

## Global Existence for a Parabolic Chemotaxis Model with Prevention of Overcrowding

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In this paper we study a version of the Keller–Segel model where the chemotactic cross-diffusion depends on both the external signal and the local population density. A parabolic quasi-linear strongly coupled system follows. By incorporation of a population-sensing (or “quorum-sensing”) mechanism, we assume that the chemotactic response is switched off at high cell densities. The response to high population densities prevents overcrowding, and we prove local and global existence in time of classical solutions. Numerical simulations show interesting phenomena of pattern formation and formation of stable aggregates. We discuss the results with respect to previous analytical results on the Keller–Segel model. © 2001 Academic Press

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## 1. INTRODUCTION

We consider the parabolic chemotaxis system

$$\begin{aligned} u_t &= \nabla(\nabla u - V(u, v)\nabla v) \\ v_t &= \mu\Delta v + g(u, v) \\ u(0, \cdot) &= u_0, \quad v(0, \cdot) = v_0 \end{aligned} \tag{1}$$

on a  $C^3$ -differentiable, compact Riemannian manifold  $\mathcal{M}$  without boundary. In particular, this includes a 1-D interval with periodic boundary conditions or a one-point compactification of  $\mathbb{R}$  and in 2-D a torus (e.g.,  $\mathbb{R}^2/\mathbb{Z}^2$ ). In  $n$ -D we consider any sphere, torus, or some appropriate compactification of  $\mathbb{R}^n$ . From solutions to homogeneous Neumann boundary conditions on intervals in one (or two) dimensions, we can construct solutions with periodic boundary conditions on a domain of double (quadruple) the size, and therefore Neumann boundary conditions on intervals in 1- and 2-D are also included.

The function  $u(t, x)$  describes the particle density at time  $t$ , at position  $x \in \mathcal{M}$ ;  $v(t, x)$  is the density of the external signal. Models of the above type were first proposed by Patlak [23] and Keller and Segel [12] to describe directed movement and aggregation of individuals in response to environmental cues. Here, the *chemotactic cross-diffusion*  $V$  is assumed to be bounded, and the function  $g(u, v)$  describes production and degradation of the external stimulus.

We will show global existence of classical solutions for

$$V(u, v) = u\beta(u)\chi(v), \tag{2}$$

where  $\beta, \chi \in C^3$  satisfy the conditions

- (i)  $\chi > 0$
- (ii)  $\beta(0) > 0$ , there exists a  $\bar{u} > 0$  such that  $\beta(\bar{u}) = 0$  and  $\beta(u) > 0$  for  $0 < u < \bar{u}$ . (3)

For the production term  $g(u, v)$  we assume that it is of birth–death structure, i.e., we assume  $g \in C^2(\mathbb{R}^2)$  and

$$g(u, v) = g_1(u, v)u - g_2(u, v)v, \tag{4}$$

with bounded death rate  $g_2 \geq \delta > 0$  and with birth rate  $g_1 \geq 0$ . Then there exists a  $\bar{v} > 0$  such that

$$g(u, \bar{v}) \leq 0 \quad \text{for all } 0 \leq u \leq \bar{u}. \tag{5}$$

The standard example for  $V$  is

$$V_0(u, v) = \chi u(1 - u), \quad (6)$$

and for  $g$  it is the linear function

$$g_0(u, v) = \gamma u - \delta v, \quad \gamma \geq 0, \delta > 0, \quad (7)$$

which has been used in related literature as well. In contrast to previous studies of parabolic chemotaxis equations, we assume that the chemotactic cross-diffusion  $V$  is bounded. It is well known that unbounded  $V(y)$  can result in finite-time blow-up of solutions, even for the case of linear  $V$  and  $g$ .

The case of  $V(u, v) = u\chi(v)$  has been studied in great detail in the literature (see, e.g., Childress and Percus [5, 6], Jäger and Luckhaus [11], Nagai [15], Gajewsky and Zacharias [7], Senba [28], Rascle and Ziti [25], Herrero and Velazques [8, 9], Yagi [31], Othmer and Stevens [21], or Levine and Sleeman [14]). The possibility of blow-up has been shown to strongly depend on space dimension. For  $V(u, v) = \chi u$  and linear reproduction,  $g_0(u, v) = \gamma u - \delta v$ , finite-time blow-up never occurs in 1-D (unless there is no diffusion of the attractant,  $v$ ) but can always occur in  $n$ -D for  $n \geq 3$ . The 2-D case is crucial, and several thresholds (for radially symmetric solutions and for nonsymmetric solutions) are found. If the initial distribution exceeds this threshold, then the solution may blow up in finite time. When the initial mass is below this threshold, the solution exists globally. The latter has been proven by using a Lyapunov functional in Gajewski and Zacharias [7]; Nagai, Senba, and Yoshida [18]; and Biler [3]. The Lyapunov technique has been generalized to obtain similar thresholds for chemotactic sensitivities  $\chi(v)$  given by a primitive  $\phi(v) = \int \chi(v)$  which is strictly sublinear (see [4]). This includes functional forms of  $\phi(v) = \log v$ ,  $\phi(v) = v^p$ , for  $0 < p < 1$  or equally bounded functions  $\phi(v)$  (see Nagai *et al.* [16, 17, 19] and Biler [4]). Post [24] considers chemotactic velocities with saturation in  $v$  and linear in  $u$ . Under modification of the Lyapunov function from [7], the global existence of solutions was shown.

In the context of pattern formation, a process leading to “blow-up” indicates permissibility of aggregative behavior: i.e., self-organization is possible. Yet, such biological processes do not end with the formation of the aggregate: the initial aggregation phase of *Dictyostelium* development leads to later stages, such as formation of the slug and fruiting body. Pertinently, the cAMP signaling mechanism responsible for initial aggregation of *Dictyostelium* is also thought to play a major role in these subsequent developmental stages [26, 29]. Throughout, a number of different processes occur, such as the cell specification of embryonic cells into prespore/prestalk cells. From such considerations, it is desirable to develop a simple chemotaxis model (like (1)) which excludes blow-up and permits global existence

independently of thresholds or of space dimensions. This will allow study of the dynamics of pattern formation during both the initial aggregation phase and the subsequent development of this pattern. A second consideration for excluding blow-up concerns the applicability of numerical tools in the studies already mentioned. The sharp gradients associated with solutions to chemotaxis systems can pose stability problems in numerical methods, resulting in confusion about whether a blow-up scenario or simply a sharp (or “spike”) aggregate is being observed.

In fact, a steady-state analysis of (1) together with (3) shows that stationary nonconstant patterns are possible for sufficiently large  $\chi$ . In 1-D the steady-state analysis leads to

$$u_x = u\beta(u)\chi(v)v_x,$$

implying that a stationary solution  $u(x)$  has an extremum when  $u = 0$  or  $u = \bar{u}$  or  $v_x = 0$ . Thus the distribution will be flat about  $u = 0$  and  $u = \bar{u}$ , which has indeed been observed in our numerical simulations (see Section 3). A detailed bifurcation analysis of steady states for a system similar to (1) can be found in Schaaf [27].

Chemotactic systems of type (1) can be derived from a biased random walk model, whereby the probability of a particle jumping is modulated by an extracellular signal and by the local population density. In particular, specific conditions for the chemotactic cross-diffusion can be derived from realistic assumptions based on how individual cells detect and interpret local environmental cues. Using plausible biological assumptions, we consider a variety of different mechanisms that can result in systems of the type given by (1) together with (3) in a separate paper [22].

