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MODELING CONTACT INHIBITION OF GROWTH: TRAVELING WAVES

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Abstract. We consider a simplified 1-dimensional PDE-model describing the effect of contact inhibition in growth processes of normal and abnormal cells. Varying the value of a significant parameter, numerical tests suggest two different types of contact inhibition between the cell populations: the two populations move with constant velocity and exhibit spatial segregation, or they stop to move and regions of coexistence are formed. In order to understand the different mechanisms, we prove that there exists a segregated traveling wave solution for a unique wave speed, and we present numerical results on the "stability" of the segregated waves. We conjecture the existence of a non-segregated standing wave for certain parameter values.

1. **Introduction.** It is observed in many types of cells *in vitro* and *vivo* that when two different types of cells touch each other, their rates of mobility and proliferation decrease. This phenomenon is called contact inhibition of growth between cells (see for example [20]). For a better theoretical understanding of the mechanism of contact inhibition between normal and abnormal cells, several mathematical models have been proposed so far (see for example [8]; abnormal cells are typically those which, potentially, become tumor cells at a later stage). In [2] we have proposed a simple PDE model for contact inhibition which describes the interaction of normal and abnormal cell growth. This model includes the effect of pushing cells away from overcrowded regions, where they feel pressed: cells move in the direction of lower overall cell density. If the average sizes of the two cells are not equal, the pressure from one cell to the other is not necessarily the same. More precisely, if n and a

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denote the densities of normal and abnormal cells, respectively, the resulting model is

$$\begin{cases} n_t = d_1 \operatorname{div}(n\nabla(n+\alpha_m a)) + \gamma_1\left(1-\dfrac{n+\alpha_g a}{k_1}\right)n \\ a_t = d_2 \operatorname{div}(a\nabla(n+\alpha_m a)) + \gamma_2\left(1-\dfrac{n+\alpha_g a}{k_2}\right)a, \end{cases} \tag{1}$$

where d_i, γ_i, k_i $(i=1,2)$, α_g and α_m are positive constants. In ecology the growth terms are known as "of Lotka-Volterra competition type". Replacing $\alpha_m a$ by a and setting $d = d_2/d_1$, $\gamma = \gamma_2/\gamma_1$, $\alpha = \alpha_g/\alpha_m$ and $k = k_2/k_1$, suitable rescaling transforms (1) into

$$\begin{cases} n_t = \operatorname{div}\big(n\nabla(n+a)\big) + \big(1-(n+\alpha a)\big)n \\ a_t = d\operatorname{div}\big(a\nabla(n+a)\big) + \gamma\left(1-\dfrac{n+\alpha a}{k}\right)a. \end{cases} \tag{2}$$

We stress that systems (1) and (2) are equivalent. In the absence of a, the first equation of (2) reduces to

$$n_t = \operatorname{div}(n\nabla n) + (1-n)n, \tag{3}$$

the so-called nonlinear degenerate Kolmogorov-Petrovsky-Piskunov (KPP) or Fisher equation ([1], [10], [16], [17], [19]). If the initial function $n(x,0)$ is nonnegative and bounded and has compact support, the spatial support of the solution $n(x,t)$ of (3) expands with finite propagation. Similarly, this property holds for the equation for a in the absence of n:

$$a_t = d\operatorname{div}(a\nabla a) + \gamma\Big(1-\frac{\alpha}{k}a\Big)a. \tag{4}$$

Therefore, if the compact supports of the initial functions $n(x,0)$ and $a(x,0)$ are distinct and nonempty, the spatial supports of the solutions $n(x,t)$ and $a(x,t)$ of (2) expand and touch each other at a certain time. Numerical evidence shows that also at all later times the populations remain segregated. Partial analytical support for the existence of such "segregated solution" was provided in [2] (in case of spatial dimension 1) and [3] (in the higher dimensional case, if $d=1$), but only with the additional assumption that $n(x,0)+a(x,0)$ is strictly positive. In the one-dimensional case it is possible to remove this additional assumption ([4]; see section 2 of the present paper for a precise statement).

In this paper we focus on the one-dimensional case and consider the system in an interval, $(-L,L)$:

$$\begin{cases} n_t = (n(n+a)_x)_x + \big(1-(n+\alpha a)\big)n \\ a_t = d(a(n+a)_x)_x + \gamma\Big(1-\dfrac{n+\alpha a}{k}\Big)a \end{cases} \qquad -L<x<L,\ t>0, \tag{5}$$

with initial and boundary conditions

$$n(x,0)=n_0(x)\ge 0 \quad\text{and}\quad a(x,0)=a_0(x)\ge 0 \quad \text{for } x\in(-L,L), \tag{6}$$

$$n(n+a)_x(\pm L,t) = a(n+a)_x(\pm L,t) = 0 \quad \text{for } t>0. \tag{7}$$

Often we shall assume that

$$k>1.$$

In Figures 1 and 2 we show a numerical simulation of problem (5)-(7), with $L=30$, $d=\gamma=\alpha=1$ and $k=2$. Initially the populations of normal and abnormal cells are segregated, and when the populations come in contact, a new interface appears. This confirms the segregation of the populations which we have discussed above. Figure 2 shows the interfacial curves indicating the separation of the two populations in the (x,t)-plane. Observe that the new interface seems to move with constant velocity, which suggests the possible existence of a *segregated traveling wave* (defined on the whole real line). Its spatial profile is suggested by Figure 1.

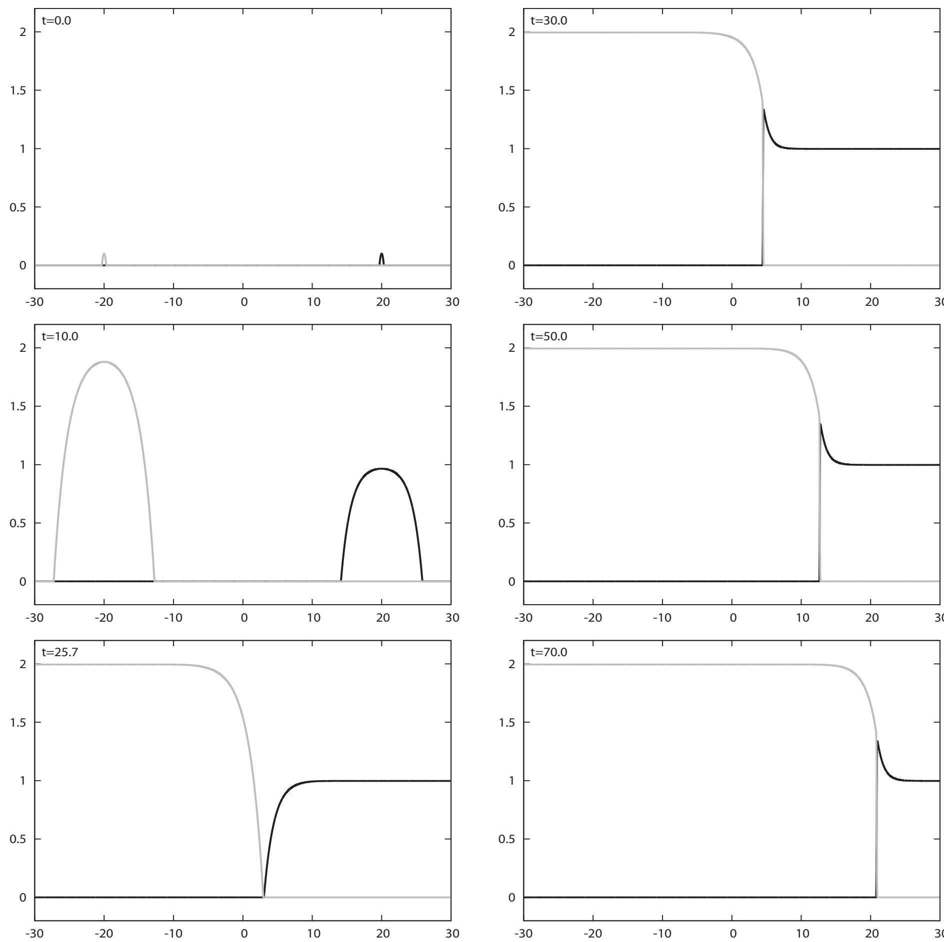

FIGURE 1. Numerical results of (5)-(7) with $L = 30$, $d = \gamma = \alpha = 1$ and $k = 2$; black curves correspond to n, gray curves to a.

