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Travelling waves for a fast reaction limit of a discrete coagulation-fragmentation model with diffusion and proliferation

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Abstract

We study traveling wave solutions for a reaction-diffusion model, introduced in the article [Calvez et al \(2023\)](#), describing the spread of the social bacterium *Myxococcus xanthus*. This model describes the spatial dynamics of two different cluster sizes: isolated bacteria and paired bacteria. Two isolated bacteria can coagulate to form a cluster of two bacteria and conversely, a pair of bacteria can fragment into two isolated bacteria. Coagulation and fragmentation are assumed to occur at a certain rate denoted by k . In this article we study theoretically the limit of fast coagulation fragmentation corresponding mathematically to the limit when the value of the parameter k tends to $+\infty$. For this regime, we demonstrate the existence and uniqueness of a transition between pulled and pushed fronts for a certain critical ratio θ^* between the diffusion coefficient of isolated bacteria and the diffusion coefficient of paired bacteria. When the ratio is below θ^* , the critical front speed is constant and corresponds to the linear speed. Conversely, when the ratio is above the critical threshold, the critical spreading speed becomes strictly greater than the linear speed.

Keywords: Reaction-diffusion systems, travelling wave, pushed and pulled fronts, fast-reaction

1 Introduction

Recent advances in both high-throughput microscopy techniques and cell segmentation techniques have significantly advanced our knowledge of bacterial populations, particularly in the bacterium *Myxococcus xanthus* (Panigrahi et al, 2021). Within a bacterial population, individuals have regular interactions with other individuals, which can be cooperative or competitive (Shapiro, 1998; Avery, 2006). In this article we are interested in the modeling of the propagation of the motile bacterium *Myxococcus xanthus* and more particularly how the interactions between the different individuals could influence the propagation speed of the bacterium. This family of bacteria forms multicellular biofilms with a complex structure that is highly heterogeneous in time and space (Rombouts, 2021; Rombouts et al, 2022). They are composed of a wide variety of bacterial cluster sizes that vary greatly with the amount of local prey. Among the bacteria within these biofilms, there is also a strong difference in behavior. Indeed, bacteria have two different motility regimes: adventurous motility A and social motility S, which depend on the expression of two distinct sets of genes (Hodgkin and Kaiser, 1979). The A cells, which move by gliding over the surface in search of prey, tend to be isolated bacteria. On the other hand, S cells tend to form large clusters and move thanks to the projection of pili allowing them to cling to other bacteria. These two motilities have synergistic roles in prey predation.

The size distribution of bacterial clusters is highly heterogeneous depending on their position in the predation front. Upstream of the front, there are mainly isolated bacteria or groups of small sizes. The further away from the invasion front, the more large clusters of bacteria are found in proportion to the distance (Rombouts et al, 2022). The speed of bacteria is also heterogeneous and depends on the size of the clusters. Indeed the average speed of isolated bacteria tends to be slower than the average speed of bacteria in clusters (Bloch et al, 2023; Rombouts et al, 2022). In this article we are mathematically interested in the possible impact of the diffusion advantage

that groups of bacteria have on the speed of invasion of the bacterium *Myxococcus xanthus*. For this, we will theoretically study the model introduced in article (Calvez et al, 2023), which models the spread of the social bacterium *Myxococcus xanthus*. We briefly explain this model below.

In this model, clusters of bacteria have two possible sizes: clusters of size 1 that we will also call isolated bacteria and clusters composed of two bacteria. The density of isolated bacteria is denoted by p_1 , while the density of pairs of bacteria is denoted by p_2 , both depending on space and time. These two densities satisfy the following system of two reaction-diffusion equations

$$\begin{cases} \partial_t p_1 = \theta_1 \Delta p_1 - \tau_1 p_1^2 + 2\tau_2 p_2 + \alpha p_1 (1 - p/K), \\ \partial_t p_2 = \theta_2 \Delta p_2 + \frac{\tau_1}{2} p_1^2 - \tau_2 p_2, \end{cases} \quad (1)$$

where p corresponds to the total number of bacteria, $p := p_1 + 2p_2$. For simplicity, we consider the problem in one-dimensional space $x \in \mathbb{R}$, so the Laplacian operator becomes $\Delta = \partial_{xx}$. The coefficients θ_1 and θ_2 correspond to the diffusion coefficients of isolated and paired bacteria respectively. For the biological reasons described above (Bloch et al, 2023), we assume that $\theta_2 > \theta_1$, i.e. the diffusion coefficient of the groups of bacteria is greater than the diffusion coefficient of the isolated bacteria. The coagulation term is represented by the term $\tau_1 p_1^2$, which models the encounter between two isolated bacteria creating a cluster of two bacteria. The term, $\tau_2 p_2$, corresponds to the fragmentation of a pair of bacteria creating two isolated bacteria. The rates τ_1 and τ_2 correspond to the coagulation rate and the fragmentation rate respectively. Finally, we assume that bacteria must be isolated to divide, this term is modeled by the growth term in the first equation of (1). This growth is assumed to be logistic, with growth rate $\alpha > 0$ and carrying capacity K . In the article Rombouts et al (2022), biological experiments on the bacterium *Myxococcus xanthus* show that the coagulation rate and

the fragmentation rate are quite similar. Therefore it is assumed that the rates τ_1 and τ_2 are both equal to the same positive constant denoted by τ .

One equivalent nondimensional system of equations (1) is given by

$$\begin{cases} \partial_t p_1 = \partial_{xx} p_1 - k p_1^2 + 2k p_2 + p_1 (1 - p), \\ \partial_t p_2 = \theta \partial_{xx} p_2 + \frac{1}{2} k p_1^2 - k p_2. \end{cases} \quad (2)$$

where $k = K\tau/\alpha$, and $\theta = \theta_2/\theta_1$ are the two free parameters of the system. The coefficient $\theta > 1$ corresponds to the diffusion advantage of groups of bacteria compared to isolated bacteria. This system (2) admits a unique positive equilibrium point which we note (p_1^*, p_2^*) , we are thus in the monostable case (Calvez et al, 2023).

In this article we are interested in the propagation speed of the system (2). It is characterized as the minimal admissible speed for a positive travelling waves solution. We are especially interested in the influence of the parameter value θ on this speed. Travelling waves for spatial fragmentation models with continuous or discrete structure have been already studied theoretically by various authors in many particular cases (See for example (Ducrot and Magal, 2009; Bouin and Calvez, 2014; Alfaro et al, 2013; Griette, 2019)). This propagation speed may sometimes correspond to the speed of the linearized problem, in which case the front is referred to as 'pulled'. Conversely, when the linear prediction is incorrect, we designate such fronts as 'pushed' fronts Van Saarloos (2003). In Section 2 of the article, we briefly recall the derivation of the linear spreading speed of the system (2) already derived in the article Holzer (2014a) and given by the following formula

$$c_{lin}(\theta, k) = \begin{cases} 2, & \text{when } \theta \leq 2 + k, \\ \sqrt{\frac{k+1}{\theta-1}} + \sqrt{\frac{\theta-1}{k+1}}, & \text{when } \theta > 2 + k. \end{cases} \quad (3)$$

Using this theoretical formula and the numerical simulations presented in the article [Calvez et al \(2023\)](#), we propose the following conjecture.

