K-l^2}}$ corresponding to stationary patterns is violated. In the latter configuration, our solutions may be either progressive ($\omega > 0$) or regressive ($\omega < 0$). The former is responsible for faster bacterial colonization of unoccupied regions, while the latter may be the signature of backward waves. In the flux limiting cases, the backward waves in a chemotactic system were shown to be responsible for a population saturation in a stable state accompanied by a transition toward unstable modes [45].

Physical acceptable solutions of Eqs.(3) correspond to positive bacterial and chemoattractant wave amplitudes. In addition, both bacterial densities and chemoattractant concentrations must remain finite, hence using Eq.(7) and assuming that $n(\xi) \geq 0$, the finiteness of the chemoattractant concentration implies the following restrictions

$$\tau_0 > \chi_0, \quad \tau_0 \neq 0, \quad c(\xi) \geq \frac{D_3}{\tau_0 - \chi_0} - \frac{D_1}{\tau_0} = c_{min}, \quad D_1 \leq \frac{D_3 \tau_0}{\tau_0 - \chi_0}. \quad (8)$$

Before proceeding further, Eqs.(8) provide important characteristics about the solutions to be found below. The traction forces must be non-null and greater than the chemotaxis strength implying that the experimenter must choose an appropriate chemoattractant substance that is consistent with Eqs.(8). Moreover, there exists a critical chemoattractant concentration that completely depends on system parameters $(\tau_0, \chi_0, D_1, D_3)$, below which the corresponding solutions are unphysical. The solutions will be viable only if the chemoattractant concentration is at least equal to c_{min} , a situation which means that chemoattractant diffusion rate is always greater or equal than a minimal value $D_3 \geq D_1 \left(1 - \frac{\chi_0}{\tau_0} \right) = D_{3min}$. The fact that $D_1 > D_{3min}$ implies $D_1 > D_3$. The latter inequality is a situation rather different from experimental values reported in [3,4,6,7,19,20,29,30]. Therefore, traction forces substantially modify the behaviors of chemotactic systems.

Balancing higher-order derivative with the higher-order nonlinear terms in Eq.(6) permits the polynomial expansion

$$n = a_0 + a_1 F(\xi) + a_2 F(\xi)^2, \quad (9)$$

where a_0, a_1, a_2 are real constants to be determined later. The function $F(\xi)$ is a solution of the auxiliary equation

$$\left(\frac{dF(\xi)}{d\xi}\right)^2 = P_4 F(\xi)^4 + P_3 F(\xi)^3 + P_2 F(\xi)^2 + P_1 F(\xi) + P_0. \quad (10)$$

P_4, P_3, P_2, P_1, P_0 are real constants. Solutions of Eq.(10) may be found in [26,44,45]. Plugging Eq.(9) into Eq.(6) and using Eq.(10) yields a set of algebraic equations that we solve for the variables $a_0, a_1, a_2, K, \beta_3$ and obtain different families of solutions presented below.

Family A: $P_0 = P_1 = P_3 = 0, P_2 > 0, P_4 < 0, F(\xi) = \sqrt{-\frac{P_2}{P_4}} \cosh^{-1}(\sqrt{P_2}\xi)$

$$a_0 = 0, \quad a_1 = 0, \quad a_2 = \frac{15\sigma_1 P_4}{2\sigma_2 P_2}, \quad K = \frac{1}{4P_2} \sqrt{-\frac{\sigma_1}{D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1}, \quad (11a)$$

$$a_0 = \frac{\sigma_1(3 + \epsilon\sqrt{105})}{\sigma_2(7 + \epsilon\sqrt{105})}, \quad a_1 = 0, \quad a_2 = -\frac{3\sigma_1 P_4(35 + \epsilon\sqrt{105})}{28P_2\sigma_2},$$

$$K = \frac{1}{4P_2} \sqrt{\frac{\sigma_1(7 + \epsilon\sqrt{105})}{14D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2(7 + \epsilon\sqrt{105})}{3\sigma_1(19 + \epsilon\sqrt{105})}. \quad (11b)$$