The main result of this paper is the global existence of solutions in time as presented in Theorem 2.5. The proof of global existence relies on the existence of an invariant region  $\Gamma$  as shown in Theorem 2.1. However, the known literature on quasi-linear parabolic systems does not present a result on local existence which fits (1) exactly. We start our analysis by showing local existence in time, using a fixed-point argument. In the case of a bounded region  $\Omega$  with Dirichlet boundary conditions, the results of Amann [2] on local existence could be applied if  $V < 2\sqrt{\mu}$ . This condition guarantees that it is a parabolic equation. As demonstrated in what follows we need no such restriction. For the proof of global existence below, we use a schematic for the regularity properties of the heat equation semigroup as given in Taylor [30] (see Lemma 2.1).

Finally, we present numerical simulations for (1) in one and two dimensions and demonstrate how the modified function results in formation of a steady pattern, as opposed to blow-up of solutions, and demonstrate the potential pattern variety. A more detailed analysis of these patterns and further numerical simulations will be presented in [22].

## 2. LOCAL AND GLOBAL EXISTENCE

We study classical solutions of (1) for some  $t_0 > 0$  in spaces

$$\mathcal{X}_u := C([0, t_0], W^{\sigma,p}(\mathcal{M})), \quad \mathcal{X}_v := C([0, t_0], W^{\sigma+\alpha,p}(\mathcal{M})),$$

with

$$1 < \sigma < 2, \quad 1 < \alpha < 2, \quad 2 < \sigma + \alpha < 3, \quad \max\left\{\frac{n}{\sigma-1}, \frac{n}{2-\sigma}\right\} < p. \quad (8)$$

For this choice of parameters we have a Sobolev imbedding  $W^{\sigma,p} \rightarrow C_b^1$  (see [1]).

Equation (1) falls into the class of quasi-linear systems with cross-diffusion. However, in its present form there is no existence result in the literature which applies directly. The works of Ladyžhenskaya, Solonnikov, and Ural'ceva [13] and Amann [2] are standard information sources in this field.

We will construct solutions using a contraction mapping argument. This involves intensive use of the following regularity properties of the solution semigroup  $e^{\Delta t}$  of the heat equation  $u_t = \Delta u$  on  $\mathcal{M}$ .

LEMMA 2.1 (Taylor, [30, p. 274]). *For all  $p \geq q > 0$  and  $s \geq r$  we have*

$$e^{\Delta t}: W^{r,q}(\mathcal{M}) \rightarrow W^{s,p}(\mathcal{M}), \quad \text{with norm } Ct^{-\kappa},$$

where  $\kappa$  is given by

$$\kappa = \frac{n}{2} \left( \frac{1}{q} - \frac{1}{p} \right) + \frac{1}{2}(s-r).$$

Our analysis starts by identifying an invariant region  $\Gamma$  for solutions in  $\mathcal{X}_u \times \mathcal{X}_v$ . We proceed to show a number of appropriate *a priori* estimates which enable a contraction mapping argument for local existence. Moreover, these estimates demonstrate bounds which grow algebraically in time, leading to global existence.

For simplicity of notation, we shall denote all constants by  $C$ , even though they might have different values in the same estimate. We will omit the argument  $(\mathcal{M})$  of the Sobolev spaces  $W^{\sigma,p}$ , and we denote the norms by  $\|\cdot\|_{\sigma,p}$ .

## 2.1. Invariant Region

The zero of the chemotactic cross-diffusion  $V(u, v)$  at  $u = \bar{u}$  permits us to demonstrate the existence of an invariant region for  $(u, v)$  in  $\mathbb{R}^2$ . This *a priori*  $L^\infty$ -estimate is the key ingredient to obtaining global existence in time.

THEOREM 2.1. *Assume (2)–(4). Then the region*

$$\Gamma := \{(u, v) \in \mathbb{R}^2 : 0 \leq u \leq \bar{u}, 0 \leq v \leq \bar{v}\}$$

*is positively invariant for solutions of (1).*

*Proof.* We explicitly prove the existence of an upper limit  $(\bar{u}, \bar{v})$ . The proof of nonnegativity uses the same construction.

Let  $(u, v) \in \mathcal{X}_u \times \mathcal{X}_v$  be a solution of (1). We define

$$u^+(t, x) := \begin{cases} u(t, x) - \bar{u}, & \text{if } u(t, x) > \bar{u}, \\ 0, & \text{otherwise.} \end{cases}$$

For each time  $t$ , where  $0 \leq t \leq t_0$ , we split the manifold  $\mathcal{M}$  into three disjoint sets  $\mathcal{M} = J_-(t) + J_0(t) + J_+(t)$ :

$$J_-(t) := \{x \in \mathcal{M} : u(t, x) < \bar{u}\}$$

$$J_0(t) := \{x \in \mathcal{M} : u(t, x) = \bar{u}\}$$

$$J_+(t) := \{x \in \mathcal{M} : u(t, x) > \bar{u}\}.$$

Since  $u(t, \cdot) \in W^{\sigma,p}$  for  $\sigma > 1$ ,  $p > n/2$  it is continuously differentiable (by the Sobolev imbedding). Thus, these sets are measurable and  $\partial J_+(t)$  is a differentiable submanifold. We can write

$$\begin{aligned} \frac{d}{dt} \frac{1}{2} \|u^+(t, \cdot)\|_2^2 &= \int_{J_-(t)} u^+ u_t^+ dx + \int_{J_0(t)} u^+ u_t^+ dx + \int_{J_+(t)} u^+ u_t^+ dx \\ &= \int_{J_+(t)} (u - \bar{u}) u_t dx \end{aligned}$$

since, on  $J_0 \cup J_-$ , we have  $u^+ = 0$ . The set  $J_+(t)$  is an open set  $T \rightarrow t$ . Then it follows from  $u^+ = u - \bar{u}$  that  $u_t^+ = u_t$  on  $J_+(t)$ . From the first equation of (1) we obtain

$$\begin{aligned} \frac{d}{dt} \frac{1}{2} \|u^+(t, \cdot)\|_2^2 &= \int_{J_+(t)} (u - \bar{u})(\nabla(\nabla u - V(u, v)\nabla v)) dx \\ &= - \int_{J_+(t)} (\nabla u)^2 + \int_{\partial J_+(t)} (u - \bar{u})(\nabla u \cdot \nu) dS \\ &\quad + \int_{J_+(t)} \nabla u V(u, v)\nabla v dx \\ &\quad - \int_{\partial J_+(t)} (u - \bar{u})V(u, v)(\nabla v \cdot \nu) dS, \end{aligned}$$

where  $\nu$  denotes the outer normal on  $\partial J_+(t)$ . On the boundary of  $J_+(t)$  we have  $u = \bar{u}$ , and the boundary integrals vanish identically. Thus,

$$\frac{d}{dt} \frac{1}{2} \|u^+(t, \cdot)\|_2^2 = - \int_{J_+(t)} (\nabla u)^2 + \int_{J_+(t)} \nabla u V(u, v)\nabla v dx. \tag{9}$$

As we are interested in solutions inside  $\Gamma$  only, we allow  $V$  outside  $\Gamma$  to be modified into

$$\tilde{V}(u, v) := \begin{cases} V(u, v), & \text{if } u \leq \bar{u} \\ 0, & \text{else,} \end{cases}$$

which is continuous at  $\bar{u}$ . Then for solutions of (1), with  $\tilde{V}$  instead of  $V$ , the estimate (9) can be reduced to

$$\frac{d}{dt} \|u^+(t, \cdot)\|_2^2 \leq 0.$$

If initially  $u_0^+ = 0$ , then  $u^+(t, \cdot) = 0$  for all times of existence. Since  $V \equiv \tilde{V}$  on  $\Gamma$  the same conclusion holds for (1) with the original  $V$ .

