How far can chemotactic cross-diffusion enforce exceeding carrying capacities?

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Chemotaxis

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- Cells secrete chemical signal substance
- Cells partially orient their movement toward increasing signal concentration

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Chemotactic movement plays a key role in many processes of communication bewteen cells, e.g. in

- formation of aggregates such as in populations of *Dictyostelium discoideum* or *Escherichia coli*
- tumor cell migration
- organization of cell positioning during embryonic development
- ...

The classical Keller-Segel model

KELLER/SEGEL 1970:

- $u = u(x,t)$: Density of cell population
- $v = v(x,t)$: Concentration of signal

$$\boxed{\begin{aligned} u_t &= \Delta u - \nabla \cdot (u \nabla v), \qquad && x\in\Omega,\ t>0, \\ v_t &= \Delta v - v + u, && x\in\Omega,\ t>0. \end{aligned}} \qquad \text{(KS)}$$

- $\Omega \subset \mathbb{R}^n$: bounded domain

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- $\Omega \subset \mathbb{R}^n$: bounded domain
- Homogeneous Neumann boundary conditions imply mass conservation:

$$\int_\Omega u(x,t)dx = \int_\Omega u_0(x)dx$$

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Some results on global well-posedness

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The classical Keller-Segel model

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- $n = 1$: All solutions are global and bounded (Osaki/Yagi 1997).
- $n = 2$: If

$$\|u_0\|_{L^1(\Omega)} < 4\pi,$$

  then (u, v) is global and bounded (Nagai/Senba/Yoshida 1997).

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- $\underline{n \geq 3:}$ Let $\delta > 0$. Then there exists $\varepsilon(\delta) > 0$ such that whenever

  $$\|u_0\|_{L^{\frac{n}{2}+\delta}(\Omega)} \leq \varepsilon(\delta) \qquad \text{and} \qquad \|v_0\|_{W^{1,n+\delta}(\Omega)} \leq \varepsilon(\delta),$$

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Many boundedness results are available for related systems, involving e.g. nonlinear diffusion or variants in cross-diffusion, signal production,...(NAGAI, SENBA, SUZUKI, YOSHIDA, LAURENÇOT, BILER, FRIEDMAN, PERTHAME, MIMURA, CARRILLO, CALVEZ, CORRIAS, HILLEN, PAINTER, TAO, TELLO, STINNER, SUGIYAMA, KOZONO, ISHIDA, YOKOTA, CIEŚLAK, WRZOSEK, WANG, OSAKI, NAKAGUCHI,...)

The classical Keller-Segel model

Detecting unbounded solutions

The classical Keller-Segel model

Detecting unbounded solutions

- If $\Omega \subset \mathbb{R}^2$ is a disk, then there exists at least one pair (u_0, v_0) such that (u, v) blows up in finite time (HERRERO/VELÁZQUEZ 1997).

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- If $\Omega \subset \mathbb{R}^2$ is simply connected, then for almost every $m > 4\pi$ there exist initial data (u_0, v_0) such that $\int_\Omega u_0 = m$, and such that (u, v) blows up either in finite or infinite time (HORSTMANN/WANG 2001).

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- If $n \geq 3$ and $\Omega \subset \mathbb{R}^n$ is a ball, then for all $m > 0$ one can find (u_0, v_0) with mass $\int_\Omega u_0 = m$ such that (u, v) blows up either in finite or infinite time (W. 2010).

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Is blow-up *in finite time* a rarely occurring phenomenon?

The classical Keller-Segel model

Finite-time blow-up

- $\underline{n \geq 3}$ Let $R > 0$ and $\Omega = B_R(0) \subset \mathbb{R}^n$. Then for all $m > 0$ there exist (u_0, v_0) with mass $\int_\Omega u_0 = m$ such that (u, v) blows up in finite time (W. 2013).

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  Moreover, for any positive radial (u_0, v_0) one can find smooth positive radial u_{0k} and v_{0k} such that $(u_{0k}, v_{0k}) \to (u_0, v_0)$ in $L^p(\Omega) \times W^{1,2}(\Omega)$ for all $p < \frac{2n}{n+2}$, but such that the corresponding solutions (u_k, v_k) blow up in finite time for each k.

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- $\underline{n = 2}$ Let $n = 2$, $R > 0$ and $\Omega = B_R(0) \subset \mathbb{R}^2$. Then for all $m > 8\pi$ there exist (u_0, v_0) with mass $\int_\Omega u_0 = m$ such that (u, v) blows up in finite time (MIZOGUCHI/W., preprint).

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In particular: All constant steady states $(u, v) \equiv (m, m)$ are highly unstable.