Conjecture 1. *There exists a threshold θ^* such that the critical nonlinear spreading speed c of the system (2) is given by*

$$c = \begin{cases} c_{lin}(\theta, k), & \text{when } \theta \leq \theta^*(k), & (\text{Pulled case}) \\ \bar{c}(\theta, k) > c_{lin}(\theta, k), & \text{when } \theta > \theta^*(k), & (\text{Pushed case}) \end{cases}$$

for $k > 0$, where c_{lin} is the linear critical speed defined in (3).

Fast reaction limit. In this paper we are mainly interested in the fast fragmentation-coagulation limit, which mathematically corresponds to the limit when k tends to $+\infty$. Biologically this corresponds to the assumption that fragmentation and coagulation occur on a faster time scale than other interactions in the system, such as diffusion or division. In the literature, this kind of fast reaction limit has already been studied and justified for models close to the system (1). For example, in the article [Carrillo et al \(2009\)](#), the authors work on the fast reaction limit for the Aizenman-Bak model of coagulation-breakup with spatial diffusion ([Desvillettes and Fellner, 2010](#); [Aizenman and Bak, 1979](#)). Under this assumption, we will see that the system (2) simplifies into a simple Fisher-KPP type equation that can be studied theoretically. This regime has already been studied numerically in the article [Calvez et al \(2023\)](#) using a shooting method. Moreover the authors show numerically that the results obtained in the asymptotic case $k = +\infty$ are similar to the numerical experiments for k assumed to be large enough.

The approximation of fast fragmentation-coagulation leads to the study of a scalar nonlinear reaction-diffusion equation, for which we prove our main result:

Main Result. *For the fast coagulation-fragmentation limit, $k = +\infty$, the linear speed is given by*

$$c_{in}(\theta, \infty) = 2.$$

Moreover the conjecture 1 is true in this case, more precisely there exists $\theta^ \in [2, 6.5]$, such that:*

- *When $\theta \in [1, \theta^*]$, the invasion speed is equal to 2, and the front is pulled. This case corresponds to a predation speed solely governed by isolated bacteria in which the diffusion advantage of the clusters does not affect the invasion of the bacterium *Myrococcus xanthus*.*
- *When $\theta > \theta^*$, the invasion speed is strictly greater than 2, and the front is pushed. In this case, the diffusion advantage of the bacterial clusters leads to a faster invasion.*

The plan of the paper is the following: In section 2, we recall the linear spreading speed and the nonlinear speed is compared numerically with the linear speed. In section 3, we study the fast fragmentation-coagulation limit. For this case, we prove the existence and the uniqueness of a transition between pulled and pushed fronts, as well as an estimate of it. In addition, estimates of the asymptotic critical speed are given.

2 General case

Theoretical linear spreading speed

In this section, we briefly recall the results obtained in article [Holzer \(2014a\)](#), which also apply to our system. The method is also explained in more detail in the article [Holzer and Scheel \(2014\)](#). The linear spreading speed corresponds to the fastest speed associated with the linearized form of the system around the state of equilibrium ($p_1 = 0, p_2 = 0$). In our case, the linearized form of the system (2) around the

equilibrium state $(0, 0)$, and in the moving frame $\xi = x - ct$, is rewritten as follows

$$\begin{cases} \partial_t p_1 = c\partial_\xi p_1 + \partial_{\xi\xi} p_1 + p_1 + 2kp_2, \\ \partial_t p_2 = c\partial_\xi p_2 + \theta\partial_{\xi\xi} p_2 - kp_2. \end{cases} \quad (4)$$

Holzer proved in the article [Holzer \(2014a\)](#) that the linear propagation speed can be deduced from the analyticity, or lack of analyticity, of the pointwise Green's function associated with the system (4). The dispersion relation for the (4) system is given by,

$$D_c(\nu, \lambda) = (\nu^2 + c\nu + 1 - \lambda) [\theta\nu^2 + c\nu - k - \lambda], \quad (5)$$

which corresponds, by the skew-product nature of the coupling, to the product of the two dispersion relations D_1 and D_2 given by

$$D_1(\nu) := \nu^2 + c\nu + 1 - \lambda = 0,$$

$$D_2(\nu) := \theta\nu^2 + c\nu - k - \lambda = 0.$$

The roots of these dispersion relations are denoted by ν_1^\pm and ν_2^\pm respectively. The singularities of Green's function correspond to pairs (s^*, λ^*) such that the dispersion relation (5) admits a pinched double root, i.e. when (s^*, λ^*) satisfies,

$$D_c(\lambda^*, \nu^*) = 0, \quad \partial_\nu D_c(\lambda^*, \nu^*) = 0, \quad \text{Re } \nu^\pm(\lambda) \rightarrow \pm\infty \text{ as } \text{Re } (\lambda) \rightarrow \infty.$$

This happens when one of these relations is satisfied

$$\nu_1^+(s, \lambda) = \nu_1^-(s, \lambda), \quad (6)$$

and

$$\nu_1^\pm(s, \lambda) = \nu_2^\mp(s, \lambda). \quad (7)$$

Equality (6) gives us the expected speed, denoted by c_1 ,

$$c_1 = 2.$$

This speed, corresponds to the speed of the problem (2) when only isolated bacteria are considered, i.e. when the problem is decoupled ($k = 0$) and without bacteria clusters at initial time (p_2^0 equal to the null function). In this case the system of equations (2) simplifies to the following Fisher-KPP scalar equation,

$$\partial_t p_1 = \partial_{xx} p_1 + p_1(1 - p_1), \quad (8)$$

This equation has been extensively studied (see (Fisher, 1937; Kolmogorov, 1937; Aronson and Weinberger, 1978), among many others), and it has been shown that the critical speed is equal to $c_1 = 2$.

The second equality (7) gives us another speed, called anomalous speed, which is given by the following formula

$$c_{anom} = \sqrt{\frac{k+1}{\theta-1}} + \sqrt{\frac{\theta-1}{k+1}}. \quad (9)$$

Anomalous propagation refers to a scenario, at first sight unexpected, in which the coupling of two equations results in a critical speed faster than those of two decoupled components. That is, in our case, a spreading speed strictly greater than $c_1 = 2$. This phenomenon was first observed in article (Weinberger et al, 2007), and subsequently rigorously studied in (Holzer, 2014a,b; Faye and Peltier, 2018).

In our case, this anomalous speed exists when the parameter value $\theta > 2 + k$, therefore the linear propagation speed c_{lin} is given by

$$c_{lin} = \begin{cases} 2, & \text{when } \theta \leq 2 + k, \\ c_{anom}, & \text{when } \theta > 2 + k. \end{cases}$$

Linear spreading speed versus Nonlinear spreading speed

In order to estimate the propagation speed, we simulate the system with initial conditions corresponding to Heaviside step functions,

$$p_1(x, t = 0) = p_1^* \mathbf{1}_{x \leq 0}(x), \quad p_2(x, t = 0) = p_2^* \mathbf{1}_{x \leq 0}(x).$$

First, we compare the linear threshold $\theta_{lin} = 2 + k$ with the threshold of the non-linear system. In figure 1, we illustrate, the separation between the two possible regimes of the linear problem. The grey area corresponds to the zone of parameter values (k, θ) for which the linear speed is strictly greater than the expected speed $c_1 = 2$.