To prove the upper bound of  $v$  we define

$$v^+(t, x) := \begin{cases} v(t, x) - \bar{v}, & \text{if } v(t, x) > \bar{v}, \\ 0, & \text{else.} \end{cases}$$

We again split  $\mathcal{M}$  according to  $v <, =, > \bar{v}$  and consider  $\frac{d}{dt} \frac{1}{2} \|v^+(t, \cdot)\|_2^2$ . Here

$$\frac{d}{dt} \|v^+(t, \cdot)\|_2^2 \leq 0$$

follows directly. This proves  $v(t, x) \leq \bar{v}$ , if initially  $v_0(x) \leq \bar{v}$ .

The nonnegativity property,  $u \geq 0, v \geq 0$ , can be shown with the use of a similar construction. ■

### 2.2. A Priori Estimates

We study first the second equation of (1).

**THEOREM 2.2.** *Assume (2)–(4) and  $p, \sigma, \alpha$  are as given in (8). Then solutions  $(u, v) \in \mathcal{X}_u \times \mathcal{X}_v$ , with  $(u(t, x), v(t, x)) \in \Gamma$ , of (1) satisfy*

$$\|v\|_{\mathcal{X}_v} \leq \|v_0\|_{\sigma+\alpha, p} + C_0 t_0^{1-h} (\|u\|_{\mathcal{X}_u} + \|u\|_{\mathcal{X}_u}^2 + \|v\|_{\mathcal{X}_v}), \tag{10}$$

where  $h = \frac{1}{2}(\sigma + \alpha - 1)$  and the constant  $C_0 > 0$  depending as

$$C_0 = C_0(\sigma, \alpha, p, \bar{u}, \|g_1\|_{C^1(\Gamma)}). \tag{11}$$

*Proof.* With the use of semigroup notation  $T_\mu(t) := e^{\mu\Delta t}$ , we can write the solution of  $v_t = \mu\Delta v + g(u, v)$ ,  $v(0, x) = v_0(x)$  formally as

$$\begin{aligned} v(t) &= T_\mu(t)v_0 + \int_0^t T_\mu(t-s)g_1(u, v)u \, ds - \int_0^t T_\mu(t-s)g_2(u, v)v \, ds \\ &\leq T_\mu(t)v_0 + \int_0^t T_\mu(t-s)g_1(u, v)u \, ds. \end{aligned} \tag{12}$$

Here we have made use of  $g_2 \geq 0, v \geq 0$  and the fact that  $T_\mu(t)$  is positive. From Lemma 2.1, we obtain  $T_\mu(t): W^{1,p} \rightarrow W^{\sigma+\alpha,p}$  with norm  $Ct^{-h}$ , where  $h := \frac{1}{2}(\sigma + \alpha - 1)$  and  $C = C(\sigma, \alpha)$ . From the assumptions on  $\sigma$  and  $\alpha$  it follows that  $0 < h < 1$ . Then we obtain (suppressing the arguments  $(t, x)$  or  $(s, \cdot)$  of the dependent functions  $u, v$ )

$$\begin{aligned} \|v\|_{\mathcal{X}_v} &\leq \|v_0\|_{\sigma+\alpha,p} + \sup_{0 \leq t \leq t_0} \int_0^t \|T_\mu(t-s)g_1(u, v)u\|_{\sigma+\alpha,p} ds \\ &\leq \|v_0\|_{\sigma+\alpha,p} + Ct_0^{1-h} \sup_{0 \leq t \leq t_0} \|g_1(u, v)u\|_{1,p} \\ &\leq \|v_0\|_{\sigma+\alpha,p} + Ct_0^{1-h} \sup_t \{ \|g_1 u\|_p + \|(g_1)_u \nabla uu\|_p \\ &\qquad\qquad\qquad + \|(g_1)_v \nabla v u\|_p + \|g_1 \nabla u\|_p \} \end{aligned} \tag{13}$$

$$\begin{aligned} &\leq \|v_0\|_{\sigma+\alpha,p} + Ct_0^{1-h} \|g_1\|_{C^1(\Gamma)} \sup_t \{ \|u\|_p + \|u \nabla u\|_p \\ &\qquad\qquad\qquad + \|u \nabla v\|_p + \|\nabla u\|_p \}. \end{aligned} \tag{14}$$

Since  $\sigma > 1$ , we have  $\|u\|_p + \|\nabla u\|_p \leq \|u\|_{\sigma,p}$ . From Hölder’s inequality it follows that  $\|u \nabla u\|_p \leq C \|u\|_{\sigma,p}^2$  and  $\|u \nabla v\|_p \leq \|u\|_{\tilde{p},p} \|v\|_{1,\tilde{q},p}$  for some  $\tilde{p}^{-1} + \tilde{q}^{-1} = 1$ . To obtain the Sobolev imbedding  $W^{2,p} \rightarrow W^{1,\tilde{q},p}$ , we choose  $1 \leq \tilde{q} \leq \frac{n}{n-p}$ . Finally, from the existence of an invariant region  $\Gamma$ , it follows that there is a constant  $C > 0$  such that  $\|u\|_{\tilde{p},p} \leq C\bar{u}$ , where  $C = C(\tilde{q}, p)$ . This gives  $\|u \nabla v\|_p \leq C\bar{u} \|v\|_{2,p}$ . Collecting these together, (10) follows from (14). ■

With this estimate, we can derive several auxiliary inequalities which will be useful in the sequel.

COROLLARY 2.1. *Assume the conditions of the above theorem.*

1. *For a choice of  $t_0 \leq (1/2C_0)^{1/(1-h)}$ , we obtain*

$$\|v\|_{\mathcal{X}_v} \leq C_1 (\|v_0\|_{\sigma+\alpha,p} + \|u\|_{\mathcal{X}_u} + \|u\|_{\mathcal{X}_u}^2), \tag{15}$$

where  $C_1 = 2 \max\{1, C_0 t_0^{1-h}\}$ .

2. *For the contraction mapping argument later we require the following. Given two functions  $\varphi_1, \varphi_2 \in \mathcal{X}_u$ , the corresponding solutions  $v_j = v_j(\varphi_j)$  of  $v_{j,t} = \mu \Delta v_j + g(\varphi_j, v_j)$ ,  $v_j(0) = v_0$ , for  $j = 1, 2$ , satisfy*

$$\|v_1 - v_2\|_{\mathcal{X}_v} \leq C_2 \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \tag{16}$$

for some constant  $C_2(C_0, \bar{v}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u}, t_0) > 0$  for sufficiently small  $t_0$  (e.g., it satisfies (17)).



*Proof.* The estimate (15) follows directly from (10) through the specific choice of  $t_0$ . To show (16), we consider the difference  $\Psi := v_1 - v_2$ . This satisfies

$$\Psi_t = \mu \Delta \Psi + g(\varphi_2, v_2) \Psi + (G_1 - G_2)v_1, \quad \Psi(0) = 0,$$

where  $G_i = g(\varphi_i, v_i)$ ,  $i = 1, 2$ . For  $\Psi$ , estimate (14) must be supplemented by the term

$$+ Ct_0^{1-h} \sup_t \|(G_1 - G_2)v_1\|_p \leq Ct_0^{1-h} \|g\|_{C^1(\Gamma)} (\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} + \|v_1 - v_2\|_{\mathcal{X}_v}) \|v_1\|_p.$$

From the existence of the invariant region  $\Gamma$  we have  $\|v_1\|_p \leq C_p \bar{v}$ . The quadratic term in (14) can be estimated as

$$\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}^2 \leq (\|\varphi_1\|_{\mathcal{X}_u} + \|\varphi_2\|_{\mathcal{X}_u}) \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}.$$

Then it follows that

$$\|v_1 - v_2\|_{\mathcal{X}_v} \leq Ct_0^{1-h} (\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} + \|v_1 - v_2\|_{\mathcal{X}_v}).$$

Assuming

$$t_0 \leq \left(\frac{1}{2C}\right)^{1/(1-h)}, \tag{17}$$

we obtain (16) with an appropriate  $C$ . ■

*Remark.* If, moreover,  $(g_1)_u = 0$  (which includes the linear functional  $g_0 = \gamma u - \delta v$ ), then

$$\|v\|_{\mathcal{X}_v} \leq C_1 (\|v_0\|_{\sigma+\alpha, p} + \|u\|_{\mathcal{X}_u}). \tag{18}$$

Under the condition  $(g_1)_u = 0$ , the term containing  $u \nabla u$  in (13) vanishes identically, and the corresponding term  $\|u\|_{\mathcal{X}_u}^2$  in estimate (10) also vanishes and (18) follows from (15).