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Too simple for reality?

Considerable efforts in modeling attempt to preclude blow-up in chemotaxis models:

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- Inhibited cross-diffusion at large (cell or signal) densities (Velázquez 2004, Othmer/Stevens 1997, Horstmann/W. 2005):

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- Saturation in signal production (Myerscough/Maini/Painter 1998, Osaki/Nakaguchi 2011):

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Chemotaxis with cell kinetics

Blow-up exclusion by logistic death effects

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\begin{aligned}
u_t &= \Delta u - \nabla \cdot (u \nabla v) + ru - \mu u^2, && x \in \Omega,\ t > 0, \\
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- $n \leq 2$: For arbitrary $\mu > 0$, all solutions are global and bounded (Osaki/Tsujikawa/Yagi/Mimura 2002, Tello/W. 2007).

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- The same conclusions hold for the parabolic-ellitpic system in which

$$0 = \Delta v - v + u.$$

Chemotaxis with logistic sources

Some simulations...

Consider

$$
\begin{array}{|ll|}
\hline
u_t = 0.0148u_{xx} - (uv_x)_x + 0.1u - 0.1u^2, & x \in (0,1),\ t>0, \\
0 = v_{xx} - v + u, & x \in (0,1),\ t>0, \\
u_x(0,t) = u_x(1,t) = v_x(0,t) = v_x(1,t) = 0, & t>0, \\
u(x,0) = 10x^2 & x \in (0,1). \\
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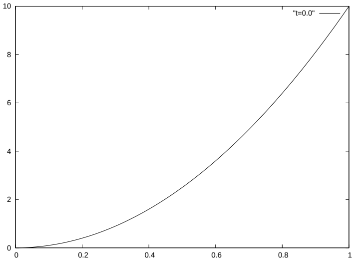

Solution for $t = 0$

Chemotaxis with logistic sources

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$$\begin{aligned}
u_t &= 0.0148u_{xx} - (uv_x)_x + 0.1u - 0.1u^2, && x\in(0,1),\ t>0,\\
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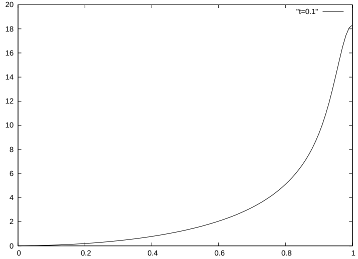
\end{aligned}$$



Solution for $t = 0.1$

Chemotaxis with logistic sources

Some simulations...

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$$
\begin{cases}
u_t = 0.0148u_{xx} - (uv_x)_x + 0.1u - 0.1u^2, & x \in (0,1),\ t > 0, \\
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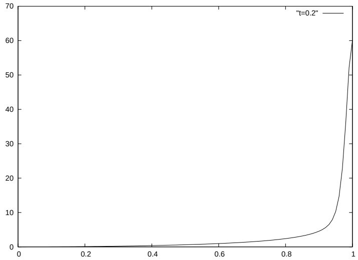

Solution for $t = 0.2$

Chemotaxis with logistic sources

Some simulations...

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$$
\begin{aligned}
&u_t = 0.0148u_{xx} - (uv_x)_x + 0.1u - 0.1u^2, && x\in(0,1),\ t>0,\\
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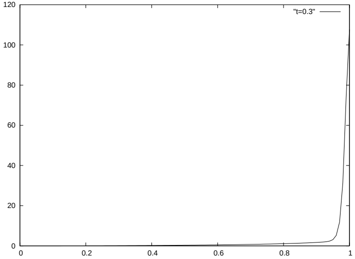

Solution for $t = 0.3$

Chemotaxis with logistic sources

Some simulations...

Consider

$$
\begin{array}{ll}
u_t = 0.0148u_{xx} - (uv_x)_x + 0.1u - 0.1u^2, & x\in(0,1),\ t>0,\\
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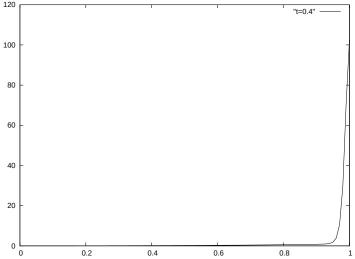

Solution for $t = 0.4$

Chemotaxis with logistic sources

Some simulations...