In the article Calvez et al (2023), the authors illustrate an equivalent figure for the general system (2). For the nonlinear system, a large part of this zone is not predicted by the linear analysis. Consequently, for the spreading speed of the system (2), the theoretical linear threshold θ_{lin} is not adequate to predict the nonlinear speed behavior. On the other hand, the numerical simulations carried out in the article Calvez et al (2023), show a notable difference concerning the exponential decay rate of the wave of $p = p_1 + 2p_2$ between the two zones separated by θ_{lin} (See Fig. 2 of (Calvez et al, 2023)). Note that the theoretical linear threshold, in the asymptotic case $k \rightarrow \infty$, corresponds to $\theta_{lin} \rightarrow +\infty$. However, as we will see in the next section, we can theoretically prove that the speed c of the system (2) is strictly greater than the speed $c_1 = 2$ for $2 < \theta < 6.6$, which theoretically demonstrates that in our case the linear speed is not a good predictor of the nonlinear speed.

We also compare the anomalous linear spreading speed given by (9) with the speed of the system (2), determined using numerical simulations. In figure 2 we plot the

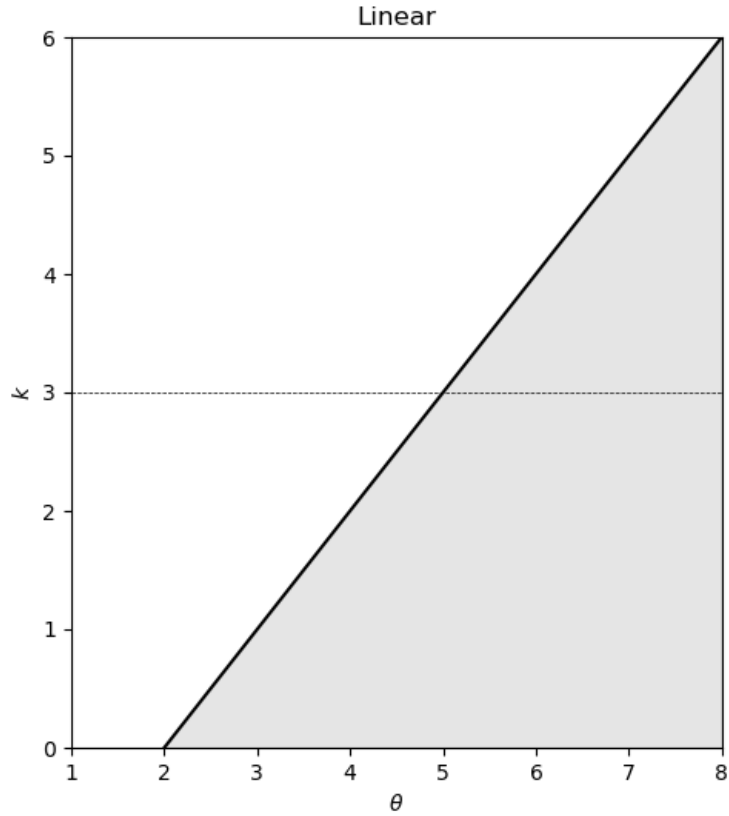


Fig. 1 The gray zones correspond to the zones for which the spreading speed is strictly greater than $c_1 = 2$. For the linear spreading speed, the threshold corresponds to the line $\theta \mapsto \theta - 2$. The horizontal dotted line, at $k = 3$, represents the choice of parameter value made for figure 2.

theoretical “normal” (in red) and anomalous (in blue) linear spreading speed given by the formula (3) as well as the nonlinear speed of the general system (in black), for different values of θ . For θ large enough, the linear speed differs greatly from the nonlinear speed. Moreover, we notice, numerically, that this linear speed is always a lower bound of the nonlinear speed. Contrary to the scalar equations, linear speed is not necessarily a lower bound of the nonlinear speed. This result was shown for a competitive Lotka-Volterra model in the article [Holzer and Scheel \(2012\)](#). We can thus conclude from figure 2 that for θ large enough, the problem is not linearly determined.

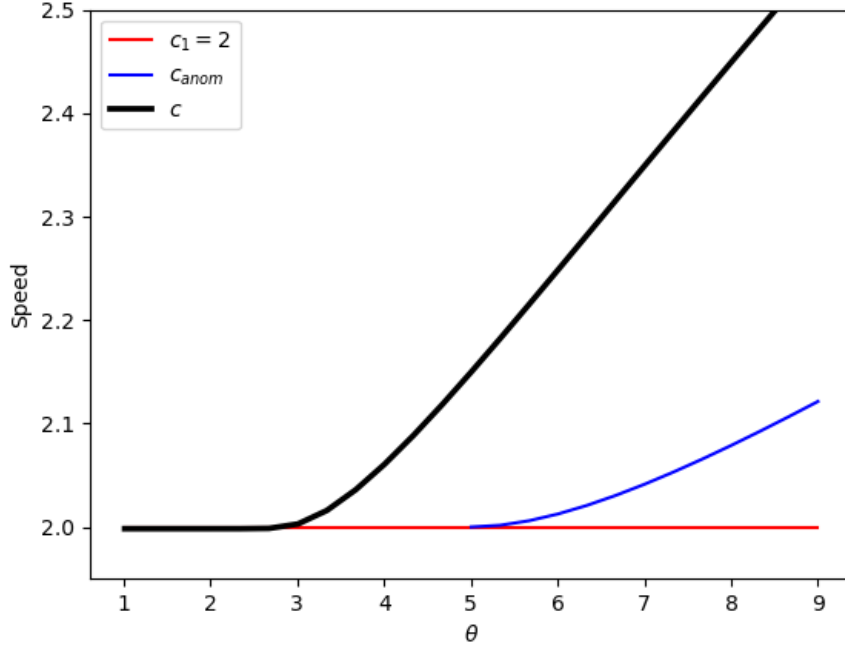


Fig. 2 Comparison of the linear spreading speed c_{lin} with the experimental speed of the system (2) for $k = 3$ and different values of θ . We notice that for θ large enough, the numerically derived spreading speeds, represented in black, are strictly greater than linear spreading speeds.

Note that in the asymptotic case $k \rightarrow 0$, the nonlinear speed seems to tend towards the linear speed. In figure 3, we represent the speed obtained using numerical experiments for the general system (black \times) and we compare it to the theoretical linear speed (red \cdot) for a chosen very small k ($k = 1e - 6$) and for different values of θ . We notice that these two speeds are very close to each other. From this figure we propose the following conjecture:

