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STATIONARY SOLUTIONS OF AEROTAXIS EQUATIONS

Abstract. We study the existence and uniqueness of the steady state in a model describing the evolution of density of bacteria and oxygen dissolved in water filling a capillary. The steady state is a stationary solution of a nonlinear and nonlocal problem which depends on the energy function and contains two parameters: the total mass of the colony of bacteria and the concentration (or flux) of oxygen at the end of the capillary. The existence and uniqueness of solutions depend on relations between these parameters and the maximum of the energy function.

1. Introduction. We study a modification of the model of aerotaxis introduced in [MZM].

A colony of bacteria lives in a capillary filled with oxygen dissolved in water. The metabolism of the bacteria depends on the concentration of oxygen, which plays the role of both an attractant (at moderate concentrations) and a repellent (at high and low concentrations). Aerotaxis is the movement of bacteria toward the concentration of oxygen optimal for their growth [T], [B], [G]. We denote by $u(x,t)$ and $p(x,t)$ respectively the density of bacteria and oxygen at a point x in the capillary, at time t. To describe the evolution of u and p we introduce the *energy function* $E(p)$, which has a maximum at a point p_o of optimal concentration of oxygen.

We make the following assumptions on E:

(i) E is a non-negative C^1 function on $\mathbb{R}$ with bounded first derivative,
(ii) $E(p) \equiv 0$ for $p \le 0$ and $E(p) > 0$ for $p > 0$,
(iii) E has only one local maximum at a point p_o,
(iv) $\lim_{p\to\infty} E(p) = 0$.

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The evolution of the density $u(x,t)$ of bacteria is given by the following one-dimensional drift-diffusion equation:

$$u_t = u_{xx} - (u(E(p))_x)_x. \tag{1.1}$$

The diffusion term u_{xx} is responsible for the random walk of bacteria, and the drift term $(u(E(p))_x)_x$ for their tendency to achieve the optimal concentration of oxygen. The assumptions on E and the form of the drift term describe the impact of oxygen concentration on bacteria movement, namely bacteria escape from regions with too high (too low respectively) concentrations of oxygen and move to the optimal one.

Oxygen diffuses in the water filling the capillary and is consumed by the cells of bacteria at a rate proportional to the density of bacteria and the energy function for a given density of oxygen. Thus the evolution of the oxygen density $p(x,t)$ is described by the equation

$$p_t = p_{xx} - E(p)u. \tag{1.2}$$

Assume that the colony lives in a capillary of unit length. This means that equations (1.1) and (1.2) are considered in the interval $[0,1]$. The density $u(x,t)$ satisfies the no-flux boundary condition, i.e.

$$u_x(0,t) - u(0,t)(E(p))_x(0,t) = u_x(1,t) - u(1,t)(E(p))_x(1,t) = 0, \tag{1.3}$$

which guarantees that the total mass of bacteria is conserved. The left end of the capillary is closed. Hence at $x=0$ we impose the no-flux condition

$$p_x(0,t) = 0. \tag{1.4}$$

At $x=1$ we may consider two distinct boundary value conditions: either a constant level of oxygen at the right end of the capillary:

$$\text{the Dirichlet condition} \quad p(1,t) = \overline{p}, \tag{1.5}$$

or a constant flow of the oxygen across the right end of the capillary:

$$\text{the Neumann condition} \quad p_x(1,t) = \overline{p}. \tag{1.6}$$

Here $\overline{p}$ is a given positive constant.

Equations (1.1), (1.2) are supplemented with the initial density of bacteria

$$u(x,0) = u_0(x) \tag{1.7}$$

and the initial density of oxygen

$$p(x,0) = p_0(x). \tag{1.8}$$

Here $u_0(x)$, $p_0(x)$ are given continuous functions on $[0,1]$.

Equations (1.1), (1.2) together with the boundary data (1.3)–(1.5), (1.6) and initial data (1.7), (1.8) describe the evolution of the density of bacteria and of oxygen.

