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TRANSPORT IN A MOLECULAR MOTOR SYSTEM *, **

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Abstract. Intracellular transport in eukarya is attributed to motor proteins that transduce chemical energy into directed mechanical energy. This suggests that, in nonequilibrium systems, fluctuations may be oriented or organized to do work. Here we seek to understand how this is manifested by quantitative mathematical portrayals of these systems.

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1. Introduction

Intracellular transport in eukarya is attributed to motor proteins that transduce chemical energy into directed mechanical motion. Muscle myosin has been known since the mid-nineteenth century and its role as a motor in muscle contraction first explained by Huxley, [10], *cf.* [9]. Kinesins and the role of motor proteins in intracellular transport were discovered around 1985. There is an extremely large active cellular biology literature in this subject and much work in biophysics. Nanoscale motors like kinesins tow organelles and other cargo on microtubules or filaments. They function in a highly viscous setting with overdamped dynamics; Reynolds' numbers about 5×10^{-2}. Taken as an ensemble, they are in configurations far from conventional notions of equilibrium even though they are in an isothermal environment. Because of the presence of significant diffusion, they are sometimes referred to as Brownian motors. Since a specific type tends to move in a single direction, for example, anterograde or retrograde to the cell periphery, these proteins are sometimes referred to as molecular rachets. Many models have been proposed to describe the functions of these proteins, or aspects of their thermodynamical behavior, beginning with Ajdari and Prost [1], Astumian and Bier, *cf. e.g.* [2], and Doering, Ermentrout, and Oster [5], Peskin, Ermentrout, and Oster [21]. They consist either in discussions of distribution functions directly or of stochastic differential equations, which give rise to the distribution functions *via* the Chapman-Kolmogorov Equation. We have also suggested an approach for motor proteins like conventional kinesin where a dissipation principle is derived based on viewing an ensemble of motors as independent conformational changing nonlinear spring mass dashpots, [4], as suggested in Howard [9]. The dissipation principle,

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which involves a Kantorovich-Wasserstein metric, identifies the environment of the system and gives rise to an implicit scheme from which evolution equations follow [3, 11, 13, 17, 18, 28]. All of these descriptions consist, in the end, of Fokker-Planck type equations coupled *via* conformational change factors, typically known as weakly coupled parabolic systems. Our own is also distinguished because it has natural boundary conditions. Transport is not *a priori* conferred by the formulation and, indeed, does not have any particular relationship to our thermodynamic view of the system. Identical thermodynamical considerations may be used to derive equations for non moving motors. Establishing the predictive authority of the equations, and the model, is a separate task and must depend on features of the equations particular to motors which move along microtubles or filiments. Our approach is to supply appropriate features and to analyze the stationary solution of the evolution equations. We also show that the time dependent solution of the evolution equation tends to the stationary solution as time becomes large.

For a brief and much oversimplified view of the motion of conventional kinesin, we note that the motor apparatus consists primarily of two heads, heavy chains, which walk in a hand over hand fashion along a microtubule. As a motor head moves it responds to a potential and, on binding to its new site, it may change conformation, and consequently its other head can move. Our dissipation principle then allows us to write a system of evolution equations for the partial probabilities $\rho = (\rho_1, \rho_2)$ of active heads in terms of nonnegative potentials ψ_1 and ψ_2 and nonnegative conformational change coefficients ν_1 and ν_2,

$$\left.\begin{aligned} \frac{\partial \rho_1}{\partial t} &= \frac{\partial}{\partial x}\left(\sigma \frac{\partial \rho_1}{\partial x} + \psi_1' \rho_1\right) - \nu_1 \rho_1 + \nu_2 \rho_2 \\ \frac{\partial \rho_2}{\partial t} &= \frac{\partial}{\partial x}(\sigma \frac{\partial \rho_2}{\partial x} + \psi_2' \rho_2) + \nu_1 \rho_1 - \nu_2 \rho_2 \end{aligned}\right\} \quad \text{in } \Omega,\ t > 0 \tag{1.1}$$