Family B: $P_0 = P_1 = P_3 = 0, P_2 < 0, P_4 > 0, F(\xi) = \sqrt{-\frac{P_2}{P_4}} \sec(\sqrt{-P_2}\xi)$

$$a_0 = 0, \quad a_1 = 0, \quad a_2 = \frac{15\sigma_1 P_4}{2\sigma_2 P_2}, \quad K = -\frac{1}{4P_2} \sqrt{-\frac{\sigma_1}{D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1}, \quad (12a)$$

$$a_0 = \frac{\sigma_1(3 + \epsilon\sqrt{105})}{\sigma_2(7 + \epsilon\sqrt{105})}, \quad a_1 = 0, \quad a_2 = -\frac{3\sigma_1 P_4(35 + \epsilon\sqrt{105})}{28P_2\sigma_2},$$

$$K = -\frac{1}{4P_2} \sqrt{\frac{\sigma_1(7 + \epsilon\sqrt{105})}{14D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2(7 + \epsilon\sqrt{105})}{3\sigma_1(19 + \epsilon\sqrt{105})}. \quad (12b)$$

Family C: $P_0 = \frac{P_2^2}{4P_4}, P_1 = P_3 = 0, P_2 < 0, P_4 > 0, F(\xi) = \sqrt{-\frac{P_2}{2P_4}} \tanh\left(\sqrt{-\frac{P_2}{2}}\xi\right)$

$$a_0 = -\frac{15\sigma_1}{2\sigma_2}, \quad a_1 = 0, \quad a_2 = \frac{15\sigma_1 P_4}{2\sigma_2 P_2}, \quad K = -\frac{1}{2P_2} \sqrt{-\frac{\sigma_1}{D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1} \quad (13a)$$

$$a_0 = -\frac{\sigma_1(543 + \epsilon 53\sqrt{105})}{\sigma_2(133 + \epsilon 13\sqrt{105})}, \quad a_1 = 0, \quad a_2 = \frac{30\sigma_1 P_4(11 + \epsilon\sqrt{105})}{\sigma_2 P_2(35 + \epsilon 3\sqrt{105})},$$

$$K = -\frac{1}{2P_2} \sqrt{\frac{\sigma_1(7 + \epsilon\sqrt{105})}{14D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2(133 + \epsilon 13\sqrt{105})}{3\sigma_1(113 + \epsilon 11\sqrt{105})}. \quad (13b)$$

Family D: $P_0 = \frac{P_2^2}{4P_4}, P_1 = P_3 = 0, P_2 > 0, P_4 < 0, F(\xi) = \sqrt{-\frac{P_2}{2P_4}} \tan\left(\sqrt{\frac{P_2}{2}}\xi\right)$

$$a_0 = -\frac{15\sigma_1}{2\sigma_2}, \quad a_1 = 0, \quad a_2 = \frac{15\sigma_1 P_4}{2\sigma_2 P_2}, \quad K = \frac{1}{2P_2} \sqrt{-\frac{\sigma_1}{D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1} \quad (14a)$$

$$a_0 = -\frac{\sigma_1(543 + \epsilon 53\sqrt{105})}{\sigma_2(133 + \epsilon 13\sqrt{105})}, \quad a_1 = 0, \quad a_2 = \frac{30\sigma_1 P_4(11 + \epsilon\sqrt{105})}{\sigma_2 P_2(35 + \epsilon 3\sqrt{105})},$$

$$K = \frac{1}{2P_2} \sqrt{\frac{\sigma_1(7 + \epsilon\sqrt{105})}{14D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2(133 + \epsilon 13\sqrt{105})}{3\sigma_1(113 + \epsilon 11\sqrt{105})}. \quad (14b)$$

Family E: $P_0 = \frac{1}{4}, P_1 = P_3 = 0, P_2 = \frac{1}{2}, P_4 = \frac{1}{4}, F(\xi) = \sin(\xi) + \epsilon \cos(\xi)$

$$a_0 = -\frac{8\sigma_1(111 + 11\epsilon\sqrt{105})}{\sigma_2(203 + 23\epsilon\sqrt{105})}, \quad a_1 = 0, \quad a_2 = -\frac{60\sigma_1(49 + 5\epsilon\sqrt{105})}{7\sigma_2(85 + 9\epsilon\sqrt{105})},$$

$$K = \sqrt{\frac{\sigma_1(7 + \epsilon\sqrt{105})}{14D_2}}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1} \quad (15)$$