Similar problems for various chemotaxis systems, even in one space dimension, lead to interesting and rich asymptotic phenomena: see e.g. [CL], [HP], [OY]. For the classical Keller–Segel model of chemotaxis the existence of global solutions in the two-dimensional case and existence or nonexistence of stationary solutions depend on one parameter, the total mass of the population of microorganisms [Bi]. In our case an analogous phenomenon occurs, but the existence of steady states depends on more parameters. Nonexistence of steady states (see Remark 2.5) suggests that a solution of the evolution problem blows up (compare [BHN]). The nonuniqueness of stationary solutions (see Th. 2.7) leads to the question of their stability and asymptotic behaviour of solutions of the evolution problem.

2. Stationary solutions. This section is devoted to the existence and uniqueness of stationary states of the model proposed in the Introduction.

The stationary density of bacteria, $U(x)$, and of oxygen, $P(x)$, satisfy the system of equations

$$U'' - (U(E(P))')' = 0, \tag{2.1}$$

$$P'' - E(P)U = 0, \tag{2.2}$$

the boundary conditions

$$U'(0) - U(0)(E(P))'(0) = U'(1) - U(1)(E(P))'(1) = 0, \tag{2.3}$$

and either

$$P'(0) = 0, \quad P(1) = \overline{p} \tag{2.4}$$

for the Dirichlet condition, or

$$P'(0) = 0, \quad P'(1) = \overline{p} \tag{2.5}$$

for the Neumann condition. Multiplying (2.1) by $Ue^{-E(P)}$ and integrating by parts we get

$$\int_0^1 (U'(x) - U(x)(E(P(x))')^2 e^{-E(P(x))}\, dx = 0.$$

Hence $U'(x) - U(x)(E(P(x)))' = 0$, so the stationary density of bacteria has the form $U(x) = Ce^{E(P(x))}$, where C is a constant. Assuming that M is the total mass of the colony of bacteria, we have the following relation for the stationary densities U and P:

$$U(x) = M\frac{e^{E(P(x))}}{\int_0^1 e^{E(P(s))}\, ds}. \tag{2.6}$$

Putting (2.6) into (2.2) we obtain a nonlocal equation for the stationary density P of oxygen:

$$P''(x) = M\mu[P]E(P(x))e^{E(P(x))}, \tag{2.7}$$

where

$$\mu[P] = \Big(\int_0^1 e^{E(P(s))}\, ds\Big)^{-1}.$$

We call equation (2.7) with the boundary conditions (2.4) the *Dirichlet problem*, and with the conditions (2.5) the *Neumann problem*. The nonlocal equation (2.7) is similar to the Poisson–Boltzmann equation which was studied in numerous papers [KN], [BN], [BHN].

2.1. Dirichlet problem. Note that the Dirichlet problem (2.7), (2.4) is nonlinear and nonlocal, so the existence and uniqueness of solutions are nontrivial questions.

First, we describe some properties of solutions of (2.7), (2.4).

LEMMA 2.1. *Each solution of* (2.7), (2.4) *is a convex, nondecreasing and positive function.*

Proof. The convexity of a solution of (2.7) follows from condition (ii) on E. Integrating (2.7) over $[0,x]$ we get

$$P'(x) = M\int_0^x \mu[P]E(P(s))e^{E(P(s))}\, ds \ge 0.$$

Hence P' is positive, so P is nondecreasing.

Assume that P is negative on some interval $(0,a)$. Condition (ii) implies that $P'' = 0$ on $(0,a)$. Thus we get

$$P'(0) = P(0) = 0. \tag{2.8}$$

It follows from assumption (i) that $P \equiv 0$ is the unique solution of the initial value problem (2.7), (2.8), so condition (2.4) is not satisfied, a contradiction. ■

To apply topological methods to prove existence of solutions of the Dirichlet problem, we transform it into an integral equation. Obviously, a solution of the Dirichlet problem is a fixed point of the following integral operator defined for $u \in C^0[0,1]$:

$$\mathcal{A}(u) = \overline{p} - \int_x^1\int_0^y M\mu[u]E(u(s))e^{E(u(s))}\, ds\, dy. \tag{2.9}$$

For $u \in C^0([0,1])$ we denote $|u|_\infty = \sup\{u(x) : x \in [0,1]\}$ and $u^* = \inf\{u(x) : x \in [0,1]\}$.

To apply the Leray–Schauder theorem or the Banach fixed point theorem for the operator (2.9), we need an auxiliary lemma.