Conjecture 2. *In the asymptotic case $k \rightarrow 0^+$, the nonlinear speed is predicted by the linear speed, i.e.*

$$\lim_{k \rightarrow 0^+} c(k, \theta) = c_{lin}(0, \theta).$$

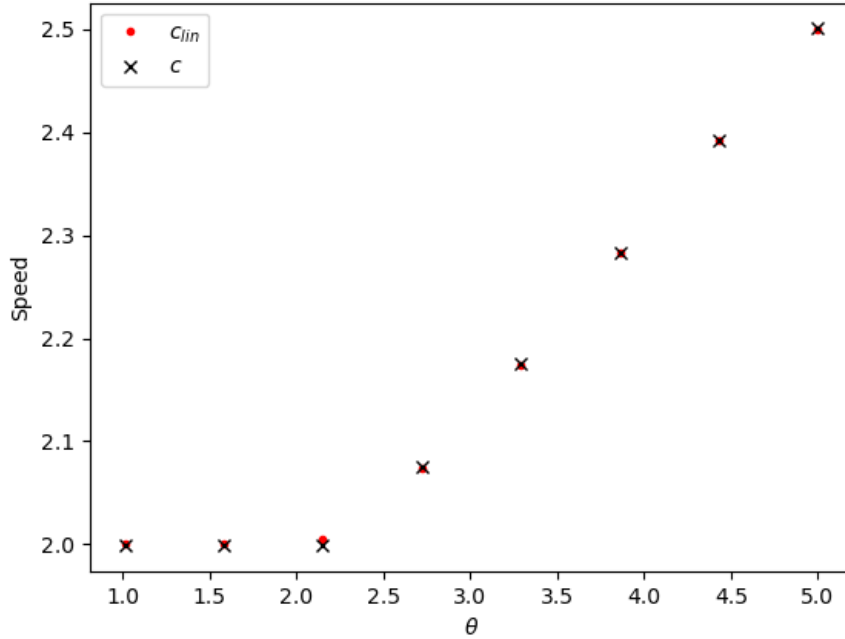


Fig. 3 Comparison of the linear spreading speed c_{lin} with the experimental speed of the system (2) for a very low parameter value k , $k = 1e - 6$. The \times in black represent numerically derived spreading speeds of the the system (2) and the red \cdot represent the linear spreading speeds given by (3). In the asymptotic case $k \rightarrow 0^+$, the linear spreading speed seems to be an accurate prediction of the critical speed of the general system.

The numerical simulations in (Calvez et al, 2023) and in this article corroborate the conjecture 1. However, they do not allow us to conclude whether or not there really is a pulled front. Indeed, with the help of numerical simulations we can obtain an experimental speed which is close, to a certain accuracy, to the real speed. Thus, using the experimental speed we cannot know for certain when we are in a pulled front regime corresponding to a critical speed equal to the linear speed. Moreover, even assuming that there is a pulled front regime for a sufficiently small θ , it is numerically very complex to identify, with certainty, the location of the transition between pulled and pushed fronts. This reason motivates us to study theoretically, the possible transition between pulled and pushed front for the system (2).

3 Fast fragmentation-coagulation regime

3.1 Derivation of an equivalent equation for travelling wave in the limit.

In the limit case $k \rightarrow +\infty$, we necessarily have $2p_2 = p_1^2$. Using the definition of p , this gives us the following relation

$$p - p_1 - p_1^2 = 0. \quad (10)$$

Therefore there is a function f such that $p_1 = f(p)$, with $f : p \rightarrow (\sqrt{1+4p} - 1)/2$. Under the assumption $k = +\infty$, the system (2) becomes a single nonlinear equation defined by

$$\partial_t p = \partial_{xx}(\phi_\theta(p)) + F(p), \quad (11)$$

with

$$F(p) = f(p)(1-p), \quad \phi_\theta(p) = f(p) + \theta f(p)^2. \quad (12)$$

We express equation (11) in the following more conventional equivalent form

$$\partial_t p = \partial_x [\psi_\theta(p) \partial_x p] + F(p), \quad (13)$$

with ψ_θ defined by

$$\psi_\theta(p) := \phi'_\theta(p) = f'(p) + 2\theta f'(p)f(p) = \frac{1}{\sqrt{1+4p}} \left(1 + \theta \left[\sqrt{1+4p} - 1 \right] \right).$$

We are interested in the existence of traveling waves for the equation (13). To investigate this, we study the equation in the moving reference frame $\xi = x - ct$. The equation (13) becomes

$$cp' + (\psi_\theta(p)p')' + F(p) = 0. \quad (14)$$

The nonlinear diffusion term complicates the study of the equation (14). The existence of traveling waves in the context of nonlinear diffusion has already been extensively studied. There are multiple theories based on different cases depending on the nonlinear diffusion term, ψ_θ , and the reaction term, F . In our case, to simplify the nonlinear diffusion term, we satisfy the assumptions to apply the change of variable initially proposed by Hadeler in the article [Hadeler \(1983\)](#) and independently by Engler in the article [Engler \(1985\)](#). Indeed we have the following conditions satisfied, $\psi_\theta(0) = 1$ and, for all $p \in [0, 1]$, the function ψ_θ is positive. The reaction term F satisfies the following properties, $F(0) = F(1) = 0$ and the function F is positive on $]0, 1[$ and negative for $p > 1$. The derivative of the function F is given by the following relation

$$F'(p) = f'(p)(1 - p) - f(p), \quad (15)$$

And applied to $p = 0$, we have $F'(0) = 1 > 0$.

In the phase plane, the equation (14) becomes the following system

$$\begin{cases} p' = q, \\ cq + (\psi_\theta(p)q)' + F(p) = 0. \end{cases} \quad (16)$$

We perform the change of variables introduced in the article [Hadeler \(1983\)](#). Rescaling the time by

$$\eta = \int_0^\xi \frac{ds}{\psi_\theta(p(s))}.$$

Setting $\rho(\eta) = p(\xi)$ and $\tilde{q}(\eta) = q(\xi)\psi_\theta(p(\xi))$, we have

$$\begin{cases} \rho' = \tilde{q}, \\ c\tilde{q} + \tilde{q}' + F(\rho)\psi_\theta(\rho) = 0. \end{cases}$$

Thus, we obtain the following equation

$$c\rho' + \rho'' + F(\rho)\psi_\theta(\rho) = 0, \quad (17)$$

without nonlinear diffusion, equivalent to the problem (14).

For this equation we want to prove the existence of a transition between pulled front and pushed front. This type of theoretical study front has already been studied for many reaction-diffusion equations. For example, the best known result concerns the Nagumo equation (Haderer and Rothe, 1975) or the more recent work on the Fisher-KPP-Burgers equation (An et al, 2021). Theoretical works on the transition between pulled and pushed fronts have also been carried out for systems of reaction-diffusion equations, notably for a system modeling autocatalytic reactions (Focant and Gallay, 1998; Billingham and Needham, 1991), or for a Lotka-Volterra competition model (Lewis et al, 2002).

3.2 Pulled case for $1 \leq \theta \leq 2$

The theoretical study of the equation (17) is much simpler than the study of the previous equation (13). In particular, it is possible to easily estimate the critical speed, c^* , by the following classical estimate

$$2 \leq c^* \leq 2\sqrt{\sup_{s \in]0,1[} \frac{\psi_\theta(s)F(s)}{s}}. \quad (18)$$

Subsequently, many authors have proposed possible improvements for the estimate of the critical speed c^* (See for example (Arias et al, 2004; Marcelli and Papalini, 2018)). For our study, we will use the following inequality, proved in (Marcelli and Papalini, 2018),

$$c^* \leq 2\sqrt{\sup_{u \in (0,1]} \frac{1}{u} \int_0^u \frac{\psi_\theta(s)F(s)}{s} ds}. \quad (19)$$

Numerically, in the article [Calvez et al \(2023\)](#), the authors noticed that a transition between pulled and pushed fronts will certainly occur when θ becomes large enough.