We now proceed with our analysis by attending to the first equation of (1).

**THEOREM 2.3.** *Assume (2)–(4) and  $p, \sigma, \alpha$  as given by (8). For solutions  $(u, v) \in \mathcal{X}_u \times \mathcal{X}_v$  of (1) with values in  $\Gamma$ , there exist constants  $C_3, C_4, C_5$  (given by (33)) such that*

$$\begin{aligned} \|u\|_{\mathcal{X}_u} \leq & 2 \left( \|u_0\|_{\sigma, p} + C_3 t_0^{1-\sigma/2} \|v\|_{\mathcal{X}_v} + C_4 t_0^{1-b} \|v\|_{\mathcal{X}_v}^2 \right. \\ & \left. + C_5 t_0^{\sigma(1-c)/(\sigma-1)} \|v\|_{\mathcal{X}_v}^{\sigma/(\sigma-1)} \right), \end{aligned} \tag{19}$$

where

$$b = \frac{n}{2p} + \frac{\sigma}{2}, \quad c = \frac{n(\sigma-1)}{2p} + \frac{\sigma}{2}. \tag{20}$$

*Proof.* We again use the semigroup approach,  $T(t) = e^{\Delta t}$ , to solve for  $u$ ,

$$u(t) = T(t)u_0 - \int_0^t T(t-s)V(u, v)\Delta v ds, \tag{21}$$

$$- \int_0^t T(t-s)V_v(u, v)(\nabla v)^2 ds \tag{22}$$

$$- \int_0^t T(t-s)V_u(u, v)\nabla u \nabla v ds, \tag{23}$$

where  $V_u, V_v$  denote the partial derivatives of  $V$  with respect to  $u, v$ , respectively. We assume  $v \in \mathcal{X}_v$  and consider these three terms separately.

Term (21). We use the regularity Lemma 2.1 for

$$T(t): L^p \rightarrow W^{\sigma,p} \quad \text{with norm } C_\sigma t^{-\sigma/2} \tag{24}$$

and obtain

$$\begin{aligned} \left\| \int T(t-s)V \Delta v ds \right\|_{\sigma,p} &\leq C_\sigma t_0^{1-\sigma/2} \sup_{0 \leq t \leq t_0} \|V \Delta v\|_p \\ &\leq C_\sigma t_0^{1-\sigma/2} \|V\|_\Gamma \sup_{0 \leq t \leq t_0} \|v(t, \cdot)\|_{2,p}, \end{aligned} \tag{25}$$

where  $C_\sigma = C_\sigma(\sigma, p)$  and  $\|V\|_\Gamma$  denotes the supremum norm on  $\Gamma \subset \mathbb{R}^2$ .

Term (22). Here we use the regularity Lemma 2.1 for

$$T(t): L^{p/2} \rightarrow W^{\sigma,p} \quad \text{with norm } C_b t^{-b}, \tag{26}$$

where  $b$  is given in (20). From the parameter conditions (8) it follows that  $b < 1$ . We obtain

$$\begin{aligned} \left\| \int T(t-s)V_v(\nabla v)^2 ds \right\|_{\sigma,p} &\leq C_b t_0^{1-b} \sup_{0 \leq t \leq t_0} \|V_v(\nabla v)^2\|_{p/2} \\ &\leq C_b t_0^{1-b} \|V_v\|_\Gamma \sup_{0 \leq t \leq t_0} \|v(t, \cdot)\|_{1,p}^2. \end{aligned} \tag{27}$$

Term (23). It turns out to be much more difficult to obtain an appropriate estimate for the product  $\nabla u \nabla v$ . We start by using Young's inequality to get

$$\begin{aligned} \|\nabla u \nabla v\|_{p/\sigma} &\leq \left\| \frac{\varepsilon}{\sigma}(\nabla u)^\sigma + \frac{1}{q\varepsilon^{q/\sigma}}(\nabla v)^q \right\|_{p/\sigma} \\ &\leq \frac{\varepsilon}{\sigma} \|u\|_{1,p}^\sigma + \frac{1}{q\varepsilon^{q/\sigma}} \|\nabla v\|_{p/(\sigma-1)}^{\sigma/(\sigma-1)}, \end{aligned}$$

where  $q = \frac{\sigma}{\sigma-1}$  and some  $\varepsilon > 0$ . We use the interpolation inequality ([30, p. 22, Proposition 6.2])

$$\|u\|_{\theta\sigma, p} \leq C(\theta)\|u\|_{\sigma, p}^{\theta}\|u\|_p^{1-\theta}$$

for  $\theta \in (0, 1)$ . If we choose  $\theta = \sigma^{-1}$ , we get

$$\|u\|_{1, p}^{\sigma} \leq C(\sigma)\|u\|_{\sigma, p}\|u\|_p^{\sigma-1}. \quad (28)$$

As  $\Gamma$  is a bounded invariant region, there exists a constant  $C = C(p, \sigma)$  such that

$$\|u\|_p^{\sigma-1} \leq C\bar{u}^{\sigma-1}. \quad (29)$$

Finally we use  $T(t): L^{p/\sigma} \rightarrow W^{\sigma, p}$  with norm  $C_c t^{-c}$ , where  $c$  is as given in (20). It is easily verified from (8) that  $c < 1$ . Thus

$$\begin{aligned} & \left\| \int_0^t T(t-s)V_u \nabla u \nabla v \, ds \right\|_{\sigma, p} \\ & \leq C_c t_0^{1-c} \sup_{0 \leq t \leq t_0} \|(V_u \nabla u \nabla v)(t, \cdot)\|_{p/\sigma} \\ & \leq C_c t_0^{1-c} \|V_u\|_{\Gamma} \sup_{0 \leq t \leq t_0} \left( \frac{\varepsilon}{\sigma} \|u\|_{\sigma, p} \bar{u}^{\sigma-1} + \frac{1}{q\varepsilon^{q/\sigma}} \|\nabla v\|_{p/(\sigma-1)}^{\sigma/(\sigma-1)} \right) \\ & \leq C_6 t_0^{1-c} \|V_u\|_{\Gamma} \left( \frac{\varepsilon}{\sigma} \|u\|_{\mathcal{X}_u} + \frac{1}{q\varepsilon^{q/\sigma}} \|v\|_{\mathcal{X}_v}^{\sigma/(\sigma-1)} \right), \end{aligned} \quad (30)$$

where  $C_6 = C_6(C_c, \bar{u})$ .