$$\left.\begin{aligned} \sigma \frac{\partial \rho_1}{\partial x} + \psi_1' \rho_1 = 0 \\ \sigma \frac{\partial \rho_2}{\partial x} + \psi_2' \rho_2 = 0 \end{aligned}\right\} \quad \text{on } \partial\Omega,\ t > 0 \tag{1.2}$$

$$\begin{aligned} &\rho_i(x, 0) = \rho_i^0 \ \geq \ 0, \qquad \text{in } \Omega, \quad i \ = \ 1, 2 \\ &\int_\Omega \left(\rho_1 + \rho_2\right)\, \mathrm{d}x = 1 \end{aligned} \tag{1.3}$$

where $\Omega = (0, 1)$. For (1.1), (1.2), (1.3) there is the stationary system of ordinary differential equations

$$\left.\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma \frac{\mathrm{d}\rho_1^\sharp}{\mathrm{d}x} + \psi_1' \rho_1^\sharp\right) - \nu_1 \rho_1^\sharp + \nu_2 \rho_2^\sharp \ &= \ 0 \\ \frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma \frac{\mathrm{d}\rho_2^\sharp}{\mathrm{d}x} + \psi_2' \rho_2^\sharp\right) + \nu_1 \rho_1^\sharp - \nu_2 \rho_2^\sharp \ &= \ 0 \end{aligned}\right\} \quad \text{in } \Omega \tag{1.4}$$

$$\left.\begin{aligned} \sigma \frac{\mathrm{d}\rho_1^\sharp}{\mathrm{d}x} + \psi_1' \rho_1^\sharp = 0 \\ \sigma \frac{\mathrm{d}\rho_2^\sharp}{\mathrm{d}x} + \psi_2' \rho_2^\sharp = 0 \end{aligned}\right\} \quad \text{on } \partial\Omega \tag{1.5}$$

$$\int_\Omega \left(\rho_1^\sharp + \rho_2^\sharp\right)\, \mathrm{d}x = 1. \tag{1.6}$$

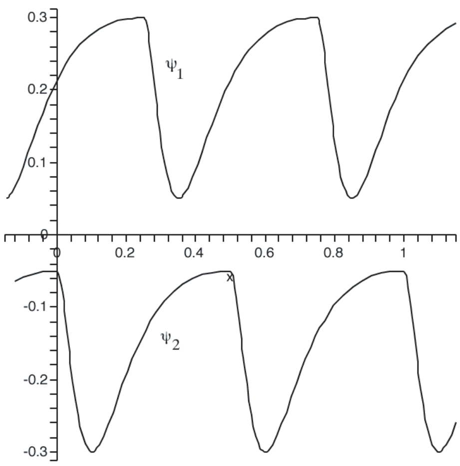

FIGURE 1. Caricature of the role of asymmetry of the potentials ψ_1 and ψ_2.

Above we think of the potentials and conformational change coefficients as periodic in Ω. Although there is no evident hint in the system itself as to why mass should be unevenly distributed, an important consideration has long been asymmetry of the potentials within their potential wells. Motor directionality is discussed in Chapter 9 of [24]. As a caricature, referring to Figure 1, suppose that type i heads are subject to the potential $\psi_i, i = 1, 2$, where one of the $\psi_i' s$ is just a half period translate of the other. A molecule of type 1 distributed near $x = 0.85$, say, may change conformation and become type 2. Then, owing to the asymmetry of ψ_2, it is likely to move to the left to the next well bottom at $x = 0.6$ with large probability p, say, $p > 1/2$ and to the right to the well bottom at $x = 1.2$ with probability $1 - p$. It may then change conformation again and become type 1. If it is at $x = 0.6$, it now moves to $x = 0.35$ with probability p or back to $x = 0.85$ with probability $1 - p$, and so forth. This corresponds to Bernoulli trials with a biased coin and, with some attention to the conditions at the first and last wells, the stationary distribution of its Markov chain decays exponentially away from the first well. Consequently, the asymmetry of the potentials in their well basins suggests exponential decay of the distribution. Unfortunately, this intuitive picture is not possible to convert into a proof. The conclusion, on the other hand, is true: the stationary distribution, referred to as $\rho^\sharp$ above, decays exponentially and thus corresponds to Bernoulli trials with a biased coin, Theorem 4.1. This is our principal result.