The speed of the linearized problem, for the equation (17), is $c_{\text{lin}} = 2$. The front is pulled if the critical speed is equal to the linear speed c^{lin} and is pushed if it is greater. First, we will show theoretically that the front is pulled for a θ assumed small enough. We are therefore interested in the upper bound of the estimate (18). In particular, one can inject the following bound in (18) or (19)

Lemma 3. *For $1 \leq \theta \leq 2$ the following inequality holds*

$$\psi_{\theta}(s)F(s) \leq s(\psi_{\theta}F)'(0) = s. \quad (20)$$

Proof. The function $\psi_{\theta}F$ is given by the following relation

$$(\psi_{\theta}F)(s) = \frac{(1-s)(\sqrt{1+4s}-1)}{4\sqrt{1+4s}} [2 + 2\theta(\sqrt{1+4s}-1)].$$

The derivative of the function $\psi_{\theta}F$ applied at $s = 0$ gives us $(\psi_{\theta}F)'(0) = 1$. By definition of F and ψ_{θ} , the inequality $(\psi_{\theta}F)(s) \leq s$ is equivalent to

$$\frac{(1-s)(\sqrt{1+4s}-1)}{4\sqrt{1+4s}} [2 + 2\theta(\sqrt{1+4s}-1)] \leq s.$$

Isolating the term θ , the condition is given by

$$\theta \leq \frac{2s\sqrt{1+4s}}{(1-s)(\sqrt{1+4s}-1)^2} - \frac{1}{\sqrt{1+4s}-1} := \mathcal{U}(s).$$

Therefore the condition (20) holds for all $\theta \leq \min_{s \in [0,1]} \mathcal{U}(s)$. The function \mathcal{U} is an increasing function, whose derivative is given by the following relation

$$\mathcal{U}'(s) = \frac{6s + 5\sqrt{4s+1} + 9}{4(s-1)^2\sqrt{4s+1}}.$$

This function is positive for $s \in (0,1)$. Therefore, thanks to the growth of \mathcal{U} the minimum of \mathcal{U} is reached at $s = 0$. To derive $\lim_{s \rightarrow 0} \mathcal{U}(s)$, we perform a Taylor series, this gives us

$$\lim_{s \rightarrow 0} \mathcal{U}(s) = \lim_{s \rightarrow 0} \frac{8s^2}{4s^2} + o(1) = 2.$$

In conclusion, we have shown that the condition (20) holds for $\theta \leq \mathcal{U}(s) = 2$.

□

Thanks to lemma 3 we directly obtain the following result

Corollary 3.1 (Pulled case for $\theta \leq 2$). *For $1 \leq \theta \leq 2$ the critical speed is equal to the linear speed*

$$c^* = 2.$$

This result is illustrated in figure 4 (Green and red areas). To prove the existence of a transition between a pulled front and a pushed front, we will use the variational principle of Benguria and Depassier (1996b,a), which we will present in the next section.

3.3 Pushed case: Application of the variational principle of Benguria and Depassier

To obtain a lower bound of the critical speed we will use the following variational principle.

Theorem 4 (Variational principle of [Benguria and Depassier \(1996b,a\)](#)). *We consider the following one-dimensional problem*

$$\partial_t u(x, t) = \partial_{xx} u(x, t) + h(u(x, t)), \quad x \in \mathbb{R}, t \geq 0.$$

Assume $h \in C^1([0, 1], \mathbb{R})$ and verify $h(0) = h(1) = 0$. We assume to be in the monostable case, i.e. $h(u) > 0$ for all $u \in]0, 1[$.

Then the critical speed c^* is given by

$$(c^*)^2 = \sup_{g \in \mathcal{G}} \left(\frac{2 \int_0^1 gh \, du}{\int_0^1 (-g^2/g') \, du} \right),$$

where

$$\mathcal{G} = \{g \in C^1(]0, 1[) \mid g(u) > 0 \text{ and } g'(u) < 0 \forall u \in]0, 1[; \int_0^1 u^2 g'(u) du > -\infty\}.$$

We characterize the threshold for transition to pushed front. Let θ^* be defined as follows

$$\theta^* = \inf\{\theta : c^*(\theta) > 2\}. \quad (21)$$

We start with

Lemma 5. *Define θ^* as in (21) then the following property holds true*

$$2 \leq \theta^* < +\infty.$$

Proof. To prove lemma 5, we denote $\psi_0 = f'$ and $\psi_1 = 2f'f$, so that we can write $\psi = \psi_0 + \theta\psi_1$. The functions ψ_0 and ψ_1 are independent of θ . This allows us to separate the part of ψ that is independent of θ and the part linearly dependent on it. Thereafter, we will denote $d\mu_g$ the measure $Fg / \int (-g^2/g')$. Under these notations, the equality

(4) of the variational principle of Benguria and Depassier becomes for our case

$$(c^*)^2 = 2 \sup_{g \in \mathcal{G}} \left(\int_0^1 (\psi_0 + \theta \psi_1) d\mu_g \right). \quad (22)$$

Therefore, since $\psi_0 \geq 0$, we have the following estimate

$$\theta \sup_{g \in \mathcal{G}} \int_0^1 \psi_1 d\mu_g \leq \frac{(c^*)^2}{2} \leq \sup_{g \in \mathcal{G}} \int_0^1 \psi_0 d\mu_g + \theta \sup_{g \in \mathcal{G}} \int_0^1 \psi_1 d\mu_g. \quad (23)$$

We define K as follows

$$K = \sup_{g \in \mathcal{G}} \int_0^1 \psi_1 d\mu_g, \quad (24)$$

by definition of μ_g and ψ_1 , this constant is positive, finite and independent of θ .

Therefore we get the following lower bound

$$2K\theta \leq (c^*)^2. \quad (25)$$

A first result, deriving from the estimate (25) and from the positivity of K , is that the transition between pulled front and pushed front, θ^* , exists and we have this following upper bound,

$$\theta^* \leq \frac{2}{K} < +\infty.$$

which ends the proof of lemma 5 □

The following lemma shows that θ^* corresponds indeed to a transition.

Lemma 6. *The function $\theta \mapsto (c^*)^2(\theta)$ is a continuous, nondecreasing convex function on $[1, +\infty[$. In particular, it is increasing on $[\theta^*, +\infty[$.*

Proof. The fact that $\theta \mapsto (c^*)^2(\theta)$ is nondecreasing is immediate. The convexity is a direct consequence of the fact that for any admissible g , $\theta \mapsto \int (\psi_0 + \theta \psi_1)$ is linear and thereby convex. As a byproduct, we establish that $\{\theta : (c^*)^2(\theta) > 4\}$ is an interval,

which is necessarily $] \theta^*, +\infty[$. Finally, by convexity, for any $\theta_1 > \theta_2 > \theta^*$, we have $(c^*)^2(\theta_2) > (c^*)^2(\theta^*) = 4$

$$\frac{(c^*)^2(\theta_1) - (c^*)^2(\theta_2)}{\theta_1 - \theta_2} \geq \frac{(c^*)^2(\theta_2) - (c^*)^2(\theta^*)}{\theta_2 - \theta^*} > 0.$$

□

Using this lemma and previous result, we can summarize the pulled pushed transition in the following

Theorem 7. *For the equation (11), let $0 < K < +\infty$ be defined by (24), there exists $\theta^* \in [2, 2/K[$, such that we have the following two results*

1. *For $\theta \in [1, \theta^*]$ the front is pulled and for $\theta > \theta^*$ the front is pushed.*
2. *The critical speed c^* of the equation (11) satisfies*

$$2K\theta \leq (c^*)^2 \leq 4 + 2K(\theta - \theta^*). \quad (26)$$

In particular

$$c^*(\theta) \underset{\theta \rightarrow +\infty}{\sim} \sqrt{2K\theta}. \quad (27)$$