Our main result is stated in section 3: the existence of a segregated traveling wave which is unique up to translation (proofs will be given in section 5). In section 4 we discuss the "stability" of the segregated waves, introducing small perturbations which destroy the complete segregation of the initial data $n(x,0)$ and $a(x,0)$. Analytically it is known ([2], [3]) that, if $d = 1$, problem (5)-(7) has a solution also for such perturbed initial data. Since we do not know if the solution of the problem (5)-(7) is unique, we are not able to discuss the concept of stability of the segregated traveling wave rigorously. Numerical evidence suggests that for certain parameter values the segregated traveling wave is "more stable" than for other values. In this sense the numerical results in section 4 should be interpreted as useful hints for further research. In particular they suggest, for certain parameter values, an entirely

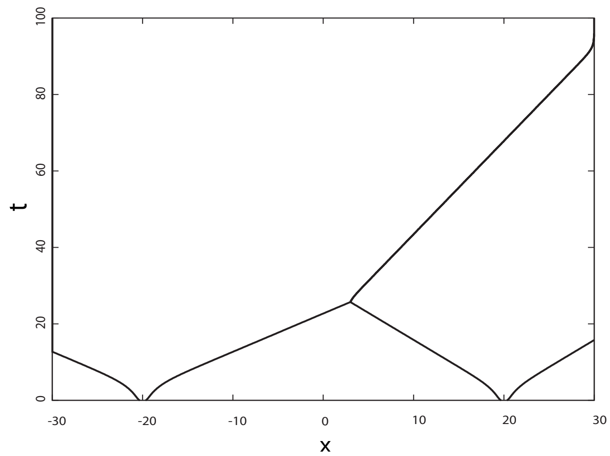

FIGURE 2. Numerical interfaces arising in Figure 1 in (x, t)- space.

new phenomenon: the existence of *standing wave*, an issue which will be discussed in a future paper ([6]).

2. **Contact inhibition: A free boundary problem.** In this section we recall some properties of segregated solutions, (n, a), of problem (5)-(7), which generalize some of the results in [2]. We assume that n and a are initially segregated: n_0 and a_0 are continuous and nonnegative functions defined in $[-L, L]$ and, for some $-L \le \ell_1 < \ell_2 < \ell_3 < \ell_4 \le L$,

$$\operatorname{supp} a_0 = [\ell_1, \ell_2], \quad \operatorname{supp} n_0 = [\ell_3, \ell_4]. \tag{8}$$

Calling $t_0 > 0$ the time at which the spatial supports of n and a touch each other, say at $x_0 \in (-L, L)$, n and a satisfy two KPP-equations for $t < t_0$. In [4] we shall prove that this solution can be continued for $t > t_0$, and at $t = t_0$ an interface $x = s(t)$ appears which separates the two populations and across which both n and a are discontinuous:

Proposition 1. *Let n_0 and a_0 be continuous and nonnegative functions on $[-L, L]$ which satisfy (8). Then there exist bounded nonnegative functions, n and a, defined on $[-L, L] \times [0, \infty)$, which solve problem (5)-(7) in the following sense: there exist $x_0 \in [\ell_2, \ell_3]$, $t_0 > 0$ and a continuous function $s : [0, \infty) \to (-L, L)$ such that*

- *(i) $s(t) = x_0$ if $0 \le t \le t_0$;*
- *(ii) n and a are continuous in $[-L, L] \times [0, \infty) \setminus \{(s(t), t), t > t_0\}$;*
- *(iii) $a = 0$ in $\mathcal{P}_+ := \{(x, t), s(t) < x < L, t > 0\}$, and n is a weak solution of the equations $n_t = (nn_x)_x + n(1 - n)$ in $\mathcal{P}_+$ and $nn_x(L, t) = 0$ for $t > 0$;*
- *(iv) $n = 0$ in $\mathcal{P}_- := \{(x, t), -L < x < s(t), t > 0\}$, and a is a weak solution of the equations $a_t = d(aa_x)_x + \gamma a(1 - a/k)$ in $\mathcal{P}_-$ and $aa_x(-L, t) = 0$ for $t > 0$;*
- *(v) $a(s(t)^-, t) = n(s(t)^+, t) > 0$ if $t > t_0$;*
- *(vi) $s \in C^1((0, \infty) \setminus \{t_0\})$ and $s'(t) = -n_x(s(t)^+, t) = -da_x(s(t)^-, t)$ if $t > 0$, $t \ne t_0$;*
- *(vii) $n(x, 0) = n_0(x)$ and $a(x, 0) = v_0(x)$ if $-L \le x \le L$.*

We call such a solution (n, a) a segregated solution of problem (5)-(7).

Proposition 1 shows that segregated solutions can be viewed as the solution of a free boundary problem: (v) and (vi) are the free boundary conditions.

3. **Segregated traveling waves.**

In this section we present our main result: the existence and uniqueness (up to translation) of a segregated traveling wave, as was suggested by the numerical test described in the introduction.

Let $x \in (-\infty, \infty)$ and set $z = x - ct$ for some constant c, the *wave speed*. We look for a segregated solution of system (5) (with $L = \infty$) which only depends on z:

$$n(x,t) = u(x-ct) \quad \text{and} \quad a(x,t) = v(x-ct).$$

Before stating the result for the system of equations, we recall the results for the scalar problem

$$\begin{cases} d(vv')' + cv' + \gamma\left(1 - \frac{\alpha}{k}v\right)v = 0 & \text{in } (-\infty,\infty) \\ v(-\infty) = k/\alpha, \quad v(\infty) = 0. \end{cases} \tag{9}$$

It is well known that there exists $c^* > 0$ such that problem (9) has a solution if and only if $c \geq c^*$ (see for example [1]). If $c \geq c*$, the solution is translation invariant and satisfies $0 \leq v(z) < k/\alpha$. If $c > c^*$ the solution is smooth and strictly positive. If instead $c = c^*$, the solution is compactly supported from the right: the traveling wave solution with minimal velocity c^* exhibits a sharp traveling front. Moreover there are explicit formula's for c^* and the corresponding traveling wave v^*:

$$v^*(z) = \frac{k}{\alpha}\left[1 - \exp\left(\sqrt{\frac{\gamma\alpha}{2dk}}z\right)\right]_+ \quad \text{and} \quad c^* = \sqrt{\frac{d\gamma k}{2\alpha}}, \tag{10}$$

where $[y]_+$ denotes the positive part of y.

It is well known that traveling waves are useful to describe the large-time profile of a solution $v(x,t)$ of the corresponding PDE (4), with $x \in (-\infty,\infty)$. For example, if the (nonnegative) initial function a_0 satisfies

$$a_0(x) > 0 \text{ if and only if } x < s_0, \text{ and } \liminf_{x\to-\infty} a_0(x) > 0,$$

then $a(x,t)$ converges, as $t \to \infty$, to a spatial translation of the traveling wave with minimal wave speed, $v^*(x - c^*t)$ ([7], [15]). Observe that in this case $v(x,t) > 0$ if and only if $x < s(t)$ for some continuous interface $x = s(t)$ (with $s(0) = s_0$).