Family F: $P_0 = P_1 = 0, P_2 > 0, P_3 = 2\epsilon\sqrt{P_2 P_4}, P_4 > 0, F(\xi) = \frac{\epsilon}{2} \sqrt{\frac{P_2}{P_4}} \frac{\cosh(\frac{\sqrt{P_2}}{2}\xi)^{-2}}{\epsilon \tanh(\frac{\sqrt{P_2}}{2}\xi) - 1}$

$$a_0 = -\frac{\sigma_1(\sqrt{105} + 21)}{14\sigma_2}, \quad a_1 = \epsilon \sqrt{\frac{P_4}{P_2}} \frac{3\sigma_1(35 - \sqrt{105})}{7\sigma_2}, \quad a_2 = -\frac{3\sigma_1 P_4(35 - \sqrt{105})}{7P_2 \sigma_2}$$

$$\beta_3 = -\frac{28\sigma_2^2}{3\sigma_1(7 + 3\sqrt{105})}, \quad K = \frac{1}{P_2} \sqrt{-\frac{\sigma_1(\sqrt{105} - 7)}{14D_2}}, \quad (16a)$$

$$a_0 = 0, \quad a_1 = \frac{30\sigma_1 \sqrt{P_2 P_4}}{\sigma_2 P_2}, \quad a_2 = \frac{30\sigma_1 P_4}{\sigma_2 P_2}, \quad K = \frac{\sqrt{-D_2 \sigma_1}}{\sigma_2 P_2}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1} \quad (16b)$$

Family G: $P_0 = P_1 = 0, P_2 < 0, P_3 = 2\epsilon\sqrt{P_2 P_4}, P_4 > 0, F(\xi) = \frac{\epsilon}{2} \sqrt{\frac{-P_2}{P_4}} \frac{\sec(\frac{\sqrt{-P_2}}{2}\xi)^2}{1 + \epsilon \tan(\frac{\sqrt{-P_2}}{2}\xi)}$

$$a_0 = -\frac{\sigma_1(\sqrt{105} + 21)}{14\sigma_2}, \quad a_1 = \epsilon \sqrt{\frac{P_4}{P_2}} \frac{3\sigma_1(35 - \sqrt{105})}{7\sigma_2}, \quad a_2 = -\frac{3\sigma_1 P_4(35 - \sqrt{105})}{7P_2 \sigma_2}$$

$$\beta_3 = -\frac{28\sigma_2^2}{3\sigma_1(7 + 3\sqrt{105})}, \quad K = -\frac{1}{P_2} \sqrt{-\frac{\sigma_1(\sqrt{105} - 7)}{14D_2}}, \quad (17a)$$

$$a_0 = 0, \quad a_1 = \frac{30\sigma_1 \sqrt{P_2 P_4}}{\sigma_2 P_2}, \quad a_2 = \frac{30\sigma_1 P_4}{\sigma_2 P_2}, \quad K = -\frac{\sqrt{-D_2 \sigma_1}}{\sigma_2 P_2}, \quad \beta_3 = -\frac{2\sigma_2^2}{15\sigma_1} \quad (17b)$$

For algebraic convenience from Eqs.(10) to Eq.(16), we set

$$\sigma_1 = \beta_1 - r\sigma - \beta_{c_{min}} \neq 0, \quad \sigma_2 = r + \frac{\beta\tau_0}{\chi_0 - \tau_0} \neq 0, \quad \tau_0 \neq \chi_0 \quad \text{and} \quad \epsilon = \pm 1.$$

2.3 Existence and dynamical behavior of solutions Eqs.(11)-(17)

A straightforward analysis of Eqs.(11)-(17) shows that bacterial and chemoattractant solutions exist if $D_2 \neq 0, \sigma_1 < 0, \sigma_2 > 0$ which lead to the constraints

$$\beta_1 < r\sigma + \beta c_{min} = \beta_{1_{crit}}, \quad \text{and} \quad r > \frac{\beta\tau_0}{\tau_0 - \chi_0} = r_{min}. \quad (18)$$

The first inequality of Eq.(18) proves that the linear chemoattractant production rate β_1 possesses a minimum value $r\sigma$, and linearly increases with chemoattractant consumption rate β . The second inequality shows that our system admits a proliferation rate always greater than the threshold value r_{min} . Eqs.(8) and Eqs.(18) describe the general conditions on the existence of bacterial and chemoattractant concentration but, do not provide any details on dynamical properties. We discuss below some dynamical properties of both bacterial and chemoattractant waves such as their profiles, velocities, amplitudes, thicknesses, and we analyze effects of τ_0, χ_0, D_2, D_1 , and β . To this end, we take $\beta_1 = \frac{\beta_{1_{crit}}}{10}, r = r_{min} + r_0, r_0 = 1.69 \cdot 10^{-9}$ being the proliferation rate given in [3].