Proof. Points 1. and 2. have already been demonstrated. It remains to prove the asymptotics on θ^* and K . We can denote that we have established with the proof that $c^* > 2$ for $\theta > 2/K$. Moreover, for $\theta \geq \theta^*$, we can improve the estimate (23) into this estimate

$$\theta \sup_{g \in \mathcal{G}} \int \psi_1 d\mu_g \leq \frac{(c^*)^2}{2} \leq \sup_{g \in \mathcal{G}} \int \psi_0 + \theta^* \psi_1 d\mu_g + (\theta - \theta^*) \sup_{g \in \mathcal{G}} \int \psi_1 d\mu_g.$$

Therefore by the definition of K , we have (26) and we obtain from this estimate the following limit

$$\lim_{\theta \rightarrow +\infty} \frac{(c^*(\theta))^2}{\theta} = 2K. \quad (28)$$

leading to (27). \square

The theorem 7 is illustrated by the figure 4. The blue region represents a lower bound of the theoretical minimal speed, which is obtained by applying the variational principle of Benguria and Depassier to a certain test function.

We end this section with some quantitative estimates on θ^* .

Lemma 8. *The following estimates hold true*

$$\theta^* \leq \frac{15\sqrt{5} + 21}{(\sqrt{5} - 1)(9 - \sqrt{5})} \approx 6.5235.$$

Proof. To show that the front is pushed for $\theta > \theta^*$, we use the Benguria-Depassier principle recalled below

$$(c^*)^2 = \sup_{g \in \mathcal{G}} \left(\frac{2 \int_0^1 g F \psi_\theta dp}{\int_0^1 (-g^2/g') dp} \right).$$

We apply the principle of Benguria and Depassier to the following family of test functions $g_\varepsilon(p) = (\sqrt{1 + 4p} - 1)^{\varepsilon-2}$. According to the principle of Benguria and Depassier we obtain the following lower bound for the critical speed

$$(c^*)^2 \geq \frac{2 \int_0^1 g_\varepsilon F \psi_\theta dp}{\int_0^1 (-g_\varepsilon^2/g'_\varepsilon) dp} =: \frac{N(\varepsilon)}{D(\varepsilon)}.$$

We compute numerator and denominator separately. Under our assumptions, the denominator becomes

$$D(\varepsilon) = \int_0^1 (-g_\varepsilon^2/g'_\varepsilon) dp,$$

$$\begin{aligned}
&= \int_0^1 \frac{(\sqrt{1+4p}-1)^{2\varepsilon-4}}{(2-\varepsilon)(\sqrt{1+4p}-1)^{\varepsilon-3} \cdot \frac{2}{\sqrt{1+4p}}} dp, \\
&= \frac{1}{4(2-\varepsilon)} \int_1^{\sqrt{5}} (u-1)^{2\varepsilon-4-\varepsilon+3} u^2 du, \\
&= \frac{1}{4(2-\varepsilon)} \int_0^{\sqrt{5}-1} v^{\varepsilon-1} (v+1)^2 dv, \\
&= \frac{1}{4(2-\varepsilon)} \int_0^{\sqrt{5}-1} (v^{\varepsilon+1} + 2v^\varepsilon + v^{\varepsilon-1}) dv, \\
&= \frac{1}{4(2-\varepsilon)} \left(\frac{(\sqrt{5}-1)^{\varepsilon+2}}{\varepsilon+2} + 2 \frac{(\sqrt{5}-1)^{\varepsilon+1}}{\varepsilon+1} + \frac{(\sqrt{5}-1)^\varepsilon}{\varepsilon} \right), \\
&= \frac{1}{4(2-\varepsilon)} (\sqrt{5}-1)^\varepsilon \frac{5\varepsilon^2 + (2\sqrt{5}+5)\varepsilon + 2}{\varepsilon(\varepsilon+1)(\varepsilon+2)},
\end{aligned}$$

leading to

$$D(\varepsilon) = \frac{(\sqrt{5}-1)^\varepsilon}{4\varepsilon(\varepsilon+1)(\varepsilon+2)} \frac{5\varepsilon^2 + (2\sqrt{5}+5)\varepsilon + 2}{(2-\varepsilon)}. \quad (29)$$

Still using the same change of variable $u = \sqrt{1+4p}$, we compute the numerator

$$\begin{aligned}
N(\varepsilon) &= 2 \int_0^1 g_\varepsilon F \psi_\theta dp, \\
&= 2 \int_1^{\sqrt{5}} (u-1)^{\varepsilon-2} \frac{(5-u^2)(u-1)}{4u} [2 + 2\theta(u-1)] \frac{u}{2} du, \\
&= \frac{1}{8} \int_1^{\sqrt{5}} (u-1)^{\varepsilon-1} (5-u^2) (1 + \theta(u-1)) du, \\
&= \frac{1}{8} \int_0^{\sqrt{5}-1} v^{\varepsilon-1} (4-2v-v^2) (1 + \theta v) dv, \\
&= \frac{1}{8} (I(\varepsilon-1) + \theta I(\varepsilon)),
\end{aligned}$$

where

$$\begin{aligned}
I(\alpha) &= \int_0^{\sqrt{5}-1} v^\alpha (4-2v-v^2) dv, \\
&= 2 \frac{(\sqrt{5}-1)^{\alpha+1}}{(\alpha+1)(\alpha+2)(\alpha+3)} \left((5-\sqrt{5})\alpha + 9 - \sqrt{5} \right).
\end{aligned}$$

So that

$$N(\varepsilon) = \frac{(\sqrt{5}-1)^\varepsilon}{4\varepsilon(\varepsilon+1)(\varepsilon+2)} \left((5-\sqrt{5})(\varepsilon-1) + 9 - \sqrt{5} + \frac{\theta\varepsilon(\sqrt{5}-1)}{\varepsilon+3} \left((5-\sqrt{5})\varepsilon + 9 - \sqrt{5} \right) \right).$$

Finally, we can make the Taylor expansion

$$\frac{N(\varepsilon)}{D(\varepsilon)} = 4 + \varepsilon \cdot \left(-7 - 5\sqrt{5} + \frac{\theta}{3} (9 - \sqrt{5}) (\sqrt{5} - 1) \right) + o(\varepsilon),$$

And therefore, for $\theta > \frac{21+15\sqrt{5}}{(9-\sqrt{5})(\sqrt{5}-1)}$, we have $(c^*)^2(\theta) \geq \frac{N(\varepsilon)}{D(\varepsilon)} > 4$ for $\varepsilon > 0$ small enough which proves the bound $\theta^* \leq \frac{21+15\sqrt{5}}{(9-\sqrt{5})(\sqrt{5}-1)}$ of lemma 8. □

This lower bound, coupled with the previous corollary 3.1, provides the following estimate $\theta^* \in [2, 6.6]$. In article [Avery et al \(2023b\)](#), the authors have developed a method to approach numerically, with good precision, the transition between pulled front and pushed front. Applying this method to the equation (17) yields the following experimental threshold: $\tilde{\theta}^* \approx 3.1489$, which is in agreement with our estimates.