We collect estimates (25, 27, 30):

$$\begin{aligned} \|u\|_{\mathcal{X}_u} & \leq \|u_0\|_{\sigma, p} + C_{\sigma} t_0^{1-\sigma/2} \|V\|_{\Gamma} \|v\|_{\mathcal{X}_v} + C_b t_0^{1-b} \|V_v\|_{\Gamma} \|v\|_{\mathcal{X}_v}^2 \\ & \quad + C_6 t_0^{1-c} \|V_u\|_{\Gamma} \left( \frac{\varepsilon}{\sigma} \|u\|_{\mathcal{X}_u} + \frac{1}{q\varepsilon^{q/\sigma}} \|v\|_{\mathcal{X}_v}^{\sigma/(\sigma-1)} \right). \end{aligned} \quad (31)$$

For given  $t_0 > 0$  we choose

$$\varepsilon = \frac{\sigma}{2t_0^{1-c} \|V_u\|_{\Gamma} C_6}. \quad (32)$$

Then, from (30), estimate (19) follows with constants  $C_3, C_4, C_5$  given by

$$C_3 = C_{\sigma} \|V\|_{\Gamma}, \quad C_4 = C_b \|V_v\|_{\Gamma}, \quad C_5 = C_6 \left( \frac{2\|V_u\|_{\Gamma} C_6}{\sigma} \right)^{\frac{1}{\sigma-1}}. \quad (33)$$

■

### 2.3. Local Existence

**THEOREM 2.4.** *Assume (2)–(4) and  $p, \sigma, \alpha$  as given by (8). For each initial datum  $u_0 \in W^{\sigma,p}$ ,  $v_0 \in W^{\sigma+\alpha,p}$  with  $(u_0(x), v_0(x)) \in \Gamma$  for all  $x \in \mathcal{M}$ , there exists a  $t_0 > 0$  and a unique solution  $(u, v) \in \mathcal{X}_u \times \mathcal{X}_v$  of (1).*

*Proof.* We use a fixed-point argument. Consider  $\varphi \in \mathcal{X}_u$  with  $\varphi(0) = u_0$  and let  $v = v(\varphi)$  denote the corresponding solution of the  $v$ -equation:

$$v_t = \mu \Delta v + g(\varphi, v), \quad v(0) = v_0. \tag{34}$$

For this  $v$  we define  $u = u(v(\varphi))$  to be the corresponding solution of

$$u_t = \nabla(\nabla u - V(u, v)\nabla v), \quad u(0) = u_0 = \varphi(0). \tag{35}$$

These solutions exist from standard theory and the *a priori* estimates (10) and (19). Moreover, the above estimates show that this procedure defines a map  $Q: \mathcal{X}_u \rightarrow \mathcal{X}_u$ ,  $Q\varphi := u(v(\varphi))$ . We first show that for  $t_0$  sufficiently small,  $Q$  maps a ball

$$\mathcal{B}_m := \{\varphi \in \mathcal{X}_u \mid \varphi(t) \in B_m(0), 0 \leq t \leq t_0\}, \quad m := 2\|u_0\|_{\sigma,p} + 1.$$

into itself. Indeed, if we combine the estimates (19) and (15) we obtain

$$\begin{aligned} \|Q\varphi\|_{\mathcal{X}_u} &\leq 2 \left( \|u_0\|_{\sigma,p} + C_3 C_1 t_0^{1-\sigma/2} (\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2) \right) \\ &\quad + C_4 C_1^2 t_0^{1-b} (\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2)^2 \\ &\quad + C_5 C_1^{(\sigma-1)/\sigma} t_0^{\sigma(\sigma-1)/(\sigma-1)} (\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2)^{(\sigma-1)/\sigma} \\ &\leq 2\|u_0\|_{\sigma,p} + 1, \end{aligned}$$

for small enough  $t_0$ .

Now we demonstrate that at small times,  $Q$  is a contraction. Consider  $\varphi_1, \varphi_2 \in \mathcal{X}_u$  and let  $v_i$  for  $i = 1, 2$  denote the corresponding solutions of the  $v$ -equation (34). Then the difference  $Q\varphi_1 - Q\varphi_2$  satisfies

$$Q\varphi_1 - Q\varphi_2 = - \int_0^t T(t-s)(V_1 \Delta v_1 - V_2 \Delta v_2) ds, \tag{36}$$

$$- \int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2) ds \tag{37}$$

$$- \int_0^t T(t-s)(V_{1,u} \nabla u_1 \nabla v_1 - V_{2,u} \nabla u_2 \nabla v_2) ds, \tag{38}$$

where  $V_i := V(\varphi_i, v_i)$  for  $i = 1, 2$  and  $V_{i,u}, V_{i,v}$  denote partial derivatives with respect to  $u$  and  $v$ , respectively. Again we study each term separately.

Term (36). We use (24), (16), and the fact that

$$\sup_{0 \leq \vartheta \leq t} \|V(\varphi_1(\vartheta, \cdot), v_1(\vartheta, \cdot)) - V(\varphi_2(\vartheta, \cdot), v_2(\vartheta, \cdot))\|_\infty \leq \|V_1 - V_2\|_\Gamma.$$

Then for  $t_0$  small enough we get

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_1 \Delta v_1 - V_2 \Delta v_2) ds \right\|_{\sigma, p} \\ & \leq C_\sigma t^{1-\sigma/2} \left( \|V_1 - V_2\|_\Gamma \sup_{0 \leq \vartheta \leq t} \|\Delta v_1(\vartheta, \cdot)\|_p \right. \\ & \quad \left. + \|V_2\|_\Gamma \sup_{0 \leq \vartheta \leq t} \|\Delta v_1 - \Delta v_2\|_p \right) \\ & \leq C t^{1-\sigma/2} \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \end{aligned} \quad (39)$$

where  $C = C(C_2, C_\sigma, \|V\|_{C^1(\Gamma)}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$ .

Term (37). Here we use (26) to obtain

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2) ds \right\|_{\sigma, p} \\ & \leq C t^{1-b} \sup_{0 \leq \vartheta \leq t} \left( \|V_{1,v} - V_{2,v}\|_\Gamma \|(\nabla v_1)^2\|_{p/2} + \|V_{2,v}\|_\Gamma \|(\nabla v_1)^2 \right. \\ & \quad \left. - (\nabla v_2)^2\|_{p/2} \right). \end{aligned}$$

With Hölder's inequality we get

$$\|(\nabla v_1)^2 - (\nabla v_2)^2\|_{p/2} \leq \|\nabla v_1 + \nabla v_2\|_p \|\nabla v_1 - \nabla v_2\|_p.$$

With estimate (16) this leads to

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2) ds \right\|_{\sigma, p} \\ & \leq C t^{1-b} \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \end{aligned} \quad (40)$$

where  $C = C(C_2, C_b, \|V\|_{C^1(\Gamma)}, \|v_1\|_{1,p}, \|v_2\|_{1,p}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$ .

Term (38). Once again, we use (24) and (16),

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_{1,u} \nabla u_1 \nabla v_1 - V_{2,u} \nabla u_2 \nabla v_2) ds \right\|_{\sigma, p} \\ & \leq C t^{1-\sigma/2} \sup_{0 \leq \vartheta \leq t} \{ \|(V_{1,u} - V_{2,u}) \nabla \varphi_1 \nabla v_1\|_p \} \end{aligned} \quad (41)$$

$$+ \|V_{2,u}(\nabla \varphi_1 - \nabla \varphi_2) \nabla v_1\|_p + \|V_{2,u} \nabla \varphi_2 (\nabla v_1 - \nabla v_2)\|_p \}$$

$$\leq C t^{1-\sigma/2} \|V\|_{C^1(\Gamma)} \sup_{0 \leq \vartheta \leq t} \{ \|\nabla \varphi_1\|_p \|\nabla v_1\|_\infty \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} \} \quad (42)$$

$$+ \|\nabla v_1\|_\infty \|\nabla \varphi_1 - \nabla \varphi_2\|_p + \|\nabla \varphi_2\|_p \|\nabla v_1 - \nabla v_2\|_\infty \}$$

$$\leq C t^{1-\sigma/2} \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \quad (43)$$

where  $C = C(C_2, C_\sigma, \|V\|_{C^1(\Gamma)}, \|v_1\|_{\mathcal{X}_v}, \|v_2\|_{\mathcal{X}_v}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$ . ■

### 2.4. Global Existence

In the foregoing estimates we saw that all bounds grow, at most, algebraically in time  $t_0$ . We will use this to show global existence in time. The procedure is standard and uses the successive application of the regularity properties of the heat equation (e.g., as given in Lemma 2.1). Starting from the known  $L^\infty$  estimates (invariant region), we develop higher order estimates for  $v$ , which lead to better estimates for  $u$  and so on. Here we work with an additional set of parameters  $(\tilde{\sigma}, \nu)$  such that one iteration step of this procedure is sufficient. At each iteration we gain an order of  $\tilde{\sigma}$ . For the original parameters  $(\sigma, \alpha)$  we would have had to use more iterations to get the same result.