Consider

$$
\begin{array}{ll}
u_t = 0.0148 u_{xx} - (u v_x)_x + 0.1u - 0.1u^2, & x \in (0,1),\ t > 0, \\
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\end{array}
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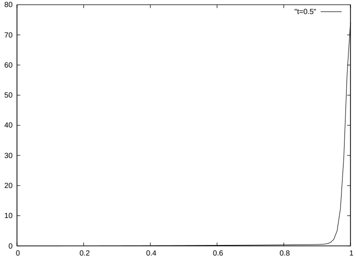

Solution for $t = 0.5$

Chemotaxis with logistic sources

Some simulations...

Consider

$$
\begin{array}{ll}
u_t = 0.0148 u_{xx} - (u v_x)_x + 0.1u - 0.1u^2, & x \in (0,1),\ t > 0, \\
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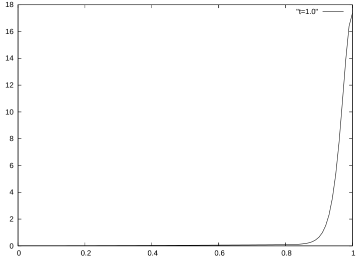

Solution for $t = 1.0$

Chemotaxis with logistic sources

Some simulations...

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\begin{array}{ll}
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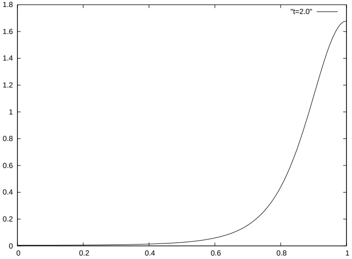

Solution for $t = 2.0$

Chemotaxis with logistic sources

Some simulations...

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\begin{cases}
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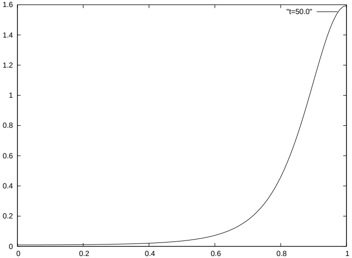

Solution for $t = 50.0$

Chemotaxis with logistic sources

...and a new challenge: A transient growth phenomenon

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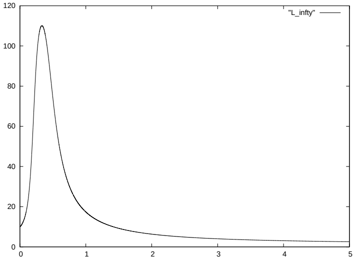
0 = v_{xx} - v + u, & x \in (0,1),\ t>0,\\
u_x(0,t) = u_x(1,t) = v_x(0,t) = v_x(1,t) = 0, & t>0,\\
u(x,0) = 10x^2 & x \in (0,1).
\end{cases}
$$



Evolution of $\|u(\cdot,t)\|_{L^\infty(\Omega)}$ for $0 \le t \le 5.0$

Going beyond carrying capacities

A refined view upon cross-diffusive destabilization

Recall: For

$$u_t = ru - \mu u^2 \tag{1}$$

there exists a **carrying capacity** $u_c := \frac{r}{\mu}$ such that $u \to u_c$ as $t \to \infty$ and

$$u \le \max\{u_0, u_c\} \qquad \text{for all } (x \text{ and}) \ t.$$

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That is: In both (1) and (2):

Populations cannot exceed the carrying capacity *dynamically*.

Going beyond carrying capacities

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Consider

$$\begin{cases} u_t = \varepsilon u_{xx} - (uv_x)_x + ru - \mu u^2, & x\in\Omega,\ t>0, \\ 0 = v_{xx} - v + u, & x\in\Omega,\ t>0. \end{cases}$$

in $\Omega = (0, L) \subset \mathbb{R}$, with $\varepsilon > 0$, $r \geq 0$ and $\mu > 0$.

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All solutions are global and bounded (Tello/W. 2007).

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How far can solutions exceed the carrying capacity u_c dynamically?

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Theorem (W.): Let $\mu < 1$. Then for all $p > \frac{1}{1-\mu}$ there exists $C(p) > 0$ such that whenever

$$
\|u_0\|_{L^p(\Omega)} > C(p) \cdot \max \left\{ \frac{1}{|\Omega|} \int_\Omega u_0 \,, \ \frac{r}{\mu} \right\},
$$

one can find $T > 0$ such that for all $M > 0$ there exists $\varepsilon_0(M) > 0$ with the following property:
For any $\varepsilon \in (0, \varepsilon_0(M))$ one can pick $t_\varepsilon \in (0, T)$ and $x_\varepsilon \in \Omega$ such that

$$
u(x_\varepsilon, t_\varepsilon) > M.
$$

Outline of proof

Analyzing a hyperbolic-elliptic limit system

Consider the case $\varepsilon = 0$, that is,

$$\begin{aligned} u_t &= -(uv_x)_x + ru - \mu u^2, && x \in \Omega,\ t > 0, \\ 0 &= v_{xx} - v + u, && x \in \Omega,\ t > 0. \end{aligned}$$