The bell-shape profile corresponds to Family A. Using parameters of Eq.(11a), explicit analytical expressions are given by

$$n(x, y, t) = -\frac{15\sigma_1}{2\sigma_2} \left(\frac{1}{\cosh [\sqrt{P_2}(kx + ly - \omega t)]} \right)^2, \quad (19a)$$

$$c(x, y, t) = -\frac{15\sigma_1\tau_0}{2\sigma_2(\chi_0 - \tau_0)} \left(\frac{1}{\cosh [\sqrt{P_2}(kx + ly - \omega t)]} \right)^2 + c_{min}, \quad (19b)$$

where the associated velocity reads:

$$\omega = \delta_{0_x} \sqrt{\frac{1}{4P_2} \sqrt{\frac{1}{D_2} [r\sigma - \beta_1 + \beta c_{min}] - l^2} + \delta_{0_y} l = \omega_{bs}. \quad (20)$$

From Eq.(20), one deduces the existence of minimal/maximal wave velocities

$$\omega_{min} = 0 \leq \omega \leq \omega_{max} = \sqrt{\frac{\delta_{0_x}^2 + \delta_{0_y}^2}{4P_2} \sqrt{\frac{1}{D_2} [r\sigma - \beta_1 + \beta c_{min}]},$$

where $\omega_{min} = \omega(l = l_{crit})$ and $\omega_{max} = \omega(l = l_0)$. l_{crit} is recovered by solving $\omega|_{l=l_{crit}} = 0$, and the maximum velocity ω_{max} is reached at l_0 . The latter is determined by solving $\frac{d\omega}{dl}|_{l=l_0}$, hence we have

$$l_{crit} = \delta_{0_x} \sqrt{\frac{\omega_0}{\delta_0^2}}, \quad l_0 = \delta_{0_y} \sqrt{\frac{\omega_0}{\delta_0^2}}, \quad \delta_0^2 = \delta_{0_x}^2 + \delta_{0_y}^2, \quad \omega_0 = \frac{1}{4P_2} \sqrt{\frac{1}{D_2} [r\sigma - \beta_1 + \beta c_{min}]}. \quad (21)$$

l_0 and l_{crit} depend on the system parameters, which means the experimenter has the potential of controlling fast or slow wave propagation if he accurately tunes the experimental setups. From Eqs.(19) $n_{\infty_{bs}} = \lim_{\xi \rightarrow \infty} n(x, y, t) \rightarrow 0$ and $c_{\infty_{bs}} = \lim_{\xi \rightarrow \infty} c(x, y, t) \rightarrow \frac{D_3}{\tau_0 - \chi_0} - \frac{D_1}{\tau_0}$, which mean that bacterial and chemoattractant wave amplitudes are finite as their associated velocity. This confirms that bell-shape solutions Eqs.(19) are physical ones. The bell-shape profile Eqs.(19) is displayed in Fig. 1 at the time $t = 100$. Bell-shape waves have been predicted analytically [24,26-30,36-38,42,47], numerically [16,19,28,30,36,40,43,48], and experimentally observed [15,19,20,30] in one dimensional chemotactic systems. Traveling waves in reactive systems are either matter carriers or information conveyors, the bell-shaped profile obtained here may explain collective bands of bacteria usually observed in reactive systems. Its velocity is depicted in panels (c)-(e) of Fig. 1. It is seen that the amplitude of ω_{bs} decreases with

Figure 1: Snapshots at $t = 100$ s of bell-shape solutions Eqs.(19) for density (a) and chemoattractant concentration (b). Wave velocity increase due to traction (c) or long-range diffusion (d) decrease, or chemotaxis increase (e). Parameters are $D_1 = 8.9 \cdot 10^{-6}$, $D_2 = 1.69 \cdot 10^{-9}$, $D_3 = 4 \cdot 10^{-6}$, $\chi_0 = 6.49 \cdot 10^{-5}$, $\tau_0 = 1.62 \cdot 10^{-3}$, $\sigma = 2.4231 \cdot 10^8$, $\beta = 3.5 \cdot 10^{-8}$, $\delta_{0x} = 1.5 \cdot 10^{-5}$, $\delta_{0y} = 4.5 \cdot 10^{-4}$, $P_2 = 4$.

increasing values of traction and long-range diffusion, respectively [see Figs. 1(c)-(d)], meaning that the traction and the long-range diffusion slowdown the waves. Conversely, the amplitude of ω_{bs} increases with increasing values of χ_0 implying that the chemotaxis strength accelerates the wave propagation. τ_0 , D_2 , and χ_0 have competing effects on the velocity of the wave. This property may be used in experiments to detect or characterize the waves. In all the cases, the velocity reduces with increasing values of l , thus thinner waves move faster than wider ones.