LEMMA 2.2. *For any* $u, v \in C^0[0,1]$,

$$|\mathcal{A}(u) - \mathcal{A}(v)|_\infty \le ML(u,v)|u-v|_\infty, \tag{2.10}$$

where

$$L(u,v) = (1+2E(p_o))e^{2E(p_o)} \sup\{|E'(p)| : p \in [\min(u^*, v^*), \max(u_\infty, v_\infty)]\}$$

and

$$(\mathcal{A}(u))'(x) \le ME(p_o)e^{E(p_o)}. \tag{2.11}$$

Proof. The elementary inequalities

$$1/e^{E(p_o)} \le \mu[w] \le 1, \qquad E(w)e^{E(w)} \le E(p_o)e^{E(p_o)} \tag{2.12}$$

hold for every $w \in C^0([0,1])$. They lead to

$$\begin{aligned}
|\mathcal{A}(u) - \mathcal{A}(v)| &\le M \int_x^1 \int_0^y |\mu[u]E(u(s))e^{E(u(s))} - \mu[v]E(v(s))e^{E(v(s))}|\, ds\, dy \\
&\le M \int_x^1 \int_0^y \big(\mu[u]|E(u(s))e^{E(u(s))} - E(v(s))e^{E(v(s))}| \\
&\qquad\qquad + E(v(s))e^{E(v(s))}|\mu[u] - \mu[v]|\big)\, ds\, dy \\
&\le M \int_0^1 \big(|E(u(s))e^{E(u(s))} - E(v(s))e^{E(v(s))}| + E(p_o)e^{E(p_o)}|\mu[u] - \mu[v]|\big)\, ds \\
&\le M \int_0^1 \Big(|E(u(s))e^{E(u(s))} - E(v(s))e^{E(v(s))}| \\
&\qquad\qquad + E(p_o)e^{E(p_o)}\mu[u]\mu[v] \int_0^1 |e^{E(v(z))} - e^{E(u(z))}|\, dz\Big)\, ds \\
&\le ML(u,v)|v-u|_\infty.
\end{aligned}$$

Now inequality (2.11) follows from (2.12). ∎

An application of the Leray–Schauder theorem gives the existence of solutions of the Dirichlet boundary problem.

Theorem 2.3. *Problem* (2.7), (2.4) *has a solution.*

Proof. Consider the family of equations

$$P = \lambda\mathcal{A}(P), \qquad \lambda \in [0,1], \tag{2.13}$$

where $P \in C^0([0,1])$ is an unknown function and λ is a parameter. Lemma 2.2 implies that $\lambda\mathcal{A}$ is a family of continuous and compact operators on $C^0([0,1])$. To apply the Leray–Schauder theorem [E], it is enough to note that the inequality $|P_\lambda|_\infty = P_\lambda(1) \le \bar{p}$ gives an a priori estimate on all solutions of (2.13). ∎

The problem of uniqueness of solutions of the Dirichlet problem is settled in

Theorem 2.4.

(i) *For a sufficiently small M the solution of* (2.7), (2.4) *is unique.*

(ii) *For each M there exists $\tilde{p}$ such that for $\overline{p} > \tilde{p}$ problem* (2.7), (2.4) *has a unique solution.*

(iii) *For $\overline{p} \in [0, p_o] \cap \{p : E(p) < 1\} =: J$ the solution of problem* (2.7), (2.4) *is unique.*

Proof. (i) is a simple consequence of the Banach fixed point theorem. In fact, the derivative E' is bounded, hence $\sup\{L(u,v) : u, v \in C^0([0,1])\} =: L < \infty$ and (2.10) gives

$$|\mathcal{A}(u) - \mathcal{A}(v)|_\infty \le ML|u - v|_\infty.$$

Thus for $M < 1/L$ the operator $\mathcal{A}$ is a contraction on $C^0([0,1])$.