Similarly, the scalar traveling wave problem

$$\begin{cases} (uu')' + cu' + (1-u)\,u = 0 & \text{in } (-\infty,\infty) \\ u(-\infty) = 0, \quad u(\infty) = 1. \end{cases} \tag{11}$$

has a solution if and only if $c \leq c_*$ and

$$c_* = -\frac{1}{\sqrt{2}}. \tag{12}$$

Now we are ready to formulate our result for the segregated traveling wave of our system. By translation invariance we may assume that the interface which separates the two populations corresponds to $z = 0$: $x = s(t) = ct$ and

$$u(z) = 0,\ v(z) > 0 \quad \text{if } z < 0, \qquad u(z) > 0,\ v(z) = 0 \quad \text{if } z > 0.$$

The natural conditions at $\pm\infty$ are

$$u(\infty) = 1 \quad \text{and} \quad v(-\infty) = \frac{k}{\alpha},$$

and the free boundary conditions (v) and (vi) in Proposition 1 translate into

$$u(0^+) = v(0^-) > 0 \quad \text{and} \quad c = -u'(0^+) = -dv'(0^-).$$

This leads to the problem

$$\begin{cases} (uu')' + cu' + (1-u)u = 0 & \text{in } (0,\infty) \\ u(0^+) = h, \quad u'(0^+) = -c \\ u(\infty) = 1, \quad u > 0 \text{ in } (0,\infty), \end{cases} \tag{13}$$

and

$$\begin{cases} d(vv')' + cv' + \gamma\left(1 - \dfrac{\alpha}{k}v\right)v = 0 & \text{in } (-\infty,0) \\ v(0^-) = h, \quad dv_z(0^-) = -c \\ v(-\infty) = k/\alpha, \quad v > 0 \text{ in } (-\infty,0), \end{cases} \tag{14}$$

where c is a real constant and $h > 0$ is a free matching parameter (i.e., (u, v) is a solution if (13) and (14) are satisfied for some $h > 0$).

Theorem 3.1. *Let d, γ, α and k be positive constants. Then there exists a unique wave speed c such that problem (13)-(14) has a solution $(u(z), v(z))$. In addition*

(i) the solution $(u(z), v(z))$ is unique;
(ii) $c_* < c < c^*$, where c^* and c_* are defined by (10) and (12);
(iii) $c > 0$ if $k/\alpha > 1$, $c < 0$ if $0 < k/\alpha < 1$ and $c = 0$ if $k/\alpha = 1$.

The proof of a slightly more general version of Theorem 3.1 will be given in section 5.

As we have seen before, the scalar problems (9) and (11) have traveling waves for infinitely many values of the wave speed c. This naturally leads to the question whether also our system has traveling wave solutions for infinitely many values of c. As we shall show in a future paper ([5]), at least for certain parameter values the answer is affirmative. The uniqueness statement in Theorem 3.1 implies that such waves will not be segregated: necessarily there will be regions where the two populations coexist.

4. **"Stability" of segregated traveling waves.** The numerical test described in the introduction suggests that segregated traveling waves are useful to describe the intermediate asymptotics of segregated solutions of problem (5)-(7) (*intermediate* asymptotics since $x \in (-L, L)$ instead of $x \in (-\infty, \infty)$). In order to discuss, at least heuristically, the stability of the segregated traveling waves, we also have to consider perturbations which break the segregation of $n(x,t)$ and $a(x,t)$.

Let $(u(x-ct), v(x-ct))$ be the segregated traveling wave defined by Theorem 3.1, with interface $x = ct$. Let (n_0, a_0) be a pair of initial functions which are "small" perturbations of $(u(x), v(x))$: $n_0(x) - u(x)$ and $a_0(x) - v(x)$ are small nonnegative functions, supported in, respectively, $(-\infty, 0)$ and $(0, \infty)$, as indicated in Figure 3. If $d = 1$, problem (5)-(7) has a solution ([2]; if $d \neq 1$ the problem of existence of a non-segregated solution is completely open). Of course the two populations are no longer segregated and it is natural to ask whether after a while the profile of the solution resembles the one of a segregated traveling wave. To answer this question correctly, one should define the concept of stability, but this goes beyond the scope of the present paper (for several reasons, first of all because the dynamical system is not well-defined since nothing is known about uniqueness of solutions of problem (5)-(7)).

Instead we describe two numerical tests for different parameter values. In the first one we choose $\gamma = 1$, $k = 2$ and $\alpha = 1$. Since $k/\alpha = 2 > 1$, the wave speed is positive: $c > 0$. As shown in Figure 3, the numerical test suggests that the intermediate asymptotics is described by a segregated traveling wave.

Next we increase the value of α and choose $\gamma = 1$, $k = 2$ and $\alpha = 4$. Since $k/\alpha = 1/2 < 1$ the speed of the segregated wave is negative, $c < 0$, and Figure 4 suggests a new phenomenon: the intermediate asymptotics is no longer described by a segregated traveling wave, but by a *standing wave*, with speed 0.

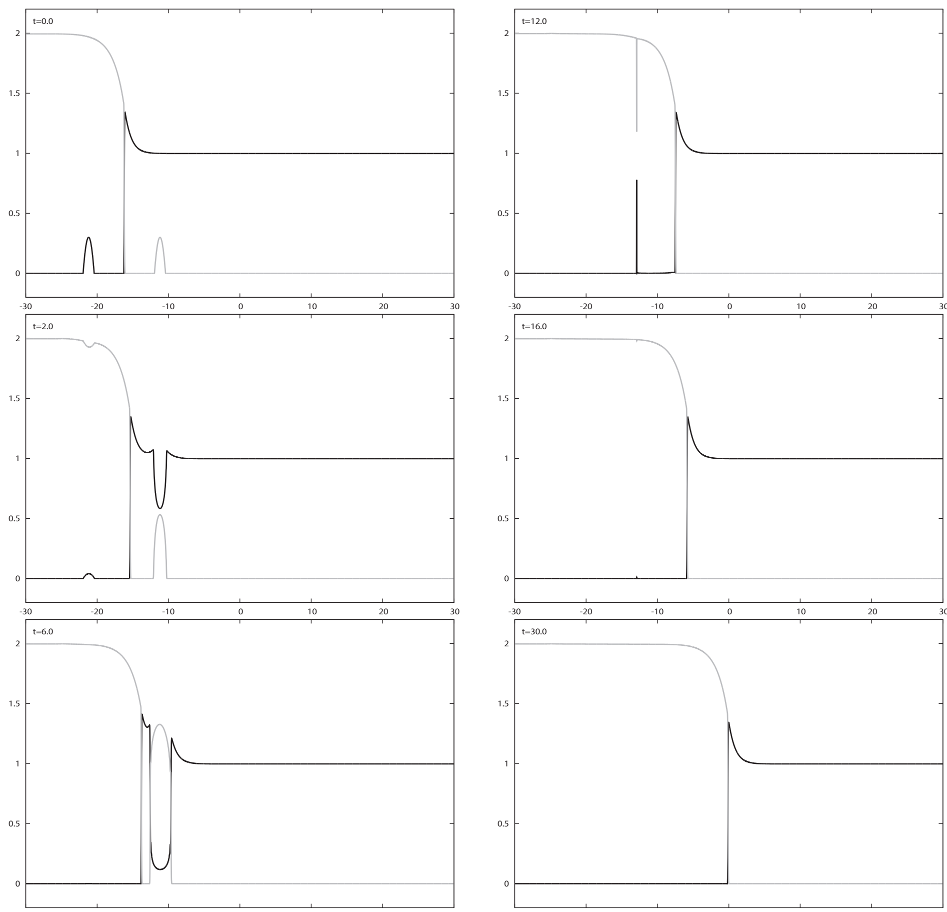

FIGURE 3. Stability of segregated traveling wave solution of (1.7)-(1.9) with $d = \gamma = 1$, $k = 2$ and $\alpha = 1$; black curves correspond to n, gray curves to a.