Considering the influences of system parameters on the bell-shaped wave, one observes that when long-range diffusion increases [Fig. 2(a)], the wave thickness widens, hence the cellular distribution occupies a larger spatial domain. At high values of long-range diffusion D_2 , the coordination degree amongst units of the bacterial population decreases, resulting in a diminution of the global velocity of the aggregation. Such a result is in accordance with the idea that diffusion of particles should break up coordination and communication degree amongst particles. Wave thickness variations are a common feature in reactive systems as extensively discussed in [19,42,48], and its occurrence in the present study signifies that cells do not lose their active properties, but rather rearrange themselves to accommodate chemoattractant concentrations across the medium. In panels (b)-(e) of Fig. 2, wave thickness variations are accompanied by an amplitude variation. Amplitude and thickness increase are observed when traction Fig. 2(b) and short range-diffusion Fig. 2(d) increase, while chemotaxis Fig. 2(c) as well as the chemoattractant consumption rate Fig. 2(e) decrease. Wave thickness reduction or increase coupled with amplitude variations in systems with uniform flows have also been reported in autocatalytic fronts [49], the Fitz-Hugh-Nagumo model [50], and the Belousov-Zhabotinsky reaction [51,52]. We propose such a coupled dynamic between wave thickness and amplitude as a tool to slice spatial domains in intervals within which cells activity remains optimized, and above which cellular density drastically reduces.

Using the parameters given in Eq.(13a) into Eq.(9) and Eq.(7) permits to recover the dip traveling

Figure 2: Influence of long-range diffusion (a), traction (b), chemotaxis (c), short-range diffusion (d) and chemoattractant consumption rate (e) upon the bell-shape bacterial wave at $y = 0$ and time $t = 100.s$. Except where mentioned, parameters are taken as in Fig. 1.

wave solutions

$$n(x, y, t) = -\frac{15\sigma_1}{4\sigma_2} \left[2 + \tanh \left(\sqrt{-\frac{P_2}{2}} (kx + ly - \omega t) \right)^2 \right], \quad (21a)$$

$$c(x, y, t) = c_{min} + \frac{15\tau_0\sigma_1}{4\sigma_2(\chi_0 - \tau_0)} \left[2 + \tanh \left(\sqrt{-\frac{P_2}{2}} (kx + ly - \omega t) \right)^2 \right]. \quad (21b)$$

In the long time/large space limits, $n_{\infty_{dw}} = \lim_{\xi \rightarrow \infty} n(x, y, t) \rightarrow -\frac{45\sigma_1}{4\sigma_2} > 0$ and $c_{\infty_{dw}} = \lim_{\xi \rightarrow \infty} c(x, y, t) \rightarrow \frac{1}{\tau_0 - \chi_0} \left[D_3 - \frac{45\sigma_1\tau_0}{4\sigma_2} \right] - \frac{D_1}{\tau_0} > 0$. The velocity associated with solutions Eqs.(22) reads

$$\omega = \delta_{0_x} \sqrt{-\frac{1}{2P_2} \sqrt{\frac{1}{D_2} [r\sigma - \beta_1 + \beta c_{min}] - l^2} + \delta_{0_y} l = \omega_{dw}. \quad (22)$$

Figs. 3(a), and 3(b) show the snapshots at time $t = 100$ of bacterial density (Eq.(21a)) and chemoattractant concentration (Eq.(21b)). The dip waves travel faster than the bell-shape waves since $\omega_{dw} > \omega_{bs}$. A straightforward comparison of Eqs.(20) and Eqs.(22) allows to figure out that the model parameters have similar effects on dip waves and their velocity ω_{dw} as on the bell-shape wave presented above.