From (2.11) we see that for any solution P,

$$\bar{p} - P(0) = P(1) - P(0) \le ME(p_o)e^{E(p_o)}. \tag{2.14}$$

It follows from conditions (iii) and (iv) on E that $\lim_{p\to\infty} E'(p) = 0$. Hence, there exists $\tilde{p}$ such that for any two solutions P_1, P_2 of (2.7), (2.4) satisfying $P_1(1) = P_2(1) = \bar{p} > \tilde{p}$ we have $L(P_1, P_2) < 1/M$. This implies that inequality (2.10) for $u = P_1$ and $v = P_2$ takes the form $|P_1 - P_2|_\infty < ML(P_1, P_2)|P_1 - P_2|_\infty < \lambda|P_1 - P_2|_\infty$ for some $\lambda < 1$. Hence $P_1 = P_2$ follows.

The proof of (iii) is based on an idea used in [KN].

Let P_i, $i = 1, 2$, satisfy

$$P_i''(x) = M\mu_i E(P_i(x))e^{E(P_i(x))} \tag{2.15}$$

with boundary condition (2.4), where $\mu_i = (\int_0^1 e^{E(P_i(x))}\,dx)^{-1}$ and $\overline{p} \in J$. We distinguish two cases: $\mu = \mu_1 = \mu_2$ and $\mu_1 \ne \mu_2$. In the first case assume that (2.15), (2.4) has two solutions P_1, P_2. Then

$$(P_1(x) - P_2(x))'' = M\mu(E(P_1(x))e^{E(P_1(x))} - E(P_2(x))e^{E(P_2(x))}). \tag{2.16}$$

Multiply (2.16) by $P_1(x) - P_2(x)$ and integrate by parts to get

$$\begin{aligned} -\int_0^1 &(P_1(x) - P_2(x))'^2\,dx \\ &= \int_0^1 M\mu\big(E(P_1(x))e^{E(P_1(x))} - E(P_2(x))e^{E(P_2(x))}\big)(P_1(x) - P_2(x))\,dx. \end{aligned} \tag{2.17}$$

The function $E(p)e^{E(p)}$ is increasing on J. Hence the right hand side of (2.17) is nonnegative. Thus

$$\int_0^1 ((P_1(x) - P_2(x))')^2\,dx = 0,$$

and consequently $P_1(x) = P_2(x)$.

Now consider the case $\mu_1 > \mu_2$. It follows from Lemma 2.10 (see Appendix) that $P_1 < P_2$ in $(0,1)$. Hence $P_1'(1) \geq P_2'(1)$.

First, we prove that $P_1'(1) \leq P_2'(1)$. Note that this inequality can be rewritten in the form

$$\int_0^1\int_0^1 \big(E(P_2(x))e^{E(P_2(x))+E(P_1(y))} - E(P_1(x))e^{E(P_1(x))+E(P_2(y))}\big)\,dx\,dy$$
$$= \frac{1}{2}\int_0^1\int_0^1 \big((E(P_2(x)) - E(P_1(y)))e^{E(P_2(x))+E(P_1(y))}$$
$$+ (E(P_2(y)) - E(P_1(x)))e^{E(P_1(x))+E(P_2(y))}\big)\,dx\,dy \geq 0.$$

We choose $x < y$ and set $a = E(P_2(x))$, $b = E(P_1(y))$, $c = E(P_2(y))$, $d = E(P_1(x))$. To prove the last displayed inequality it is enough to show that

$$(a-b)e^{a+b} + (c-d)e^{c+d} \geq 0$$

for $0 < d < a < b < c < 1$. We postpone the proof of this elementary inequality to Lemma 2.9 (see Appendix). Thus we have

$$(P_1 - P_2)'(1) = 0. \tag{2.18}$$

It follows from the inequality $\mu_1 > \mu_2$ that $(P_1 - P_2)'' > 0$ on an interval $(1-\varepsilon, 1]$. Hence $(P_1 - P_2)' < 0$ and so $P_1 > P_2$ on this interval, contrary to Lemma 2.10. ∎

2.2. Neumann problem. This section is devoted to the Neumann problem (2.7), (2.5).

Integrating (2.7) on $(0,1)$ we obtain

$$\overline{p} = P'(1) = \int_0^1 M\mu[P]E(P(x))e^{E(P(x))}\,dx. \tag{2.19}$$

Hence $\overline{p} \leq ME(p_o)$, which implies:

Remark 2.5. If $\overline{p} > ME(p_o)$ then there exists no solution of (2.7), (2.5).