To get some more insight in the dependence on the parameter α, we recall the stability properties of the the following system of ordinary differential equations for $n(t)$ and $a(t)$, the *kinetic system* related to (2):

$$\begin{cases} n_t = \big(1 - (n + \alpha a)\big)n & t > 0 \\ a_t = \gamma\Big(1 - \dfrac{n + \alpha a}{k}\Big)a & t > 0 \\ n(0) = n_0 > 0,\ a(0) = a_0 > 0. \end{cases} \tag{15}$$

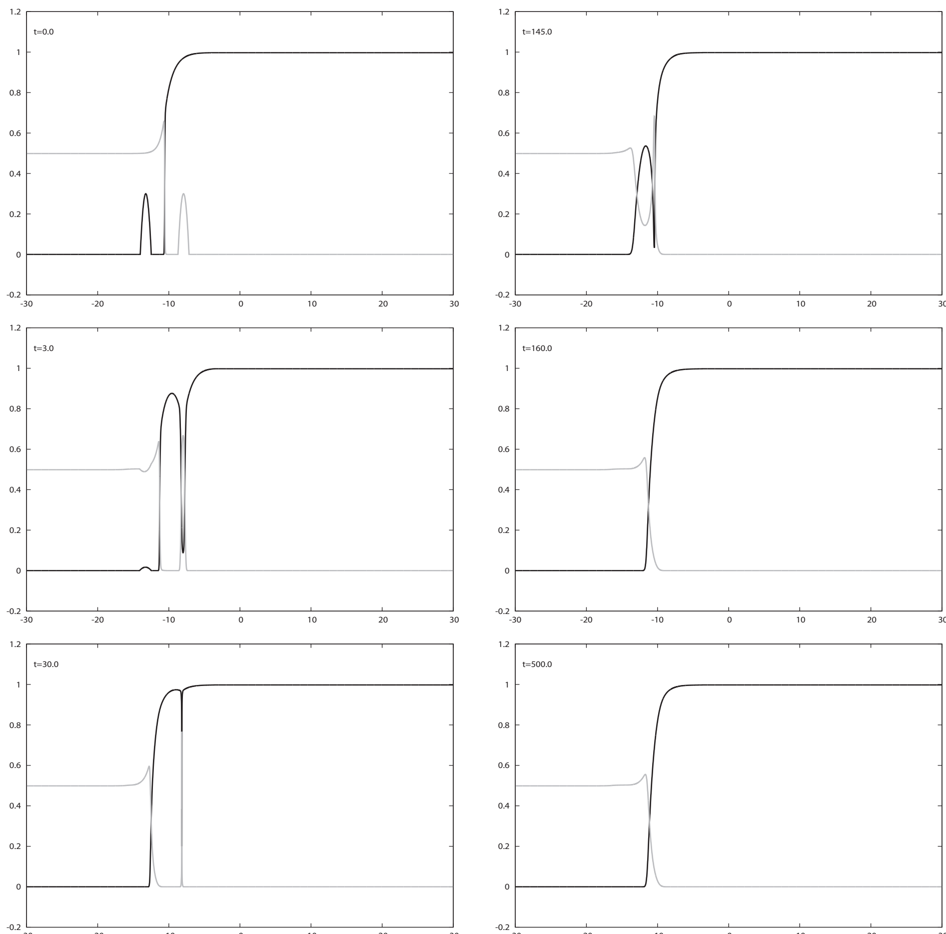

FIGURE 4. Appearance of standing wave solution of (1.7)-(1.9) with $d = \gamma = 1$, $k = 2$ and $\alpha = 4$; black curves correspond to n, gray curves to a.

If $k \neq 1$, (15) admits the equilibrium points $(0,0)$, $(1,0)$ and $(0,k/\alpha)$. The point $(0,0)$ is always unstable, but the stability of $(1,0)$ and $(0,k/\alpha)$ depends on k: $(1,0)$ is unstable and $(0,k/\alpha)$ is asymptotically stable if and only if $k > 1$ (i.e., $n(t) \to 0$ and $a(t) \to k/\alpha$ as $t \to \infty$).

The analysis of the kinetic system (15) suggests that, if $k > 1$, the population $a(x,t)$ is dominant with respect to $n(x,t)$ and "tries to invade" the domain $(-L,L)$. If $k/\alpha > 1$ (as in the first numerical test, see Figure 3), this is compatible with the positivity of the speed of the segregated traveling wave. But if $k/\alpha < 1$, the negativity of the speed of the segregated wave does not match with the tendency of a to invade the domain, and apparently this leads to the coexistence of the two populations.

Hence, if

$$k > 1,$$

the segregated traveing wave seems numerically more stable if $k/\alpha > 1$. In addition the numerical tests described in this section lead to the conjecture that there exists a non-segregated standing wave if $k/\alpha < 1$. In a future paper ([6]) we shall elaborate these ideas, in particular we shall prove that there exists a non-segregated standing wave if $k/\alpha < 1$.

5. **Proof of Theorem 3.1.** As announced in section 3, we shall prove in this section a slightly more general version of Theorem 3.1, which is motivated by the model introduced in [2]. We replace (13) and (14) by

$$\begin{cases} (u\chi'(u)u_z)_z + cu_z + (1-u)u = 0 \quad \text{in } (0,\infty) \\ u(0^+) = h, \quad \chi'(h)u_z(0^+) = -c \\ u(\infty) = 1, \quad u > 0 \text{ in } (0,\infty) \end{cases} \tag{16}$$

and, respectively,

$$\begin{cases} d(v\chi'(v)v_z)_z + cv_z + \gamma\left(1 - \dfrac{\alpha}{k}v\right)v = 0 \quad \text{in } (-\infty,0) \\ v(0^-) = h, \quad d\chi'(h)v_z(0^-) = -c \\ v(-\infty) = k/\alpha, \quad v > 0 \text{ in } (-\infty,0). \end{cases} \tag{17}$$

Here the function χ represents the population pressure ([2]), and we assume that

$$\chi \text{ is smooth in } [0,\infty) \text{ and } \chi'(s) > 0 \text{ if } s > 0. \tag{18}$$

If $\chi(s) = s$, (16) and (17) reduce to (13) and (14). The more general version of Theorem 3.1 will be given at the end of this section.

If $z < 0$, we may replace z by $\tilde{z} = z/d$. Denoting $\tilde{z}$ again by z, (17) becomes

$$\begin{cases} \left(v\chi'(v)v_z\right)_z + cv_z + d\gamma\left(1 - \dfrac{\alpha}{k}v\right)v = 0 \quad \text{in } (-\infty,0) \\ v(0^-) = h, \quad \chi'(h)v_z(0^-) = -c \\ v(-\infty) = k/\alpha, \quad v > 0 \text{ in } (-\infty,0). \end{cases} \tag{19}$$

Observe that in the rescaled problem (16) and (19), u and v are connected at $z = 0$ with C^1-continuity.

We first settle property (iii) of Theorem 3.1:

Proposition 2. *Let $u(z)$ and $v(z)$ satisfy (16) and (19) for some $d, \gamma, k, \alpha, h > 0$ and $c \in (-\infty,\infty)$. Then*

$$\begin{cases} c > 0,\ 1 < h < k/\alpha,\ u' < 0 \text{ in } (-\infty,0],\ v' < 0 \text{ in } [0,\infty) & \text{if } k > \alpha \\ c < 0,\ k/\alpha < h < 1,\ u' > 0 \text{ in } (-\infty,0],\ v' > 0 \text{ in } [0,\infty) & \text{if } k < \alpha \\ c = 0,\ h = 1,\ u = 1 \text{ in } (-\infty,0],\ v = 1 \text{ in } [0,\infty) & \text{if } k = \alpha. \end{cases}$$

Proof. By standard ODE-theory u is either strictly increasing in $[0,\infty)$ (with $h < 1$ and $c > 0$), strictly decreasing (with $h > 1$ and $c < 0$), or identically equal to 1 (with $h = 1$ and $c = 0$). Since a similar result holds for v, the desired result follows immediately. □

Let $\tilde{k}, \tilde{\gamma}$ and σ be arbitrary positive numbers. We consider the equation

$$\left(\varphi\chi'(\varphi)\varphi_z\right)_z + \sigma\varphi_z + \tilde{\gamma} f\left(\frac{\varphi}{\tilde{k}}\right)\varphi = 0, \tag{20}$$

where $f(s) = 1 - s$. When we investigate (16) and (19), we choose $(\tilde{k},\tilde{\gamma}) = (1,1)$ and $(\tilde{k},\tilde{\gamma}) = (k/\alpha, d\gamma)$, respectively. Given a solution of (20), we set

$$\psi(z) := \frac{1}{\sigma}\chi'(\varphi(z))\varphi_z(z).$$

Then (20) defines a dynamical system for $(\varphi(z), \psi(z))$:

$$\frac{d}{dz}\begin{bmatrix} \varphi \\ \psi \end{bmatrix} = \begin{bmatrix} \dfrac{\sigma}{\chi'(\varphi)}\psi \\ -\dfrac{1}{\sigma\varphi\chi'(\varphi)}\Big(\sigma^2\psi(1+\psi) + \tilde{\gamma}\varphi\chi'(\varphi)f\Big(\dfrac{\varphi}{\tilde{k}}\Big)\Big) \end{bmatrix}. \tag{21}$$

To complete the proof of Theorem 3.1, we need the following four lemmata, which will be proved in subsection 5.1.