Plugging the parameters Eq.(16a) into Eq.(7) and Eq.(8) allows us to construct step traveling waves

Figure 3: Dip traveling waves for bacterial density (a) and chemoattractant concentration (b) given by Eqs.(23). Same parameters as in Fig. 1 except for $P_2 = -2$.

whose analytical formula are

$$n(x, y, t) = -\frac{\sigma_1(21 + \sqrt{105})}{14\sigma_2} - \frac{3\sigma_1(35 - \sqrt{105})}{28\sigma_2} \frac{\cosh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right)^{-2}}{\tanh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right) - 1} \times \left[-2 + \frac{\cosh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right)^{-2}}{\tanh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right) - 1} \right], \quad (23a)$$

$$c(x, y, t) = -\frac{D_1}{\tau_0} - \frac{1}{\chi_0 - \tau_0} \left[D_3 - \frac{\tau_0\sigma_1(21 + \sqrt{105})}{14\sigma_2} \right] + \frac{3\sigma_1\tau_0(35 - \sqrt{105})}{28\sigma_2(\chi_0 - \tau_0)} \frac{\cosh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right)^{-2}}{\tanh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right) - 1} \left[-2 + \frac{\cosh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right)^{-2}}{\tanh\left(\sqrt{\frac{P_2}{4}}(kx + ly - \omega t)\right) - 1} \right]. \quad (23b)$$

The corresponding velocity associated with solutions Eqs.(23) is

$$\omega = \delta_{0_x} \sqrt{\frac{1}{P_2} \sqrt{\frac{\sqrt{105} - 7}{14D_2}} [r\sigma - \beta_1 + \beta c_{min}] - l^2} + \delta_{0_y} l = \omega_{sw}. \quad (24)$$

Furthermore, $n_{-\infty_{sw}} = \lim_{\xi \rightarrow -\infty} n(x, y, t) \rightarrow -\frac{\sigma_1(21 + \sqrt{105})}{14\sigma_2}$, $c_{-\infty_{sw}} = \lim_{\xi \rightarrow -\infty} c(x, y, t) \rightarrow \frac{D_3}{\tau_0 - \chi_0} - \frac{D_1}{\tau_0} - \frac{\sigma_1\tau_0(21 + \sqrt{105})}{14\sigma_2(\tau_0 - \chi_0)}$, and $n_{+\infty_{sw}} = \lim_{\xi \rightarrow +\infty} n(x, y, t) \rightarrow -\frac{\sigma_1(420 - 11\sqrt{105})}{14\sigma_2}$, $c_{+\infty_{sw}} = \lim_{\xi \rightarrow +\infty} c(x, y, t) \rightarrow \frac{D_3}{\tau_0 - \chi_0} - \frac{D_1}{\tau_0} - \frac{\sigma_1\tau_0(420 - 11\sqrt{105})}{14\sigma_2(\tau_0 - \chi_0)}$. Step waves obtained here translate the transition process happening between two different levels of bacteria as well as chemoattractant distribution. The gap between the levels depends on system parameters, which means that the experimenter has the potential of choosing how and the position at which the transition happens. Figs. (4) display bacterial and chemoattractant step waves Eqs.(23) in panels (a), (b), respectively.

Figure 4: Step traveling waves for bacterial density (a) and chemoattractant concentration (b) (Eqs.(23)). $P_2 = 4$, other parameters taken as in Fig. 1.

Numerical values of short-range diffusions D_1, D_3 , chemotaxis strength χ_0 , chemoattractant consumption rate β , and medium carrying capacity σ were chosen as in [3,19,29,30]. The fluids flow rate was taken according to experimental studies [18-20,29,30]. The other parameters $\tau_0, D_2, \beta_1, \beta_3$ to the best of our knowledge are not yet available. While the analytical formalism used allows to determine β_3 as given by Eqs.(11)-(17), the existence of solutions discussed yields a minimum value of β_1 . Though traction forces dominate the chemotaxis strength, the latter is shown to still have strong effects on wave characteristics namely the velocity, amplitude, and thickness. These observations are consistent with conclusions reported in [30]. More importantly, for the same set of parameter values, comparison of Eq.(20), Eq.(22) and Eq.(24) yields $\omega_{dw} > \omega_{sw} > \omega_{bs}$: the dip waves travel faster than the step and the bell-shaped waves. In other words, dip waves are better candidates to achieve fast coordination of cells or to quickly convey a piece of information within a bacterial population. From Eqs.(19), Eqs.(21) and Eqs.(23), one derives the inequalities $n_{sw} > n_{dw} > n_{bs}$. Step waves carry a higher amount of particles compared to dip and bell-shape waves. Generally speaking, an optimal transport is expected for higher velocities and wave amplitudes, but the results obtained here draw the roadmap to characterizing an optimal transport as follows: while step waves ensure the transport of a higher number of particles, a faster transport is guaranteed through dip wave structures. In reactive systems without traction and long-range diffusion, it has been shown that optimal transport necessitates the coupled dynamic between short-range diffusion and feedback [53]. However, the present study stresses that traction and long-range diffusion deeply alter the optimal transport of waves, hence must be taken into account for a better description of waves propagation.