The situation is, nonetheless, subtle, and involves delicate interplay between the potentials and the conformational change coefficients. At the beginning of Section 4 we give a synopsis of the analysis. The potentials represent all the interactions involved with the motion, including the substrate microtubule. The conformational change is a result of ATP-hydrolysis. For transport, the hydrolysis step should take place at the binding site of the protein, *cf.* Hackney [7]. To promote this we ask the ψ_i and the ν_i to be synchronized so that

$$\nu_i > 0 \quad \text{where} \quad \psi_i = \min.$$

A statistical interpretation of this is that the ν_i are active where we expect the distribution to be highly populated. We may choose ν_i so that (1.4) decouple, for example, with

$$\frac{\nu_1}{\nu_2} = a\mathrm{e}^{\frac{1}{\sigma}(\psi_1 - \psi_2)},$$

for which

$$\rho^\sharp \propto \left(a\mathrm{e}^{-\frac{1}{\sigma}\psi_1}, \mathrm{e}^{-\frac{1}{\sigma}\psi_2}\right).$$

Here the mass in each period interval is about the same and the system lacks transport. The decoupling situation has an interpretation in terms of detailed balance.

There are rich and diverse expressions of Brownian motors, or the orientation of fluctuations in nonequilibrium systems, available for study [8,20,23,27]. The flashing rachet [2] consists in alternation of diffusion and transport in an asymmetric potential [6, 12, 15, 16]. The Janossy effect in a dichroic dye/nematic liquid crystal system consists in destabilizing an equilibrium state in an asymmetric fashion [19]. The mathematical examples are only shadows of the complexity found in nature.

The methods we employ come from partial differential equations, ordinary differential equations, and functional analysis. In the presentation, we have striven for accessibility; our intention is not to write a sequence of puzzles for the reader. The expert in any given field will no doubt find some familiar arguments.

2. Stationary solution: Schauder method

In this section we discuss a proof of existence of a solution to (1.4), (1.5) based on the Schauder fixed point theorem.

Theorem 2.1. *Suppose that $\psi_i \geqq 0$ and $\nu_i \geqq 0$ are smooth, $\sigma > 0$, and $\nu_i \not\equiv 0$, $i = 1, 2$. There is a unique solution $\rho^\sharp \in H^{1,1}(\Omega)$ of (1.4),(1.5) with*

$$\rho_i^\sharp > 0 \text{ in } \Omega$$

and

$$\int_\Omega \left(\rho_1^\sharp + \rho_2^\sharp\right) \mathrm{d}x = 1.$$

We show this in several steps with the Schauder Fixed Point Theorem. In the sequel we shall generally suppress the symbol $^\sharp$. First we recall some versions of a maximum principle [22].

Proposition 2.2 (elementary maximum principle)**.** *Let α, λ be smooth in $\overline{\Omega}$ with $\alpha \geqq \alpha_0 > 0$ and $\lambda \geqq 0$. Suppose $w \in C^2(\overline{\Omega})$ satisfies*

$$-\frac{\mathrm{d}}{\mathrm{d}x}\left(\alpha \frac{\mathrm{d}w}{\mathrm{d}x}\right) + \lambda w \geqq 0 \quad in \quad \Omega. \tag{2.7}$$

Then

(i) w does not attain a negative minimum in the open interval Ω;
(ii) $w \geqq 0$ and $w \not\equiv 0 \Longrightarrow w > 0$ in Ω;
(iii) $w \geqq 0$, $w \not\equiv 0$, and $\inf_\Omega w = 0 \Longrightarrow \inf_\Omega w$ is attained at $a = 0$ or 1 and $w_x(a) \neq 0$.