To prove the existence of solutions of (2.7), (2.5) we consider the auxiliary problem

$$P_b''(x) = M\mu[P_b]E(P_b(x))e^{E(P_b(x))}, \quad P'(0) = 0, \quad P(0) = b \geq 0. \tag{2.20}$$

Note that if P_b is a solution of (2.20) and satisfies

$$\overline{p} = \int_0^1 M\mu[P_b]E(P_b(x))e^{E(P_b(x))}\,dx, \tag{2.21}$$

then $P = P_b$ is a solution of (2.7), (2.5).

Integrating (2.20) we get

$$P_b'(x) = \int_0^x \mu[P_b]E(P_b(s))e^{E(P_b(s))}\,ds, \tag{2.22}$$

which implies that for $b > 0$ the solution P_b of (2.20) is a convex increasing function.

Integrating (2.22) we obtain the integral form of problem (2.20):

$$P_b(x) = b + \int_0^x\int_0^y M\mu[P_b]E(P_b(s))e^{E(P_b(s))}\,ds\,dy. \tag{2.23}$$

The inequality $P_b \ge b$ follows immediately from (2.23).

The Banach fixed point theorem applied to (2.23) shows that for sufficiently small M the solution exists and is unique. For this range of M we consider the function

$$H(b) = \int_0^1 M\mu[P_b]E(P_b(x))e^{E(P_b(x))}\,dx.$$

Lemma 2.6. *The function $H(b)$ is continuous and not injective.*

Proof. We need to show that the solution $P_b(x)$ depends continuously on b. Let $\{b_n\}_{n\in\mathbb{N}}$ be a sequence of real numbers converging to b. Since $\sup_n |P_{b_n}(\cdot)|_\infty \le \sup_n |b_n| + ME(p_o)$ and $|P_{b_n}'(\cdot)|_\infty \le ME(p_o)$, it follows that $\{P_{b_n}(\cdot)\}_{n\in\mathbb{N}}$ is uniformly bounded and equicontinuous. The Arzelà–Ascoli theorem implies that the sequence $\{P_{b_n}(\cdot)\}_{n\in\mathbb{N}}$ is precompact in $C^0([0,1])$. Hence we can choose a subsequence $\{P_{b_{n_k}}(\cdot)\}_{k\in\mathbb{N}}$ converging in $C^0([0,1])$ to a function $\varphi(\cdot)$. Using the Lebesgue dominated convergence theorem we obtain

$$\varphi(x) = b + \int_0^x\int_0^y M\mu[\varphi]E(\varphi(s))e^{E(\varphi(s))}\,ds\,dy.$$

The uniqueness of solution of (2.20) for the range of M in question gives $\varphi(x) \equiv P_b(x)$, and continuous dependence of P_b on b follows. Since $b \le P_b(x) \le b + ME(p_o)$, by the Lebesgue dominated convergence theorem we get

$$\lim_{b\to\infty} H(b) = \lim_{b\to\infty} \int_0^1 M\mu[P_b]E(P_b(x))e^{E(P_b(x))}\,dx = 0. \tag{2.24}$$

Note that $H(0) = 0$ and (2.24) imply that $H(b)$ is not injective. ∎

We are ready to prove

Theorem 2.7. *For sufficiently small M and $\overline{p} \in [0, \sup_b H(b)]$, problem (2.7), (2.5) has a solution. If $\overline{p} \in [0, \sup_b H(b))$ then this solution is not unique.*

Proof. As we proved above, for sufficiently small M the function H is well defined and not injective. If we choose $\overline{p} \in [0, \sup_b H(b))$ then the equation $\overline{p} = H(b)$ has at least two solutions, so nonuniqueness follows. ∎

The above theorem partially solves the problem of existence of solutions of the Neumann problem. To make our presentation more complete we state the next theorem.