**THEOREM 2.5.** *Assume (2)–(4) and  $p, \sigma, \alpha$  as given by (8). For each initial datum  $u_0 \in W^{\sigma, p}, v_0 \in W^{\sigma+\alpha, p}$  with  $(u_0(x), v_0(x)) \in \Gamma$  for all  $x \in \mathcal{M}$ , there exists a unique global solution*

$$(u, v) \in C([0, \infty), W^{\sigma, p} \times W^{\sigma+\alpha, p})$$

of (1).

*Proof.* We start with the global  $L^\infty$  estimate (i.e., the invariant region  $\Gamma$ ) to successively derive higher order estimates. For technical reasons we choose parameters  $\tilde{\sigma} > 0$  and  $\nu > 0$  such that

$$2 > \tilde{\sigma} > \max\left\{\sigma, \frac{5}{3}\right\} \tag{44}$$

$$2 - \tilde{\sigma} < \nu < \frac{\tilde{\sigma} - 1}{2} \tag{45}$$

$$1 - \nu + \tilde{\sigma} = \sigma + \alpha. \tag{46}$$

It is easy to check that these three conditions can be simultaneously satisfied.

**LEMMA 2.2.** *There exists a constant  $\kappa_1 = \kappa_1(\tilde{\sigma}, p, \bar{u}, \bar{v}, \|g\|_{C^1(\Gamma)})$  such that the solution of Theorem 2.4 satisfies*

$$\|v\|_{\tilde{\sigma}, p} \leq \|v_0\|_{\tilde{\sigma}, p} + \kappa_1 t_0^{1-\tilde{\sigma}/2} =: K_1(t_0). \tag{47}$$

*Proof.* We consider the solution of the  $v$ -equation as represented by (12), and we use (24) with  $\tilde{\sigma}$  replacing  $\sigma$ . ■

Now, with the use of  $T_\mu(t): W^{1-\nu-\tilde{\sigma}, p} \rightarrow W^{1-\nu, p}$  with norm  $C_{\tilde{\sigma}} t^{-\tilde{\sigma}/2}$ , we obtain from  $u(t) = T(t)u_0 - \int T(t-s)\nabla(V\nabla v)ds$  that

$$\|u(t)\|_{1-\nu, p} \leq \|u_0\|_{1-\nu, p} + C_{\tilde{\sigma}} t^{1-\tilde{\sigma}/2} \sup_{0 \leq \vartheta \leq t} \|\nabla(V\nabla v)\|_{1-\nu-\tilde{\sigma}, p}.$$

Since  $\nu > 2 - \tilde{\sigma}$  we have  $2 - \nu - \tilde{\sigma} < 0$ . Then there is a constant  $C = C(\tilde{\sigma}, \nu)$  such that

$$\|\nabla(V\nabla v)\|_{1-\nu-\tilde{\sigma}, p} \leq C\|V\nabla v\|_{2-\nu-\tilde{\sigma}, p},$$

and we get

$$\begin{aligned} \|u(t)\|_{1-\nu, p} &\leq \|u_0\|_{1-\nu, p} + Ct^{1-\tilde{\sigma}/2} \sup_{0 \leq \vartheta \leq t} \|V\nabla v\|_{2-\nu-\tilde{\sigma}, p} \\ &\leq \|u_0\|_{1-\nu, p} + Ct^{1-\tilde{\sigma}/2} \|V\|_{\Gamma} \sup_{0 \leq \vartheta \leq t} \|v\|_{1, p}. \end{aligned}$$

We apply Lemma 2.2 to show

$$\|u(t)\|_{1-\nu, p} \leq \|u_0\|_{1-\nu, p} + Ct^{1-\tilde{\sigma}/2} \|V\|_{\Gamma} K_1(t_0) =: K_2(t_0).$$

We use this estimate to get a better estimate for  $v$ , as in the previous lemma. Since on the compact set  $\Gamma$  the function  $h(u, v) = g_1(u, v)u$  is uniformly bounded in  $C^2(\Gamma)$ , it follows that the map  $h: W^{1-\nu, p} \rightarrow W^{1-\nu, p}$  is Lipschitz continuous, where the Lipschitz constant is bounded by  $H := \|h\|_{C^2(\Gamma)}$ . Then, from (12), it follows that

$$\begin{aligned} \|v(t)\|_{1-\nu+\tilde{\sigma}, p} &\leq \|v_0\|_{1-\nu+\tilde{\sigma}, p} + \int_0^t \|T_{\mu}(t-s)g_1(u, v)u\|_{1-\nu+\tilde{\sigma}, p} ds \\ &\leq \|v_0\|_{1-\nu+\tilde{\sigma}, p} + Ct^{1-\tilde{\sigma}/2} \sup_{0 \leq \vartheta \leq t} \|g_1(u, v)u\|_{1-\nu, p} \\ &\leq \|v_0\|_{1-\nu+\tilde{\sigma}, p} + Ct^{1-\tilde{\sigma}/2} \sup_{0 \leq \vartheta \leq t} \|h\|_{C^2(\Gamma)} \|u\|_{1-\nu, p} \\ &\leq \|v_0\|_{1-\nu+\tilde{\sigma}, p} + Ct^{1-\tilde{\sigma}/2} HK_2(t_0). \end{aligned} \tag{48}$$

To complete the proof of global existence we use  $1 - \nu + \tilde{\sigma} = \sigma + \alpha$  (46). Then from (48) it follows that

$$\|v\|_{\mathcal{X}_v} \leq \|v_0\|_{\sigma+\alpha, p} + Ct_0^{1-\tilde{\sigma}/2} K_2(t_0) =: K_3(t_0). \tag{49}$$

Hence  $\|v\|_{\mathcal{X}_v}$  grows, at most, algebraically in time with maximal order of  $2 - \tilde{\sigma}$ .

Finally, to estimate  $\|u\|_{\mathcal{X}_u}$ , we consider (30). For each time  $t_0 > 0$  we choose  $\varepsilon = \varepsilon(t_0)$  according to (32) and obtain (19). With the use of (49) we observe that

$$\begin{aligned} \|u\|_{\mathcal{X}_u} &\leq 2\left(\|u_0\|_{\sigma, p} + C_3 t_0^{1-\sigma/2} K_3(t_0) + C_4 t_0^{1-b} K_3(t_0)^2\right. \\ &\quad \left.+ C_5 t_0^{\sigma(1-c)/(\sigma-1)} K_3(t_0)^{(\sigma-1)/\sigma}\right), \end{aligned}$$

which also grows algebraically in time. Global existence in  $\mathcal{X}_u \times \mathcal{X}_v$  follows. ■

### 3. NUMERICAL SIMULATIONS

In this section we consider one- and two-dimensional numerics to the model (1) with chemotactic cross-diffusion  $V(u, v) = \chi u(1 - u)$ . These simulations demonstrate interesting spatial and temporal behavior. Whereas finite-time blow-up of solutions in the classical model (see Figs. 2a and 3a) prevents study of behavior beyond a certain time, here we can study the subsequent interplay between the different maxima (see Fig. 3b) and other pattern phenomena (Fig. 4).