Proof. We give a proof for the convenience of the reader. If strict inequality holds, *i.e.*,

$$-\frac{\mathrm{d}}{\mathrm{d}x}\left(\alpha \frac{\mathrm{d}w}{\mathrm{d}x}\right) + \lambda w > 0 \quad in \quad \Omega \tag{2.8}$$

then, obviously, w does not have a negative minimum in Ω. If $w \geqq 0$ then $w > 0$ in Ω. Suppose then that (2.7) holds and that for some $a \in \overline{\Omega}$,

$$w(a) = \min \ w = 0.$$

Assume that $a \in \Omega$. Suppose, without loss of generality that $w(a + \delta) > 0$ and set

$$\zeta(x) = 1 - \mathrm{e}^{\kappa(x-a)}$$

with κ chosen large enough that

$$-\frac{\mathrm{d}}{\mathrm{d}x}(\alpha\zeta_x) + \lambda\zeta > 0.$$

Let $\varphi(x) = w(x) + \epsilon\zeta(x)$. Then $\varphi(a) = 0$, so min $\varphi \leqq 0$, and for ϵ sufficiently small

$$-\frac{\mathrm{d}}{\mathrm{d}x}(\alpha\varphi_x) + \lambda\varphi > 0$$
$$\varphi(a-\delta) > 0 \quad \text{and} \quad \varphi(a+\delta) > 0$$
$$\text{and} \quad \min_{|x-a|<\delta} \varphi(x) \leqq \varphi(a) \leqq 0.$$

This is a contradiction to (2.8). The boundary point condition is proven similarly. □

Proposition 2.3 (elementary maximum principle redux)**.** *Let $\sigma > 0$ and ψ and $\mu \geqq 0$ be smooth in $\overline{\Omega}$. Suppose that $u \in C^2(\overline{\Omega})$ satisfies*

$$-\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}u}{\mathrm{d}x} + \psi' u\right) + \mu u \geqq 0 \quad \text{in } \Omega. \tag{2.9}$$

Then

(i) u does not attain a negative minimum in the open interval Ω;
(ii) $u \geqq 0$ and $u \not\equiv 0 \Longrightarrow u > 0$ in Ω;
(iii) $u \geqq 0$, $u \not\equiv 0$, and $\inf_\Omega u = 0 \Longrightarrow \inf_\Omega u$ is attained at $a = 0$ or 1 and

$$\sigma\frac{\mathrm{d}u}{\mathrm{d}x} + \psi' u|_{x=a} \neq 0. \tag{2.10}$$

Proof. Define w by $w(x) = \mathrm{e}^{\frac{1}{\sigma}\psi(x)}$ and apply Proposition 2.2.

The point here is that we shall be able to apply Proposition 2.3, for example, component wise to solutions of the stationary system when all components are non-negative.

Step 1. Existence. Look at the scalar equation

$$-\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}u}{\mathrm{d}x} + \psi' u\right) + \mu u = \hat{\mu} f \quad \text{in } \Omega \tag{2.11}$$

$$\sigma\frac{\mathrm{d}u}{\mathrm{d}x} + \psi' u = 0 \quad \text{on} \quad \partial\Omega \tag{2.12}$$

where $\mu, \hat{\mu} \geqq 0$ and μ not identically 0. Assume $f \in L^1(\Omega)$.

The mapping

$$T_0 : L^1(\Omega) \to L^1(\Omega)$$
$$f \to u$$

is compact. The reader may employ his favorite technique at this point. For example, (2.11), (2.12) has a bounded Green's Function. So,

$$|u(x)| \leqq \frac{C_0}{\sigma}\|\hat{\mu} f\|_{L^1(\Omega)} \tag{2.13}$$

then integrating (2.11) gives the estimate

$$|u_x(x)| \leqq \frac{C}{\sigma}\|\hat{\mu} f\|_{L^1(\Omega)}$$

from which the compactness of T_0 follows by the Ascoli-Arzela' theorem. In particular note that when $f \geqq 0$ from (2.11),

$$\|u\|_{L^1(\Omega)} = \int_\Omega u \ \mathrm{d}x \leqq \frac{C_0}{\sigma}\int_\Omega \hat{\mu} f \ \mathrm{d}x. \tag{2.14}$$