Lemma 5.1. *Let χ satisfy (18) and let $\tilde{k}, \tilde{\gamma} > 0$. There exists $\sigma^+ = \sigma^+(\tilde{k}, \tilde{\gamma}) \in (0, \infty]$ such that*

(i) if $0 < \sigma < \sigma^+$, there exists a unique solution (φ, ψ, h) of (21) and

$$\begin{bmatrix} \varphi(\infty) \\ \psi(\infty) \end{bmatrix} = \begin{bmatrix} \tilde{k} \\ 0 \end{bmatrix}, \quad \begin{bmatrix} \varphi(0) \\ \psi(0) \end{bmatrix} = \begin{bmatrix} h \\ -1 \end{bmatrix}, \tag{22}$$

we denote this solution by $(\varphi^+_{\tilde{k},\tilde{\gamma},\sigma}(z), \psi^+_{\tilde{k},\tilde{\gamma},\sigma}(z), h^+_{\tilde{k},\tilde{\gamma},\sigma})$;

(ii) if $\sigma^+ < \infty$ and $\sigma \geq \sigma^+$, there is no solution (φ, ψ, h) (with $h > 0$) of (21) and (22).

Lemma 5.2. *Let σ^+ be defined by Lemma (5.1) and let the function $h^+_{\tilde{k},\tilde{\gamma}} : (0, \sigma^+) \to (k, \infty)$ be defined by $h^+_{\tilde{k},\tilde{\gamma}}(\sigma) := h^+_{\tilde{k},\tilde{\gamma},\sigma}$. Then*

(i) $h^+_{\tilde{k},\tilde{\gamma}}$ is continuous in $(0, \sigma^+)$;

(ii) $h^+_{\tilde{k},\tilde{\gamma}}$ is monotone increasing in $(0, \sigma^+)$;

(iii) $\lim_{\sigma\to 0} h^+_{\tilde{k},\tilde{\gamma}}(\sigma) = \tilde{k}$ and $\lim_{\sigma\to(\sigma^+)^-} h^+_{\tilde{k},\tilde{\gamma}}(\sigma) = \infty$.

Lemma 5.3. *Let χ satisfy (18) and let $\tilde{k}, \tilde{\gamma} > 0$. Then there exists $\sigma^- = \sigma^-(\tilde{k}, \tilde{\gamma}) > 0$ such that*

(i) if $0 < \sigma < \sigma^-$, there exists a unique solution (φ, ψ, h) of (21) and

$$\begin{bmatrix} \varphi(-\infty) \\ \psi(-\infty) \end{bmatrix} = \begin{bmatrix} \tilde{k} \\ 0 \end{bmatrix}, \quad \begin{bmatrix} \varphi(0) \\ \psi(0) \end{bmatrix} = \begin{bmatrix} h \\ -1 \end{bmatrix}, \tag{23}$$

we denote this solution by $(\varphi^-_{\tilde{k},\tilde{\gamma},\sigma}(z), \psi^-_{\tilde{k},\tilde{\gamma},\sigma}(z), h^-_{\tilde{k},\tilde{\gamma},\sigma})$;

(ii) if $\sigma \geq \sigma^-$, there is no solution (φ, ψ, h) (with $h > 0$) of (21) and (23).

Lemma 5.4. *Let σ^- be defined by Lemma 5.3 and let the function $h^-_{\tilde{k},\tilde{\gamma}} : (0, \sigma^-) \to (0, k)$ be defined by $h^-_{\tilde{k},\tilde{\gamma}}(\sigma) := h^-_{\tilde{k},\tilde{\gamma},\sigma}$. Then*

(i) $h^-_{\tilde{k},\tilde{\gamma}}$ is continuous in $(0, \sigma^-)$;

(ii) $h^-_{\tilde{k},\tilde{\gamma}}$ is monotone decreasing in $(0, \sigma^-)$;

(iii) $\lim_{\sigma\to 0} h^-_{\tilde{k},\tilde{\gamma}}(\sigma) = \tilde{k}$ and $\lim_{\sigma\to(\sigma^-)^-} h^-_{\tilde{k},\tilde{\gamma}}(\sigma) = 0$.

Now we are ready to state the more general version of Theorem 3.1 and complete its proof. We set

$$c^* = \sigma^-(k/\alpha, d\gamma) \quad \text{and} \quad c_* = -\sigma^-(1, 1), \tag{24}$$

where σ^- is defined by Lemma 5.3. Under some additional conditions on χ, for example if $\chi'(0) \neq 0$ ([1], [13], [19]; see also Remark 2), it is possible to show that the function $v(z) = \lim_{\sigma \to (\sigma^*)^-} \varphi^-_{k/\alpha, d\gamma, \sigma}(z/d)$ is a solution of

$$\begin{cases} d(v\chi'(v)v_z)_z + c^* v_z + \gamma \left(1 - \dfrac{\alpha}{k} v\right) v = 0 \quad \text{in } (-\infty, 0) \\ v(0^-) = 0, \quad d\chi'(0)v_z(0^-) = -c^* \\ v(-\infty) = k/\alpha, \quad v > 0 \text{ in } (-\infty, 0). \end{cases}$$

In this sense definition of c^* is the natural generalization of the one in the case $\chi(s) = s$ (see (10)). Similarly, c_* generalizes the previous definition to the case of general χ.

Theorem 5.5. *Let d, γ, α and k be positive constants, and let χ satisfy (18). Then there exists a unique wave speed c such that problem (16)-(17) has a solution $(u(z), v(z))$. In addition*

(i) the solution $(u(z), v(z))$ is unique;
(ii) $c_* < c < c^*$, where c^* and c_* are defined by (24);
(iii) $c > 0$ if $k/\alpha > 1$, $c < 0$ if $0 < k/\alpha < 1$ and $c = 0$ if $k/\alpha = 1$.

Observe that we do not require $\chi'(0) \neq 0$.

Let $k > \alpha$ and, in view of Proposition 2, $c > 0$. By Lemma 5.1, there exists a unique $(\varphi^+_{1,1,c}(z), \psi^+_{1,1,c}(z))$ of (21) and (22) if and only if $c \in (0, \sigma^+(1,1))$. Similarly, it follows from Lemma 5.3 that there exists a unique $(\varphi^-_{k/\alpha,d\gamma,c}(z), \psi^-_{k/\alpha,d\gamma,c}(z))$ of (21) and (23) if and only if $c \in (0, \sigma^-(k/\alpha, d\gamma)) = (0, c^*)$. Setting

$$\overline{\sigma}(k/\alpha, d\gamma) := \min\{\sigma^+(1,1), \sigma^-(k/\alpha, d\gamma)\},$$

it follows immediately from Lemma 5.2 and 5.4, that the equation

$$h^+_{1,1}(c) = h^-_{k/\alpha,d\gamma}(c) \tag{25}$$

has a unique solution $c = c(k/\alpha, d\gamma) \in (0, \overline{\sigma}(k/\alpha, d\gamma))$. Therefore,

$$(u(z), v(z), c) = (\varphi^+_{1,1,c}(z), \varphi^-_{k/\alpha,d\gamma,c}(z), c)$$

is the desired solution of (16) and (19), with $h = h^+_{1,1}(c) = h^-_{k/\alpha,d\gamma}(c)$.

If $0 < k < \alpha$ the proof is similar:

$$(u(z), v(z), c) = (\varphi^-_{1,1,-c}(-z), \varphi^+_{k/\alpha,d\gamma,-c}(-z), c)$$

is a solution of (16) and (19), where $-c = -c(k/\alpha, d\gamma)$ is the unique solution of

$$h^-_{1,1}(\sigma) = h^+_{k/\alpha,d\gamma}(\sigma) \text{ for } \sigma \in (0, \underline{\sigma}), \qquad \underline{\sigma} := \min\{\sigma^+(k/\alpha, d\gamma), \sigma^-(1,1)\}. \tag{26}$$

Observe that $\underline{\sigma} = \min\{\sigma^+(k/\alpha, d\gamma), -c_*\}$.