3 Numerical experiments

In this section, we ascertain the ability of waves discussed above to propagate in a stable fashion way in model Eqs.(3). To this end, direct numerical integrations of Eqs.(3) on a square spatial domain of length $L = 100$ are performed. We take $N = 1024$ points along each spatial direction with a time step is $dt = 10^{-3}$. Integrations are performed through the pseudo-spectral method. We initially launched the simulations by introducing perturbed analytical solutions with a noise strength of ten percent of the initial amplitude of the wave. Simulations are ran over a final time $t_{fin} = 200$ s and results are displayed in Figs. 5-7. To be precise, panels (a), (b), (c) of Figs. 5-7 (resp. panels (d), (e), (f)) display snapshots of the bacterial density (resp. chemoattractant concentration) at $t = 0$ s, 100 s, 200 s respectively, obtained with the analytical solutions Eqs.(19), (21), (23) as initial conditions. Though we

inserted a random perturbation at the initial time, results depicted in Figs. 5-7 show that initial solutions evolve without undergoing any collapses nor explosions. Our solutions are numerically stable ones. In addition, from Eqs.(19), (21), and (23), the analytical solutions found above predict waves whose profiles, widths, amplitudes, and velocities remain unchanged during their evolutions, but slightly displaced due to small velocities of magnitude about 10^{-5} . Snapshots of waves displayed in Figs.(5)-(7) are in good agreement with analytical predictions. Our solutions are therefore stable ones, such that they are likely to be observed in experiments. Our results are new ones and we do believe this work may motivate further two-dimensional experimental investigations in chemotaxis systems where traction forces, advection, and long-range diffusion are at play. To the best of our knowledge, such experimental investigations that take into account the latter effects are still missing.

Figure 5: Snapshots of stable numerical bell-shape solutions for bacterial (chemoattractant) wave at $t = 0$ s (a) [(d)], $t = 100$ s (b) [(e)], and $t = 200$ s (c) [(f)]. Parameters as in Figs. 1.

4 Conclusion

We discussed the existence and the dynamical behaviors of bacterial and chemical waves propagating in a $(2 + 1)$ -dimensional chemotactic system. We introduced a new model that takes into consideration several processes including a uniform advection, long-range diffusion, chemotaxis, traction, cellular proliferation, and chemoattractant production and degradation. The traveling wave variable is assumed and an extended F-expansion method is used to construct new traveling wave solutions like step, dip, and bell-shape waves. The quest for physically acceptable solutions enforces the existence of a minimum chemoattractant concentration which depends on both traction, chemotaxis strength, bacterial and chemical short-range diffusions. We showed that traction, short-range diffusion and chemotaxis, and chemoattractant consumption rate have competing effects on the number of particles transported. The former parameters decrease the number of particles transported while the latter ones increase wave amplitudes. Increasing values of long-range diffusion decrease wave velocity but increase the wave width, the amplitude remaining unchanged. Besides, by comparing velocities and amplitudes of solutions presented, we observed that while dip waves travel faster hence are better candidates to explaining fast bacterial coordination, step waves have the potential of carrying a higher number of cells, hence may be considered

Figure 6: Stable propagation of dip bacterial (chemoattractant) wave at $t = 0$ s (a) [(d)], $t = 100$ s (b) [(e)], and $t = 200$ s (c) [(f)]. Parameters as in Fig. 1.

Figure 7: Stable evolutions of step waves of bacterial (chemoattractant) at $t = 0$ s (a) [(d)], $t = 100$ s (b) [(e)], and $t = 200$ s (c) [(f)]. Parameters as in Figs. 1.

as robust structures to perform transport in a highly dense system. The stability of solutions constructed is analyzed through direct numerical integration of the original model. Both numerical and analytical solutions remain very close hence ascertaining our theoretical predictions.

Statement of data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Conflict of Interest:

The authors declare that they have no conflict of interest.

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