All simulations use model (1) with kinetics given by (7). Initially we set  $u(x, 0) = u_0$  constant and a random spatial perturbation about the homogeneous steady state for the chemical concentration. For simulations we use homogeneous Neumann boundary conditions on an interval in 1-D or in 2-D. These boundary conditions can be arranged into dynamics on the circle or on the 2-torus, respectively. Indeed, one-dimensional simulations with periodic boundary data show no appreciable difference in behavior.

#### 3.1. *One-Dimensional Simulations*

As mentioned previously, our modified system permits the global existence of solutions, enabling exploration of the temporal behavior. Figure 1 shows the space-time evolution for the population density  $u$ . Initially many peaks develop, the wavelength of which can be predicted by a linear stability analysis. In contrast to simulations of Turing systems (where the pattern evolves to a heterogeneous steady state), solutions to the chemotaxis system continue to evolve in a manner leading to the gradual disappearance of the total number of peaks. This occurs either via collision of two peaks into a single one or by the collapse of a single peak. When the simulation is allowed to run for sufficient time, this results in a single boundary peak.

The above behavior is not restricted to the chemotactic velocities considered here. Merging of peaks also occurs for the classical problem, yet the steepening of the peaks creates numerical problems, and a detailed study is difficult.

#### 3.2. *Two Dimensions*

As reported in the Introduction, the behavior in classical models has been shown to depend strongly on the space dimension. In particular, blow-up of solutions occurs in two dimensions for sufficiently strong chemotactic velocities, and a threshold phenomenon is known. The results presented earlier preclude such behavior for the modified model, and we demonstrate this numerically via comparison with the classical case. Figure 2, sequence (a), plots the evolving two-dimensional cell density patterns for  $u\beta(u)\chi(v) = \chi_0 u$ . An aggregation grows in the corner of the domain,



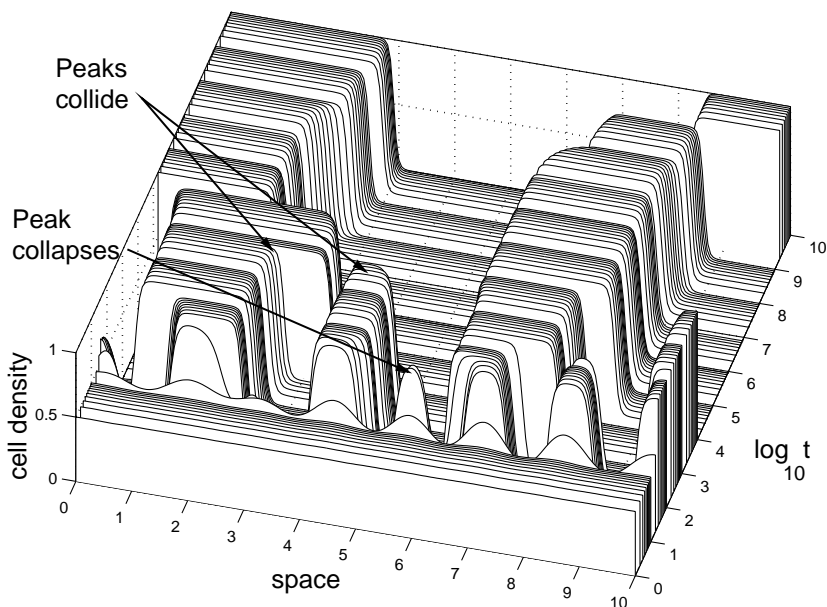


FIG. 1. Time evolution of numerical simulations to the chemotaxis problem with  $\beta(u) = 1 - u$  and  $\chi(v) = 0.5$ . Numerical simulations show a collapse/collision of peaks: examples are illustrated by the arrows. Other parameters and initial conditions are as follows: length = 10.0,  $D_u = 0.025$ ,  $D_v = 0.1$ ,  $\gamma = \delta = 1.0$ ,  $u(x, 0) = 0.5$ . The chemical concentration is initially given a small (1%) random spatial perturbation of its steady-state value (0.5).

eventually blowing up in finite time. In contrast, choosing the modified chemotactic cross-diffusion ( $u\beta(u)\chi(v) = \chi_0 u(U_0 - u)$ ) with the same initial data prevents this behavior, as we would expect from the earlier analysis. Figure 2, sequence (b), shows how the initial aggregations eventually flatten out, forming a globally existing spatial pattern. A comparison of the rate of growth of the maximum cell density, Fig. 2c demonstrates how the two models initially grow at a similar rate before diverging. As one may predict from a linear analysis of the system in the vicinity of the homogeneous solution, domain size has an important role in the number and position of aggregates that develop. In the classical system the blow-up tends to occur on the boundary of the domain, although for larger domain sizes interior blow-ups can also occur, as shown in Fig. 3, sequence (a). Blow-up prevents further numerical study of the solution behavior. However, by using the modified model we can analyze the subsequent interplay between the multiple aggregate peaks. Fig. 3b considers model data identical to that of Fig. 3a, yet using the modified chemotactic cross-diffusion. This example demonstrates how the cell density evolves in time, showing a rearrangement of the pattern consistent with the collapse and collision of the peaks

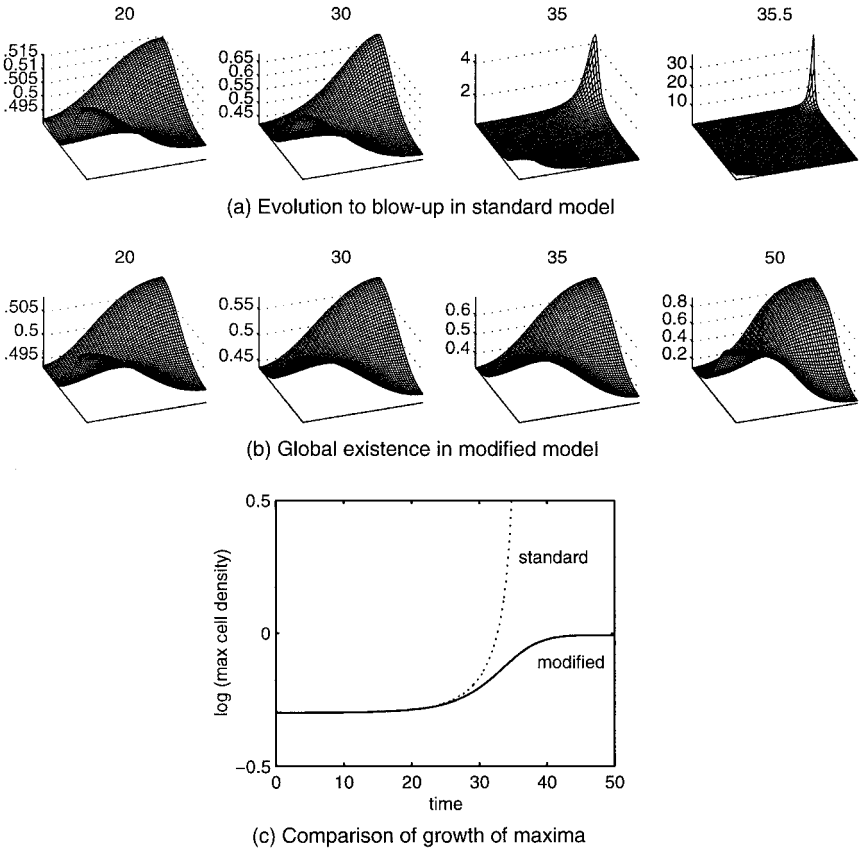


FIG. 2. Comparison of evolving cell density  $u$  in two dimensions for the classical model ((a),  $u\beta(u)\chi(v) = 5u$ ) and the modified model ((b),  $u\beta(u)\chi(v) = 10u(1 - u)$ ). Numerical time is as indicated at the top of the figures. For sufficiently strong chemotactic sensitivities, solutions for the classical model blow up in finite time. Cell densities for the modified model show similar dynamics during early stages, yet the functional form prevents blow-up. (c) Comparison of (log of) maximum particle density as a function of time for sequences (a) and (b). In both sequences we use  $D_u = 1$ ,  $D_v = 1$ ,  $\beta = 1$ ,  $\gamma = \delta = 1$ ,  $u_0 = 0.5$ . Domain dimensions =  $[0, 2\pi] \times [0, 2\pi]$ . Initially we set  $u_0 = 0.5$  and randomly perturb  $v_0$  about its steady state.

observed for the one-dimensional numerics above. Intriguingly, the modified model demonstrates a variety of pattern types under certain parameter modulation. In Fig. 4 we demonstrate how a transition between spotted, striped, and inverted spots can occur under variation of the initial cell density,  $u_0$ . We explore both of the above phenomena more comprehensively, together with implications for biological pattern formation, in a separate paper [22].