□

Returning now to (1.4), (1.5), given $f_1, f_2 \in L^1(\Omega)$, let

$$T : L^1(\Omega) \times L^1(\Omega) \to L^1(\Omega) \times L^1(\Omega)$$

$$\eta = Tf$$

denote the solution of

$$\begin{aligned} -\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}\eta_1}{\mathrm{d}x} + \psi_1'\eta_1\right) + \nu_1\eta_1 = \nu_2 f_2 \ \text{ in } \ \Omega \\ -\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}\eta_2}{\mathrm{d}x} + \psi_2'\eta_2\right) + \nu_2\eta_2 = \nu_1 f_1 \ \text{ in } \ \Omega \\ \sigma\frac{\mathrm{d}\eta_1}{\mathrm{d}x} + \psi_1'\eta_1 = 0 \ \text{ on } \ \partial\Omega \\ \sigma\frac{\mathrm{d}\eta_2}{\mathrm{d}x} + \psi_2'\eta_2 = 0 \ \text{ on } \ \partial\Omega \end{aligned}$$

T is compact. Let $K \subset L^1(\Omega) \times L^1(\Omega)$ denote the $f = (f_1, f_2)$ which satisfy

$$f_i \geqq 0, \quad i = 1, 2 \tag{2.15}$$

$$\int_\Omega (\nu_1 f_1 + \nu_2 f_2)\ \mathrm{d}x = 1 \tag{2.16}$$

$$\int_\Omega (\nu_1 f_1 - \nu_2 f_2)\ \mathrm{d}x = 0 \tag{2.17}$$

$$0 \leqq \int_\Omega f_i\ \mathrm{d}x \leqq \frac{C_0}{\sigma}, \quad i = 1, 2. \tag{2.18}$$

K is a bounded convex subset in $L^1(\Omega) \times L^1(\Omega)$. For $\eta = Tf$, with $f \in K$, we have $\eta_i \geqq 0$ from the maximum principle already cited. Adding and subtracting the equations for η_i, we check that (2.16), (2.17) are satisfied. Now (2.16) implies in particular that

$$0 \leqq \int_\Omega \nu_i f_i\ \mathrm{d}x \leqq 1.$$

Hence from (2.14),

$$0 \leqq \int_\Omega \eta_i\ \mathrm{d}x \leqq \frac{C_0}{\sigma}, \quad i = 1, 2.$$

Thus $\eta \in K$. Hence $T(K) \subset K$. Now we apply the Schauder Fixed Point Theorem to T and K to conclude that T has a fixed point

$$f = Tf.$$

Let ρ denote the normalized fixed point with total mass 1.

Step 2. Uniqueness. From the existence, we know that $\rho_i \geqq 0$ in Ω. Rewrite the system, considering it to be independent equations for the components as

$$\begin{aligned} &-\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}\rho_1}{\mathrm{d}x} + \psi_1'\rho_1\right) + \nu_1\rho_1 = \nu_2\rho_2 \geqq 0 \text{ in } \Omega \\ &\sigma\frac{\mathrm{d}\rho_1}{\mathrm{d}x} + \psi_1'\rho_1 = 0 \text{ on } \partial\Omega \end{aligned}$$

and

$$
\begin{aligned}
&-\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}\rho_2}{\mathrm{d}x}+\psi_2'\rho_2\right)+\nu_2\rho_2=\nu_1\rho_1\geqq 0 \text{ in } \Omega\\
&\sigma\frac{\mathrm{d}\rho_2}{\mathrm{d}x}+\psi_2'\rho_2=0 \text{ on } \partial\Omega.
\end{aligned}
$$

By the elementary maximum principle redux, Proposition 2.3, quoted prior to the proof, we know that $\rho_i > 0$ in $\overline{\Omega}$.

Suppose we have two solutions, ρ and $\hat{\rho}$ with non-negative components. Hence for $\epsilon > 0$ small enough,

$$\rho_i - \epsilon\hat{\rho}_i > 0 \ \text{ in } \Omega.$$

Choose ϵ as large as possible:

$$
\begin{aligned}
\rho_i - \epsilon\hat{\rho}_i &> 0 \ \text{ in } \Omega, \quad i=1,2\\
\rho_j(x_0) - \epsilon\hat{\rho}_j(x_0) &= 0, \quad \text{for some } j=1,2, \text{ and } x_0\in\overline{\Omega}.
\end{aligned}
$$

So $\rho - \epsilon\hat{\rho}$ is a solution with non-negative components and with minimum zero. Just as above, each component satisfies a differential inequality with a homogeneous boundary condition. Again according to Proposition 2.3, $\rho_i = \epsilon\hat{\rho}_i$ and, by the mass requirement, $\epsilon = 1$. This verifies the uniqueness.