4 Conclusion

We exhibit numerically that for $k \geq 0$ the linear speed of model (2) is not a good prediction of the nonlinear speed. Moreover, in the asymptotic case, $k = +\infty$, we can, with a change of variables, simplify the system (2) into a single reaction-diffusion equation. Thanks to this simplification, we have demonstrated the existence of a transition between pulled and pushed fronts, as well as an estimate of the critical threshold.

Note that if we replace the coagulation term with a linear transfer term, the resulting model is a special case of the general system studied in the article [Elliott and Cornell \(2012\)](#). In this paper, the authors show the existence of zones for which the speed is anomalous, and also exhibit the importance of the critical threshold $\theta^* = 2$.

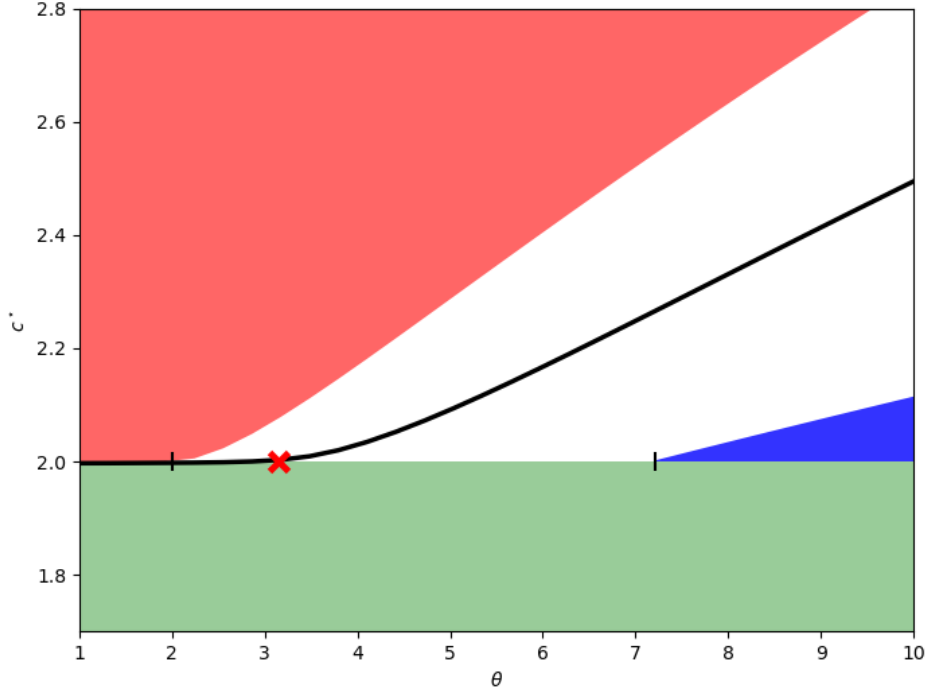


Fig. 4 The black curve represents the evolution of the critical speed of the numerical solution of the asymptotic problem (13) as a function of θ . It is obtained numerically using a shooting method. The green area corresponds to the inequality $c^* \geq c^{\text{lin}} = 2$. The area in red corresponds to the upper bound of the estimate (19) introduced in the article Marcelli and Papalini (2018). The blue area is obtained using the variational principle of Benguria and Depassier (4) applied to the family of test functions $\tilde{g}_\varepsilon(p) = (\sqrt{1+4p} - 1)^{\varepsilon-2}$. For this figure the value of the parameter ε is $\varepsilon = 0.09$. This value of ε is not optimal for estimating the transition between pulled and pushed front. The zone in white corresponds theoretically to the area in which the critical speed is admissible. We observe a transition between pulled and pushed fronts which takes place between the positions, $x = 2$ and $x \approx 7.2$, symbolized by the two markers. The red cross corresponds to the experimental transition threshold between pulled front and pushed front, obtained using the theory and the codes of the article Avery et al (2023b).

In their case, however, the linear speed predicts the non-linear speed; in our case, the addition of the non-linear coagulation term disturbs this prediction when θ is large enough.

In this article we have demonstrated the existence of a transition between pulled and pushed fronts only in the asymptotic case $k = +\infty$. For the case $k > 0$, this

result is more complex to prove. In the article [Focant and Gally \(1998\)](#), the authors theoretically prove the existence of a transition between pulled and pushed fronts for a system of reaction-diffusion equations using phase space techniques. However, for the system (2), the eigenvectors of the linearization around the positive equilibrium point are explicit but highly complex, making it impossible to use these techniques.

It could be interesting to determine if and how our result for $k = +\infty$ persists for sufficiently large values of k . The resolution of this type of problem is generally carried out using the implicit function theorem. However, the application of this theorem can be complex in the context of traveling wave solutions ([Volpert, 2014](#); [Volpert et al, 1994](#); [Banerjee et al, 2017](#)). There are several possibilities to overcome these problems, for example, refer to the theory presented in the book [Volpert \(2014\)](#). Moreover, new methods for the persistence of pulled fronts have been recently introduced in the articles [Avery and Scheel \(2022\)](#); [Avery et al \(2023a,b\)](#); [Avery and Garénaux \(2023\)](#). Regardless of the method used, the nonlinear diffusion in the asymptotic case of $k = +\infty$ considerably complicates the analysis.

It should also be noted that the numerical simulations carried out in the article [Calvez et al \(2023\)](#) can be improved. In particular, the recent results obtained by [Avery et al \(2023b\)](#), based on the far field decomposition, would allow us to obtain an experimental transition between the pulled and the pushed fronts with an extreme accuracy compared to the previous numerical simulations.

There are multiple possible future directions to improve modeling of the spread of the bacterium *Myxococcus xanthus*.

First of all it would be interesting to complexify the size structure of the model (2), by including also larger clusters of bacteria. In the article [Calvez et al \(2023\)](#), the authors show numerically, for a similar model structured in continuous size, the existence of numerical results very close to those obtained for the system (2). In particular, the authors show, numerically, the existence of a phenomenon equivalent to

a transition between pulled and pushed front. Another possibility, concerning the size of the clusters, would be to use the classification recently introduced in biology between 3 types of families: the “scouts” which are small groups of bacteria, the “loners” the medium-sized groups and finally the “swarms” corresponding to the largest clusters (Rombouts et al, 2022).

Another interesting axis would be to complexify the reaction terms of the model (1) to model as well as possible the behavior of the bacterium *Myxococcus xanthus*. For example, when the bacterium divides, it remains motionless during the time of the division. In this article we assume that this time is negligible. Nevertheless it would be interesting to study the effect on the speed of such counterpart on the division. Such an addition would tend to increase the area in which the front regime is pushed. From a mathematical point of view, there already exist in the literature systems modeling division terms close to the desired one. For these models built with a delay term, traveling wave solutions have already been studied (see for example (Adimy et al, 2017, 2022) and the references therein).

Finally, it is necessary for the future to take into account the fact that the bacterium *Myxococcus xanthus* is a predatory bacterium attacking prey bacteria such as *E.Coli*. Biologically, the amount of prey and its evolution over time has a major impact on the different motilities of *Myxococcus xanthus* as well as on its speed of propagation. This will be a subject of our future study.