If $k \neq \alpha$, the uniqueness of the segregated traveling wave solution is assured by the relations

$$\begin{cases} h^+_{1,1}(c) = h = h^-_{k/\alpha,d\gamma}(c) \\ \psi^+_{1,1,c}(0) = -1 = \psi^-_{k/\alpha,d\gamma,c}(0) \end{cases} \quad \text{and} \quad \begin{cases} h^-_{1,1}(-c) = h = h^+_{k/\alpha,d\gamma}(-c) \\ \psi^-_{1,1,-c}(0) = -1 = \psi^+_{k/\alpha,d\gamma,-c}(0), \end{cases}$$

and the uniqueness of solutions of (25) and (26).

If $k = \alpha$ it follows easily from Proposition 2 that $(u, v, h, c) = (1, 1, 1, 0)$ is the unique solution of (16) and (17).

5.1. **Proofs of Lemmata 5.1-5.4.** It remains to prove the lemmata announced in section 5. In order to keep notations as simple as possible, we shall denote the constants $\tilde{k}$ and $\tilde{\gamma}$ in (21) by k and γ.

The dynamical system (21) has a singularity at $\varphi = 0$, which we remove by a change of the independent variable (see [1], [19]):

$$\tau(z) = \int_0^z \frac{1}{\sigma\varphi(s)\chi'(\varphi(s))}ds, \quad \tilde{\varphi}(\tau) := \varphi(z^{-1}(\tau)), \quad \tilde{\psi}(\tau) := \psi(z^{-1}(\tau)),$$

where we assume that $\varphi > 0$ in $[0,\infty)$. Denoting $\tilde{\varphi}$ and $\tilde{\psi}$ again by φ and ψ, (21) reduces to

$$\frac{d}{d\tau}\left[\begin{array}{c}\varphi\\ \psi\end{array}\right] = \left[\begin{array}{c}\sigma^2\varphi\psi\\ F_{k,\gamma,\sigma}(\varphi,\psi)\end{array}\right], \tag{27}$$

where

$$F_{k,\gamma,\sigma}(\varphi,\psi) := -\left(\sigma^2\psi(1+\psi) + \gamma\varphi\chi'(\varphi)f\left(\frac{\varphi}{k}\right)\right). \tag{28}$$

Vice versa, for any solution $(\tilde{\varphi}(\tau),\tilde{\psi}(\tau))$ of (27) with $\tilde{\varphi}(\tau) > 0$, we can solve $\tau(z)$ from

$$\frac{d\tau}{dz} = \frac{1}{\sigma\tilde{\varphi}(\tau)\chi'(\tilde{\varphi}(\tau))}, \quad \tau(0) = 0,$$

whence the pair $(\varphi(z),\psi(z)) = (\tilde{\varphi}(\tau(z)),\tilde{\psi}(\tau(z)))$ solves (21).

We shall prove Lemmata 5.1-5.4 for the dynamical system (27). Fixing $k,\gamma > 0$, we shall denote $\varphi^{\pm}_{k,\gamma,\sigma}$ and $F_{k,\gamma,\sigma}$ by $\varphi^{\pm}_{\sigma}$ and F_σ. The solution of (27) with initial condition $(\varphi(0),\psi(0)) = (\xi,\eta)$ will be denoted by $(\varphi_\sigma(\tau;\xi,\eta),\psi_\sigma(\tau;\xi,\eta))$. Observe that if $\sigma = 0$,

$$(\varphi_0(\tau;\xi,\eta),\psi_0(\tau;\xi,\eta)) = \left(\xi, \eta - \gamma\xi\chi'(\xi)f\left(\frac{\xi}{k}\right)\tau\right) \tag{29}$$

(see Fig.5.1(0)). If $\sigma > 0$, the equilibrium points of (27) are

$$(\bar{\varphi},\bar{\psi}) = (0,0),\ (k,0),\ (0,-1).$$

The following proposition is an immediate consequence of the continuous parameter dependence of solutions of ordinary differential equations.

Proposition 3. *Let $k,\gamma > 0$, let χ satisfy (18), and let $(\xi,\eta) \neq (0,0),(k,0),(0,-1)$. If $\psi_{\sigma_0}(T_{\sigma_0};\xi,\eta) = 0$ for some $\sigma_0 \geq 0$ and $T_{\sigma_0} \in (-\infty,\infty)$, then there exists a neighborhood Σ_0 of σ_0 such that for any $\sigma \in \Sigma_0$ there exists $T_\sigma \in (-\infty,\infty)$ such that $\psi_\sigma(T_\sigma;\xi,\eta) = 0$, $T_\sigma \to T_{\sigma_0}$ as $\sigma \to \sigma_0$, and*

(i) *if $\varphi_{\sigma_0}(T_{\sigma_0};\xi,\eta) > k$, then $\varphi_\sigma(T_\sigma;\xi,\eta) > k$ for $\sigma \in \Sigma_0$;*
(ii) *if $0 < \varphi_{\sigma_0}(T_{\sigma_0};\xi,\eta) < k$, then $0 < \varphi_\sigma(T_\sigma;\xi,\eta) < k$ for $\sigma \in \Sigma_0$.*

If $\psi_\sigma(\tau;\xi,\eta) \neq 0$ for all τ, the orbit $(\varphi_\sigma(\tau;\xi,\eta),\psi_\sigma(\tau;\xi,\eta))$ can be viewed as an integral curve of

$$\left\{\begin{array}{l}\dfrac{d\Psi}{d\varphi} = -\dfrac{1+\Psi}{\varphi} - \dfrac{\gamma\chi'(\varphi)f(\varphi/k)}{\sigma^2\Psi}\\ \Psi(\xi) = \eta.\end{array}\right. \tag{30}$$

The following result follows at once from the comparison principle for first order ordinary differential equations:

Proposition 4. *Let $k,\gamma > 0$ and let χ satisfy (18). Let $0 < \sigma_1 < \sigma_2$, and let Ψ_{σ_1} and Ψ_{σ_2} be the unique solutions of (30) with $\sigma = \sigma_1$ and $\sigma = \sigma_2$, respectively. Then,*

(i) *if $\xi > k$ and $\eta < 0$, then $\Psi_{\sigma_1}(\varphi) < \Psi_{\sigma_2}(\varphi)$ for $\varphi > \xi$;*
(ii) *if $0 < \xi < k$ and $\eta < 0$, then $\Psi_{\sigma_1}(\varphi) < \Psi_{\sigma_2}(\varphi)$ for $0 < \varphi < \xi$.*

Now we are ready to prove Lemmata 5.1-5.4. Linearization of (27) around $(k, 0)$ leads to the matrix

$$L_\sigma \ (= L_{k,\gamma,\sigma}) = \begin{pmatrix} 0 & \sigma^2 k \\ -f'(1)\gamma\chi'(k) & -\sigma^2 \end{pmatrix},$$

with eigenvalues and corresponding eigenvectors

$$\lambda_\sigma^\pm \ (= \lambda_{k,\gamma,\sigma}^\pm) = -\frac{\sigma^2}{2}\left(1 \pm \sqrt{1 - \frac{4f'(1)\gamma k\chi'(k)}{\sigma^2}}\right), \quad p_\sigma^\pm \ (= p_{k,\gamma,\sigma}^\pm) = \begin{bmatrix} \sigma^2 k \\ \lambda_{k,\gamma,\sigma}^\pm \end{bmatrix}.$$

Observe that $\lambda_\sigma^+ < 0$ and $\lambda_\sigma^- > 0$. Hence standard theory of dynamical systems yields the existence a local stable and unstable curve near $(k, 0)$ for the nonlinear equation (27): for sufficiently small $\delta = \delta_\sigma > 0$,

$$\mathcal{M}_\sigma^{+,\,loc} = \{(\xi, \eta) \in B((k, 0); \delta_\sigma) \mid (\varphi_\sigma(\tau; \xi, \eta), \psi_\sigma(\tau; \xi, \eta)) \to (k, 0) \text{ as } \tau \to \infty\}$$

and

$$\mathcal{M}_\sigma^{-,\,loc} = \{(\xi, \eta) \in B((k, 0); \delta_\sigma) \mid (\varphi_\sigma(\tau; \xi, \eta), \psi_\sigma(\tau; \xi, \eta)) \to (k, 0) \text{ as } \tau \to -\infty\}$$

exist and are C^1-curves which, at $(k, 0)$, are tangent to $p_\sigma^\pm$, respectively.