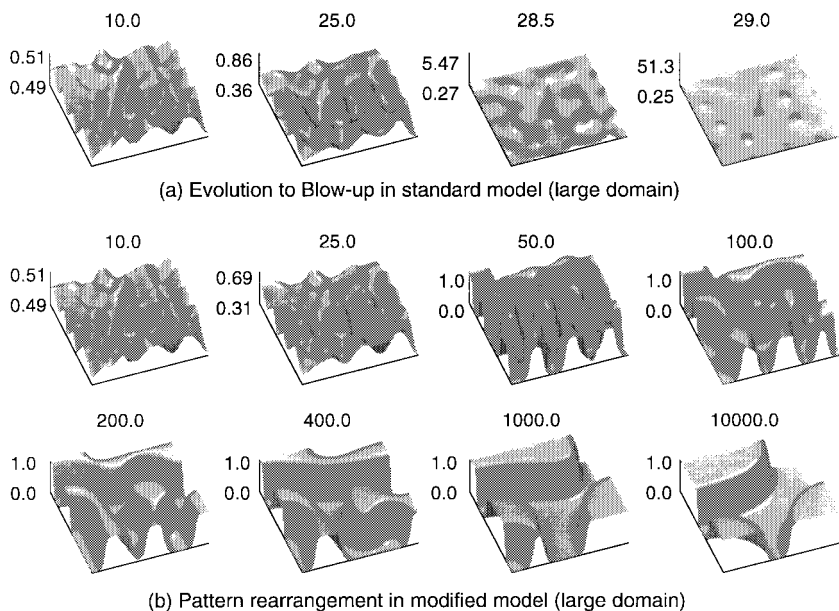


FIG. 3. Comparison of evolving cell density  $u$  in two dimensions for the classical model ((a),  $u\beta(u)\chi(v) = 5u$ ) and the modified model ((b),  $u\beta(u)\chi(v) = 10u(1 - u)$ ), using a larger domain size  $([0, 10\pi] \times [0, 10\pi])$ . Numerical time is as indicated at the top of the figures. For larger domains, multiple aggregates initially develop, yet the finite-time blow-up behavior in the classical model prevents exploration of the subsequent behavior. For the modified model, we observe how the peaks subsequently collapse and coalesce in a manner analogous to the one-dimensional behavior above. Other parameters and initial conditions are as previously.

*Remark 3.1.* The stiffness associated with chemotactic problems requires close attention when the validity of numerical simulations is considered. One-dimensional simulations have been conducted using two separate methods, with a variety of space and time discretizations. Two-dimensional simulations have been performed using an alternating direction implicate (ADI) method

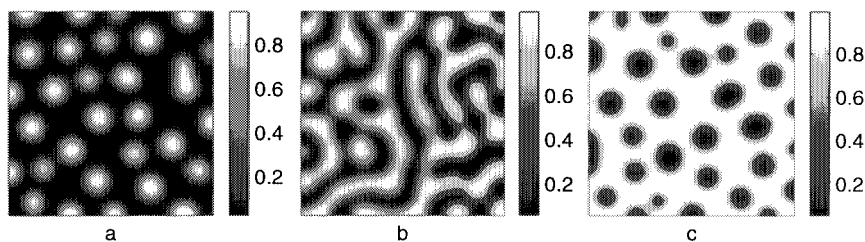


FIG. 4. A variety of pattern types demonstrated by the modified model under variation of the initial cell density,  $u_0$ . (a)  $u_0 = 0.25$ ; (b)  $u_0 = 0.5$ ; (c)  $u_0 = 0.75$ . A transition between spotted, striped, and inverse spots is observed. Parameters and initial conditions are as for the previous figure with the domain size  $[0, 20\pi] \times [0, 20\pi]$ .

augmented by an upwind scheme to calculate the chemotactic components. All 2-D simulations have been checked with a variety of mesh and time discretizations.

#### 4. DISCUSSION

To prevent misunderstanding, the aim of this paper is not to oppose those publications focusing on finite-time blow-up of chemotaxis systems. Rather, we hope that this provides a continuation of the stimulating analysis of such systems that may yield useful insights into additional phenomena, for example, long-time behavior. Historically, the mathematical analysis of chemotaxis systems was partly motivated by the question of whether the models of Patlak [23] and Keller and Segel [12] are able to show strong aggregational tendencies and thus are candidates for population models of grouping in cells or organisms. Indeed, it was possible to prove the existence of solutions which blow up in finite time. A number of mathematical directions have developed from the early studies (for example, Nanjundiah [20], Childress and Percus [5, 6], Jäger and Luckhaus [11], and Nagai [15]). One question concerns the form of blow-up and the problem of continuation after blow-up [9]. Another aspect relates to the variety of functional forms for the chemotactic sensitivity ( $\chi(v)$  in our notation). Certain choices will lead to global existence (see the references given in the Introduction). Our ansatz relates the local particle density to the chemotactic sensitivity (via  $\beta(u)$ ), and, under realistic assumptions, global existence follows. These results on global existence address the question of what patterns evolve and the dynamic behavior observed. Our numerical investigations emphasize interesting phenomena such as “tabletop” peaks and merging peaks in one dimension and coarsening in two dimensions.

Our observation that different peaks merge or disappear reflects the parabolic nature of the model. Due to long-range interactions, all peaks interact with all others. It would be interesting to consider how the same conditions with the hyperbolic chemotaxis model of Hillen and Stevens [10] compare with those of the parabolic system. The hyperbolic model has a finite range of interaction of peaks such that coexistence and stability of smaller peaks may be possible.

The results on global existence presented here place a number of restrictions on various aspects of the model (e.g., form of chemotactic cross-diffusion, form of initial conditions). Although a variety of plausible biological mechanisms can be considered which give rise to the class of models considered here (see [22]), an important future goal is to extend the existence results to more general models for chemotaxis. Chemotactic behavior is a highly complicated process, with a variety of different

factors contributing to the movement response. Consequently, models incorporating different factors can lead to a wide class of parabolic PDE systems. An understanding of the model classes either leading or not leading to global existence would improve understanding of the relative importance of the different factors.

The derivation of our model relies on the hypothesis that populations (e.g., of bacteria) possess some form of regulatory mechanism which allows them to control the size of the aggregate. Indeed, as previously mentioned, such behavior is crucial for populations such as *Dictyostelium*, which accumulate into fruiting bodies of up to  $10^5$  cells. Of course, while we have considered a regularity mechanism of the bacteria themselves, more physical models could be developed which allow limiting of the population size. For example, cells may be repelled by neighbors when they come too close. Many biological systems use quorum sensing systems to regulate behavior, and failure of such mechanisms can result in abnormal functioning. Other derivations for incorporating a density effect in the movement may simply rely on space considerations—only a finite number of particles can fit into a certain volume. We explore the derivation and behavior of different models in a second paper [22].

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