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References

- Adimy M, Chekroun A, Kazmierczak B (2017) Traveling waves in a coupled reaction–diffusion and difference model of hematopoiesis. *Journal of Differential Equations* 262(7):4085–4128
- Adimy M, Chekroun A, Kazmierczak B (2022) Traveling waves for reaction-diffusion pde coupled to difference equation with nonlocal dispersal term and time delay. *Mathematical Modelling of Natural Phenomena* 17:17
- Aizenman M, Bak TA (1979) Convergence to equilibrium in a system of reacting polymers. *Communications in Mathematical Physics* 65(3):203–230
- Alfaro M, Coville J, Raoul G (2013) Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypic trait. *Communications in Partial Differential Equations* 38(12):2126–2154
- An J, Henderson C, Ryzhik L (2021) Pushed, pulled and pushmi-pullyu fronts of the burgers-fkpp equation. arXiv preprint arXiv:210807861
- Arias M, Campos J, Robles-Pérez A, et al (2004) Fast and heteroclinic solutions for a second order ode related to fisher-kolmogorov's equation. *Calculus of Variations and Partial Differential Equations* 21(3):319–334
- Aronson DG, Weinberger HF (1978) Multidimensional nonlinear diffusion arising in population genetics. *Advances in Mathematics* 30(1):33–76
- Avery M, Garénaux L (2023) Spectral stability of the critical front in the extended fisher-kpp equation. *Zeitschrift für angewandte Mathematik und Physik* 74(2):71

- Avery M, Scheel A (2022) Universal selection of pulled fronts. *Communications of the American Mathematical Society* 2(05):172–231
- Avery M, Holzer M, Scheel A (2023a) Pushed and pulled fronts in a logistic keller-segel model with chemorepulsion. arXiv preprint arXiv:230801754
- Avery M, Holzer M, Scheel A (2023b) Pushed-to-pulled front transitions: continuation, speed scalings, and hidden monotonicity. *Journal of Nonlinear Science* 33(6):102
- Avery SV (2006) Microbial cell individuality and the underlying sources of heterogeneity. *Nature Reviews Microbiology* 4(8):577–587
- Banerjee M, Vougalter V, Volpert V (2017) Doubly nonlocal reaction–diffusion equations and the emergence of species. *Applied Mathematical Modelling* 42:591–599
- Benguria R, Depassier M (1996a) Speed of fronts of the reaction-diffusion equation. *Physical review letters* 77(6):1171
- Benguria R, Depassier M (1996b) Variational characterization of the speed of propagation of fronts for the nonlinear diffusion equation. *Communications in mathematical physics* 175:221–227
- Billingham J, Needham D (1991) The development of travelling waves in quadratic and cubic autocatalysis with unequal diffusion rates. i. permanent form travelling waves. *Philosophical Transactions of the Royal Society of London Series A: Physical and Engineering Sciences* 334(1633):1–24
- Bloch H, Calvez V, Gaudeul B, et al (2023) Modelling, analysis, and simulation of traffic jam in colonies of *myxococcus xanthus* (in preparation). In preparation

- Bouin E, Calvez V (2014) Travelling waves for the cane toads equation with bounded traits. *Nonlinearity* 27(9):2233
- Calvez V, El Abdouni A, Estavoyer M, et al (2023) Regime switching on the propagation speed of travelling waves of some size-structured myxobacteriapopulation models. In preparation
- Carrillo JA, Desvillettes L, Fellner K (2009) Rigorous derivation of a nonlinear diffusion equation as fast-reaction limit of a continuous coagulation-fragmentation model with diffusion. *Communications in Partial Differential Equations* 34(11):1338–1351
- Desvillettes L, Fellner K (2010) Large time asymptotics for a continuous coagulation-fragmentation model with degenerate size-dependent diffusion. *SIAM journal on mathematical analysis* 41(6):2315–2334
- Ducrot A, Magal P (2009) Travelling wave solutions for an infection-age structured model with diffusion. *Proceedings of the Royal Society of Edinburgh Section A: Mathematics* 139(3):459–482
- Elliott EC, Cornell SJ (2012) Dispersal polymorphism and the speed of biological invasions. *PloS one* 7(7):e40496
- Engler H (1985) Relations between travelling wave solutions of quasilinear parabolic equations. *Proceedings of the American Mathematical Society* 93(2):297–302
- Faye G, Peltier G (2018) Anomalous invasion speed in a system of coupled reaction-diffusion equations. *Communications in Mathematical Sciences* 16(2):441–461
- Fisher RA (1937) The wave of advance of advantageous genes. *Annals of eugenics* 7(4):355–369

- Focant S, Gally T (1998) Existence and stability of propagating fronts for an autocatalytic reaction-diffusion system. *Physica D: Nonlinear Phenomena* 120(3-4):346–368
- Griette Q (2019) Singular measure traveling waves in an epidemiological model with continuous phenotypes. *Transactions of the American Mathematical Society* 371(6):4411–4458
- Hadeler K (1983) Free boundary problems in biological models. *Free boundary problems: Theory and applications* 2:664–671
- Hadeler KP, Rothe F (1975) Travelling fronts in nonlinear diffusion equations. *Journal of Mathematical Biology* 2(3):251–263
- Hodgkin J, Kaiser D (1979) Genetics of gliding motility in *myxococcus xanthus* (myxobacterales): two gene systems control movement. *Molecular and General Genetics* 171(2):177–191
- Holzer M (2014a) Anomalous spreading in a system of coupled fisher–kpp equations. *Physica D: Nonlinear Phenomena* 270:1–10
- Holzer M (2014b) A proof of anomalous invasion speeds in a system of coupled fisher–kpp equations. *arXiv preprint arXiv:14098641*
- Holzer M, Scheel A (2012) A slow pushed front in a lotka–volterra competition model. *Nonlinearity* 25(7):2151
- Holzer M, Scheel A (2014) Criteria for pointwise growth and their role in invasion processes. *Journal of Nonlinear Science* 24:661–709
- Kolmogorov A (1937) Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow Univ Bull Math* 1:1–25

- Lewis MA, Li B, Weinberger HF (2002) Spreading speed and linear determinacy for two-species competition models. *Journal of mathematical biology* 45:219–233
- Marcelli C, Papalini F (2018) A new estimate on the minimal wave speed for travelling fronts in reaction–diffusion–convection equations. *Electronic Journal of Qualitative Theory of Differential Equations* 2018(10):1–13
- Panigrahi S, Murat D, Le Gall A, et al (2021) Mistic, a general deep learning-based method for the high-throughput cell segmentation of complex bacterial communities. *Elife* 10:e65151
- Rombouts S (2021) Advanced microscopies for the study of motility behavior in predated myxococcus xanthus. PhD thesis, Université Montpellier
- Rombouts S, Mas A, Le Gall A, et al (2022) Multi-scale dynamic imaging reveals that cooperative motility behaviors promote efficient predation in bacteria. *bioRxiv* pp 2022–12
- Shapiro JA (1998) Thinking about bacterial populations as multicellular organisms. *Annual review of microbiology* 52(1):81–104
- Van Saarloos W (2003) Front propagation into unstable states. *Physics reports* 386(2-6):29–222
- Volpert AI, Volpert VA, Volpert VA (1994) Traveling wave solutions of parabolic systems, vol 140. American Mathematical Soc.
- Volpert V (2014) Elliptic partial differential equations, vol 2. Springer
- Weinberger HF, Lewis MA, Li B (2007) Anomalous spreading speeds of cooperative recursion systems. *Journal of mathematical biology* 55:207–222