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Lemma 1: Let $q > 1$ and $u_0 \in W^{1,q}(\Omega)$. Then there exist $T_{\max} \leq \infty$ and a generalized solution for $t \in (0, T_{max})$ such that for all $q > 1$,

$$u \in L^\infty((0,T); W^{1,q}(\Omega)) \qquad \text{for all } T < T_{max},$$

and such that

$$\text{if } T_{max} < \infty \quad \text{then} \quad \limsup_{t \nearrow T_{max}} \|u(\cdot,t)\|_{L^\infty(\Omega)} = \infty.$$

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Main Estimate:

$$\int_\Omega |u_x|^q \leq \left\{ \int_\Omega |u_{0x}|^q + q\int_0^t \Big(\int_\Omega u(\cdot,s)\Big)^{q+1} ds \right\} \cdot \exp\left(4q\int_0^t \|u(\cdot,s)\|_{L^\infty(\Omega)} ds + qrt\right)$$

Outline of proof

Analyzing a hyperbolic-elliptic limit system

Formally, for any $p > 1$,

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\end{aligned}$$

that is,

$$\frac{d}{dt}\int_\Omega u^p = pr\int_\Omega u^p - (1-p+\mu p)\int_\Omega u^{p+1} - (p-1)\int_\Omega u^p v.$$

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Since the rightmost term is nonpositive:

Corollary 2: If $\mu \geq 1$, then all solutions are global and bounded.

Outline of proof

Analyzing a hyperbolic-elliptic limit system

Procedure for $\mu < 1$:

- Derive rigorous justification for

$$\frac{d}{dt}\int_\Omega u^p = pr\int_\Omega u^p + (p - \mu p - 1)\int_\Omega u^{p+1} - (p-1)\int_\Omega u^p v.$$

- Absorb last term appropriately.

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- Absorb last term appropriately.

Result:

$$\int_\Omega u^p(\cdot, t) \geq C_1 \int_0^t \int_\Omega u^{p+1} + \int_\Omega u_0^p - C_2 \int_0^t \Big(\int_\Omega u\Big)^{p+1}$$

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Since $\int_\Omega u^{p+1} \ge C(\int_\Omega u^p)^{\frac{p+1}{p}}$, by a Grønwall-type lemma this implies a blow-up criterion:

Lemma 3. Let $\mu \in (0,1)$ and $(1-\mu)p > 1$. Then there exists $C(p) > 0$ with the following property: Whenever $q > 1$ and $u_0 \in W^{1,q}(\Omega)$ is nonnegative and such that

$$\|u_0\|_{L^p(\Omega)} > C(p) \cdot \max\left\{ \frac{1}{|\Omega|} \int_\Omega u_0 \, , \, \frac{r}{\mu} \right\},$$

the solution (u,v) of the hyperbolic-elliptic problem blows up in finite time; that is, we have $T_{max} < \infty$ and

$$\limsup_{t \nearrow T_{max}} \|u(\cdot,t)\|_{L^\infty(\Omega)} = \infty.$$

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By

- uniqueness in the hyperbolic-elliptic problem and – thereby implied –
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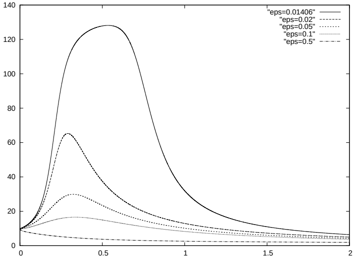
Thus, if $u(x_0, t_0) > 2M$ then $u_\varepsilon(x_0, t_0) > M$ for all small ε.

Exceeding carrying capacities

A transient small diffusion phenomenon



Solution for $r = 0.1, \mu = 0.1, u_0(x) = 10x^2$

Evolution of $\|u(\cdot, t)\|_{L^\infty(\Omega)}$ for $0 \leq t \leq 2.0$

Comparing different values of ε: $\varepsilon \in \{0.01406, 0.02, 0.05, 0.1, 0.5\}$

Conclusion

Chemotactic cross-diffusion can enforce dynamical exceedance of carrying capacities

- to an arbitrary extent, provided that diffusion is sufficiently weak;
- even in spatially one-dimensional systems, where solutions always are bounded.

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Open problems concern e.g.

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- blow-up in (three-dimensional) system with diffusion and small logistic absorption;
- problems involving degenerate diffusion instead of a constantly small diffusivity.

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Thank you!