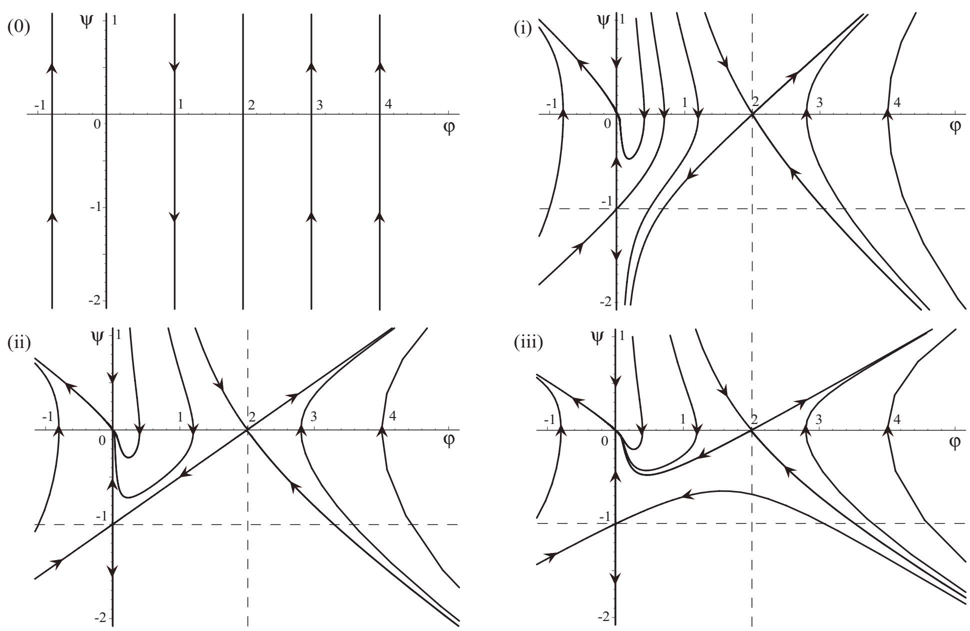

FIGURE 5. (φ, ψ)-phase planes for (27) with $\chi(s) = s$, $\gamma = 1$, $k = 2$: (0) $\sigma = 0$, (i) $\sigma = 0.8 (< \sigma^*)$, (ii) $\sigma = 1 (= \sigma^*)$, (iii) $\sigma = 1.2 (> \sigma^*)$.

Proof of Lemma 5.1. Fix $k, \gamma > 0$ and set

$$R^+ := \{(\varphi, \psi) \mid \varphi > k, -1 < \psi < 0\}.$$

Let $\sigma > 0$ and fix $(\xi_\sigma, \eta_\sigma) \in \mathcal{M}_\sigma^{+,\,loc} \cap R^+$. We set

$$\underline{T}_\sigma := \inf\{T < 0 \mid (\varphi_\sigma(\tau; \xi_\sigma, \eta_\sigma), \psi_\sigma(\tau; \xi_\sigma, \eta_\sigma)) \in R_+ \text{ for } \tau \in (T, 0)\},$$

$$\mathcal{M}_\sigma^{+,R^+} := \{(\varphi_\sigma(\tau; \xi_\sigma, \eta_\sigma), \psi_\sigma(\tau; \xi_\sigma, \eta_\sigma)) \mid \tau \in (\underline{T}_\sigma, \infty)\},$$

and

$$\Sigma := \{\sigma > 0 \mid \mathcal{M}_\sigma^{+,R^+} \text{ is bounded}\}.$$

Since $\psi \in (-1,0)$ in R^+, the solution $\Psi_\sigma(\varphi)$ of (30) with $(\xi,\eta) = (\xi_\sigma,\eta_\sigma)$ is decreasing and $\mathcal{M}_\sigma^{+,R^+}$ is the graph of the decreasing function. Hence $\underline{T}_\sigma > -\infty$ if $\sigma \in \Sigma$, and

$$(\varphi_\sigma(\underline{T}_\sigma;\xi_\sigma,\eta_\sigma), \psi_\sigma(\underline{T}_\sigma;\xi_\sigma,\eta_\sigma)) = (h_\sigma^+, -1) \quad \text{if } \sigma \in \Sigma$$

for some h_σ^+ $(= h_{k,\gamma,\sigma}^+) > k$.

Observe that $\Sigma \neq \emptyset$: by (29) and Proposition 3(i) we can take σ so small that the orbit $(\varphi_\sigma(\tau;2k,-1), \psi_\sigma(\tau;2k,-1))$ intersects the half-line $\{(\varphi,0) \mid \varphi > k\}$, and therefore $\sigma \in \Sigma$ for sufficiently small $\sigma > 0$.

A similar argument shows that Σ is open. We claim that Σ is also connected. Let $\sigma_1 < \sigma_2$ with $\sigma_2 \in \Sigma$. Since the slope of p_σ^+,

$$\frac{\lambda_\sigma^+}{\sigma^2 k} = -\frac{1}{2k}\left(1 + \sqrt{1 - \frac{4f'(1)\gamma k \chi'(k)}{\sigma^2}}\right).$$

is increasing with respect to σ, we can choose $(\xi_{\sigma_1},\eta_{\sigma_1})$ and $(\xi_{\sigma_2},\eta_{\sigma_2})$ such that $\xi_{\sigma_1} = \xi_{\sigma_2}$ and $\eta_{\sigma_1} < \eta_{\sigma_2}$. Let $\Psi_{\sigma_i}(\varphi)$ be the solution of (30) with $(\xi,\eta) = (\xi_{\sigma_i},\eta_{\sigma_i})$, $i = 1,2$. By Proposition 4, $\Psi_{\sigma_1}(\varphi) < \Psi_{\sigma_2}(\varphi)$ if $\varphi > k$, so that also $\sigma_1 \in \Sigma$. Hence Σ is connected.

Summarizing these results, we obtain $\Sigma = (0,\sigma^+)$ for some $\sigma^+ \in (0,\infty]$. Setting

$$(\varphi_\sigma^+(\tau), \psi_\sigma^+(\tau)) = (\varphi(\tau + \underline{T}_\sigma;\xi_\sigma,\eta_\sigma), \psi(\tau + \underline{T}_\sigma,\xi_\sigma,\eta_\sigma)),$$

we have found the solutions of (20) and (22) for $\sigma \in (0,\sigma^+)$. Their uniqueness follows from the uniqueness of $\mathcal{M}_\sigma^{+,loc}$.

Finally we note that $\mathcal{M}_\sigma^{+,R^+}$ cannot intersect $\{(\varphi,-1) \mid \varphi > 0\}$ if $\sigma \notin \Sigma$, i.e. if $\sigma \geq \sigma^+$. This completes the proof of Lemma 5.1. □

Remark 1. Using the explicit formula $f(s) = 1-s$, one easily shows that $\sigma^+(k,\gamma) = \infty$. Arguing by contradiction we suppose that $\mathcal{M}_\sigma^{+,R^+}$ is unbounded for some $\sigma > 0$. Then $\varphi(\tau)$ is unbounded and $\psi(\zeta)$ bounded, which implies that $\Psi_\sigma^* = \lim_{\varphi\to\infty} \Psi_\sigma(\varphi) \in [-1,0)$ exists. But this leads to a contradiction:

$$0 = \lim_{\varphi\to\infty} \frac{d\Psi_\sigma}{d\varphi} = -\frac{\gamma}{\sigma^2\Psi_\sigma^*} \lim_{\varphi\to\infty} \chi'(\varphi) f(\varphi/k) \neq 0.$$

Proof of Lemma 5.2. (i) The proof of the stable manifold theorem (see for example, Coddington-Levinson [9]) implies that the constant δ_σ in the definition of $\mathcal{M}_\sigma^{+,loc}$ can be chosen uniformly with respect to σ, locally in $(0,\sigma^+(k,\gamma))$. Hence we may choose, in Lemma 5.1, ξ_σ and η_σ in such a way that they depend continuously on σ. Since also (27) depends continuously on σ, we conclude that $h_{k,\gamma}^+$ is continuous with respect to σ.