THEOREM 2.8. *If $\overline{p}/M$ is sufficiently small, then problem* (2.7), (2.5) *has a solution.*

Proof. For given nonnegative parameters μ and b we consider the following local initial value problem:

$$P''_{\mu,b}(x) = M\mu E(P_{\mu,b}(x))e^{E(P_{\mu,b}(x))}, \quad P'_{\mu,b}(0) = 0,\ P_{\mu,b}(0) = b \geq 0. \tag{2.25}$$

This problem has a unique solution $P_{\mu,b}(\cdot)$, which is a C^1 function of the parameters μ and b ([H]). We define the functions

$$T(\mu, b) = \frac{1}{\int_0^1 e^{E(P_{\mu,b}(s))}\, ds}, \qquad G(\mu, b) = T(\mu, b) - \mu.$$

To prove the existence of solution of the nonlocal problem (2.7), (2.5) we need to show the existence of μ and b such that $G(\mu, b) = 0$. Differentiating $T(\mu, b)$ with respect to μ we get

$$\begin{aligned} &T_\mu(\mu, b) \\ &= \Big(\int_0^1 \exp(E(P_{\mu,b}(s)))\, ds\Big)^{-2} \int_0^1 \exp(E(P_{\mu,b}(s)))E'(P_{\mu,b}(s))(P_{\mu,b}(s))_\mu\, ds. \end{aligned} \tag{2.26}$$

Note that $(P_{\mu,b}(s))_\mu(1, 0) = 0$. Hence $T_\mu(1, 0) = 0$. Thus, by the implicit function theorem there exists a continuous function $\mu(\cdot)$ defined in some open neighbourhood V_0 of 0 such that $\mu(0) = 1$ and $G(\mu(b), b) = 0$. Hence $P_{\mu(b),b}$ is a solution of (2.20). To solve (2.7), (2.5) we have to check that

$$H^*(b) := P'_{\mu(b),b}(1) = \int_0^1 \mu(b)E(P_{\mu(b),b}(x))e^{E(P_{\mu(b),b}(x))}\, dx = \frac{\overline{p}}{M}. \tag{2.27}$$

The function $H^*(b)$ is positive for $b > 0$, continuous and $H(0) = 0$. Hence if we choose $\overline{p}/M$ sufficiently small, then condition (2.27) is fulfilled. ∎

The last theorem says that for an arbitrary $\overline{p}$ the Neumann problem has a solution if the mass of the bacteria is large enough.

2.3. Appendix

LEMMA 2.9. *If $0 < d < a < b < c < 1$, then*

$$(a - b)e^{a+b} + (c - d)e^{c+d} \geq 0. \tag{2.28}$$

Proof. Let
$$A = b - a, \quad B = c - d.$$
We have $0 < A < B < 1$. The inequality (2.28) can be written in the form $-Ae^{-A} + Be^{B-2(b-d)} \geq 0$. The function xe^{-x} is increasing on $[0,1]$, hence
$$-Ae^{-A} + Be^{B-2(b-d)} \geq -Ae^{-A} + Be^{B-2B} = -Ae^{-A} + Be^{-B} \geq 0. \ \blacksquare$$

LEMMA 2.10. *Let F be an increasing function and P_i be the solutions of the boundary value problem*
$$P_i'' = \lambda_i F(P_i), \quad P_i'(0) = 0, \quad P_i(1) = \overline{p} > 0, \quad \textit{for } i = 1, 2,$$
where λ_1, λ_2 are real parameters. If $\lambda_1 < \lambda_2$, then $P_1(x) > P_2(x)$ for $x \in (0,1)$.

Proof. Assume that there exists $x_0 \in [0,1)$ such that $P(x) := P_1(x) - P_2(x)$ attains a nonpositive minimum at x_0. If $x_0 \in (0,1)$ then $P''(x_0) = \lambda_1 F(P_1(x_0)) - \lambda_2 F(P_2(x_0)) < 0$, a contradiction.

Consider the case $x_0 = 0$. At the point $\overline{x} := \inf\{x \in [0,1] : P(x) = 0\}$ we have $P'(\overline{x}) \geq 0$ and $P(x) < 0$ for $[0, \overline{x})$. Hence $\lambda_1 F(P_1(x)) < \lambda_2 F(P_2(x))$ for $[0, \overline{x})$ and $P'(\overline{x}) = \int_0^{\overline{x}} (\lambda_1 F(P_1(s)) - \lambda_2 F(P_2(s)))\, ds < 0$, which leads to a contradiction. $\blacksquare$

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