(ii) The monotonicity of $h_{k,\gamma,\sigma}^+$ with respect to σ follows easily from the monotonicity of $\Psi_\sigma(\varphi)$ (see the proof of Lemma 5.1).

(iii) Let $\varepsilon > 0$. Proposition 3(i) implies that, for sufficiently small $\sigma > 0$, the orbit $(\varphi_\sigma(\tau;k+\varepsilon,-1), \psi_\sigma(\tau;k+\varepsilon,-1))$ intersects the half-line $\{(\varphi,0) \mid \varphi > k\}$ at a point $(\xi_1,0)$ with $\xi_1 > k$. Hence $h_{k,\gamma,\sigma}^+ \to k$ as $\sigma \to 0$.

It remains to prove that $h^+_{k,\gamma,\sigma} \to \infty$ as $\sigma \to \sigma^+ = \infty$ (see Remark 1). The change of variable $\tau \mapsto \tau/\sigma^2$, modifies (27) into

$$\frac{d}{d\tau}\begin{bmatrix} \varphi \\ \psi \end{bmatrix} = \begin{bmatrix} \varphi\psi \\ \dfrac{1}{\sigma^2}F_\sigma(\varphi,\psi) \end{bmatrix}. \tag{31}$$

Letting $\sigma \to \infty$, the limiting system of (31) is

$$\frac{d}{d\tau}\begin{bmatrix} \bar\varphi \\ \bar\psi \end{bmatrix} = \begin{bmatrix} \bar\varphi\bar\psi \\ -\bar\psi(1+\bar\psi) \end{bmatrix}. \tag{32}$$

Any orbit of the limiting system, $\{\bar\varphi(\tau;\xi,\eta), \bar\psi(\tau;\xi,\eta)\}$, with $\bar\psi(\tau) \neq 0$, can be represented as an integral curve, $\{(\bar\varphi,\bar\psi) \mid \bar\psi = \bar\Psi(\bar\varphi)\}$:

$$\frac{d\bar\Psi}{d\varphi} = -\frac{1+\bar\Psi}{\varphi} \quad \text{and} \quad \bar\Psi = -1 + \frac{\xi(\eta+1)}{\bar\varphi}.$$

Arguing by contradiction we suppose that $\sup\limits_{\sigma\in(0,\sigma^+)} h^+_{k,\gamma,\sigma} < h^* < \infty$. We consider an orbit $(\varphi_\sigma(\tau;h^*,-1+\varepsilon), \psi_\sigma(\tau;h^*,-1+\varepsilon))$. If σ is sufficiently large, it follows from (32) that there exists $\varepsilon > 0$ such that the orbit has an intersection with $\{(k,\psi) \mid -1 < \psi < 0\}$. This leads to a contradiction and completes the proof of Lemma 5.2. □

Proof of Lemma 5.3. Let $k, \gamma > 0$ be fixed and set

$$R^- := \{(\varphi,\psi) \mid 0 < \varphi < k, -1 < \psi < 0\}.$$

For any $\sigma > 0$ we fix $(\xi,\eta) = (\xi_\sigma,\eta_\sigma) \in \mathcal{M}_\sigma^{-,\,loc} \cap R^-$. The set $\mathcal{M}_\sigma^{-,\,loc} \cap R_-$ can be extended to

$$\mathcal{M}_\sigma^{-,R^-} := \{(\varphi_\sigma(\tau;\xi,\eta), \psi_\sigma(\tau;\xi,\eta)) \mid \tau \in (-\infty, \bar T_\sigma)\},$$

where

$$\bar T_\sigma := \sup\{T > 0 \mid (\varphi_\sigma(\tau;\xi_\sigma,\eta_\sigma), \psi_\sigma(\tau;\xi_\sigma,\eta_\sigma)) \in R^- \text{ for } \tau \in (-\infty, T)\}.$$

Observe that $\mathcal{M}_{k,\gamma,\sigma}^{-,R^-}$ is an integral curve, $\psi = \Psi_\sigma(\varphi)$, of (30), with $(\xi,\eta) = (\xi_\sigma,\eta_\sigma)$.

We distinguish three cases:

(C-1) $\bar T_\sigma < \infty$ and $\mathcal{M}_\sigma^{-,R^-}$ intersects the segment $\{(\varphi,-1) \mid 0 < \varphi < k\}$ (Fig. 5(i));
(C-2) $\bar T_\sigma = \infty$ and $\mathcal{M}_\sigma^{-,R^-}$ connects to the equilibrium $(0,-1)$ (Fig. 5(ii));
(C-3) $\bar T_\sigma = \infty$ and $\mathcal{M}_\sigma^{-,R^-}$ connects to the equilibrium $(0,0)$ (Fig. 5(iii)).

We set, for $i = 1, 2, 3$,

$$\Sigma_i := \{\sigma > 0 \mid \text{case (C-}i\text{) occurs}\}.$$

Arguing as in the proof of Lemma 5.1, it follows from Proposition 4(ii) and a "monotonic choice" of η_σ that $\Psi_\sigma(\varphi)$ is increasing with respect to σ for $\varphi \in (0,k)$. Hence $\sigma_1 < \sigma_2 < \sigma_3$ if $\sigma_1 \in \Sigma_1$, $\sigma_2 \in \Sigma_2$, $\sigma_3 \in \Sigma_3$. In particular Σ_1, Σ_2 and Σ_3 are connected.

Following the proof of Lemma 5.1, Proposition 3(ii) implies that $\Sigma_1 = (0,\sigma^*)$ for some $\sigma^* \in (0,\infty]$. We claim that also $\Sigma_3 \neq \emptyset$: if σ is sufficiently large, then

$$S^- := \left\{(\varphi,\psi) \in R^- \mid -\tfrac{1}{2} < \psi < 0\right\}$$

is positively invariant; hence $\sigma \in \Sigma_3$ if σ is large enough: $\mathcal{M}_\sigma^{-,R^-} \in S^-$, $\bar T_{k,\gamma,\sigma} = \infty$, and $(\varphi_\sigma(\tau;\xi_\sigma,\eta_\sigma), \psi_\sigma(\tau;\xi_\sigma,\eta_\sigma)) \to (0,0)$ as $\tau \to \infty$.

Finally we show that Σ_3 is open. Let $\sigma_0 \in \Sigma_3$ and let $\xi > 0$ be so small that $F_{\sigma_0}(\xi, -1/2) > 0$. Hence $(\varphi_{\sigma_0}(\tau; \xi, -1/2), \psi_{\sigma_0}(\tau; \xi, -1/2)) \to (0, 0)$ as $\tau \to \infty$ and

$$(\varphi_{\sigma_0}(T_{\sigma_0}; \xi, -1/2), \psi_{\sigma_0}(T_{\sigma_0}; \xi, -1/2)) = (k, \psi_{\sigma_0}) \quad \text{for some } T_{\sigma_0} < 0,\ \psi_{\sigma_0} \in (-1, 0).$$

Using a continuity argument similar to Proposition 3, $(\varphi_\sigma(\tau; \xi, -1/2), \psi_\sigma(\tau; \xi, -1/2))$ satisfies the same properties if σ sufficiently close to σ_0. Hence $\sigma \in \Sigma_3$ if σ is sufficiently close to σ_0, and $\Sigma_3 = (\sigma^{**}, \infty)$ for some $\sigma^{**} > 0$.

Summarizing these results we conclude that there exists $\sigma^* \le \sigma^{**} < \infty$ such that

$$\Sigma_1 = (0, \sigma^*), \quad \Sigma_2 = [\sigma^*, \sigma^{**}], \quad \Sigma_3 = (\sigma^{**}, \infty).$$

Setting $\sigma^-(k, \gamma) = \sigma^*$, parts (i) and (ii) of Lemma 5.3 can be proved in the same way as in the proof of Lemma 5.1. □

Remark 2. If $\sigma^* = \sigma^{**}$ in the proof of Lemma 5.3, then there exists a unique nonsmooth traveling wave of (20). This case appears under suitable additional conditions for χ, for instance if $\chi'(0) \neq 0$ (see [1], [13], [19]).

The proof of Lemma 5.4 is similar to the one of Lemma 5.2 and we omit it.

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