We shall use variations of this argument many times.

3. Stationary solution: shooting method

In this section, we give an alternate proof of existence and uniqueness while setting up the apparatus for discussion of the behavior of the solution. Let $\rho = (\rho_1, \rho_2)$ be the solution of (1.4), (1.5) and set

$$\phi_i = \sigma\frac{\mathrm{d}\rho_i}{\mathrm{d}x} + \psi_i'\rho_i, \quad i=1,2$$

so (1.4), (1.5) may be written as the first order system

$$
\begin{aligned}
\sigma\frac{\mathrm{d}\rho_1}{\mathrm{d}x} &= \phi_1 - \psi_1'\rho_1\\
\sigma\frac{\mathrm{d}\rho_2}{\mathrm{d}x} &= \phi_2 - \psi_2'\rho_2\\
\frac{\mathrm{d}\phi_1}{\mathrm{d}x} &= \nu_1\rho_1 - \nu_2\rho_2\\
\frac{\mathrm{d}\phi_2}{\mathrm{d}x} &= -\nu_1\rho_1 + \nu_2\rho_2
\end{aligned}
$$

with

$$\phi_1(0) = \phi_2(0) = \phi_1(1) = \phi_2(1) = 0.$$

Observe from the last two equations of the system that $\phi_1 + \phi_2 = \text{const}$ and this const $= 0$ by the boundary conditions, so we may write the first order system in terms of three functions, with $\phi = \phi_1$ as

$$\sigma \frac{\mathrm{d}\rho_1}{\mathrm{d}x} = \phi - \psi_1' \rho_1 \tag{3.19}$$

$$\sigma \frac{\mathrm{d}\rho_2}{\mathrm{d}x} = -\phi - \psi_2' \rho_2 \qquad \text{in } \Omega \tag{3.20}$$

$$\frac{\mathrm{d}\phi}{\mathrm{d}x} = \nu_1 \rho_1 - \nu_2 \rho_2 \tag{3.21}$$

$$\phi(0) = \phi(1) = 0. \tag{3.22}$$

Introduce

$$p = \begin{pmatrix} \rho_1 \\ \rho_2 \\ \phi \end{pmatrix} \quad \text{and} \quad A = \frac{1}{\sigma} \begin{pmatrix} -\psi_1' & 0 & 1 \\ 0 & -\psi_2' & -1 \\ \sigma\nu_1 & -\sigma\nu_2 & 0 \end{pmatrix}$$

so the system of ODE's assumes the form

$$\frac{\mathrm{d}}{\mathrm{d}x} p = Ap, \quad \phi(0) = \phi(1) = 0. \tag{3.23}$$

We shall now prove Theorem 1 again. Let $p^{(1)}$ and $p^{(2)}$ be the solutions of (3.23) with

$$p^{(1)}(0) = (1, 0, 0) \ \text{ and } \ p^{(2)}(0) = (0, 1, 0).$$

Lemma 3.1. *For $p^{(1)}$ we have that $\rho_1 \geqq 0, \rho_2 \leqq 0$ and $\phi \geqq 0$ and for $p^{(2)}$ we have that $\rho_1 \leqq 0, \rho_2 \geqq 0$ and $\phi \leqq 0$.*

Proof. Suppose first that $\nu_1 > 0$ and $\nu_2 > 0$ in $\overline{\Omega}$ and consider $p^{(1)}$. Here

$$\rho_2(0) = 0$$
$$\rho_2'(0) = 0$$
$$\rho_2''(0) = -\phi'(0) = -\nu_1(0) < 0.$$

So there is an initial interval $(0, \epsilon)$ in which

$$\rho_1 > 0, \quad \rho_2 < 0, \quad \phi > 0, \quad x \in [0, \epsilon).$$

Suppose there is a first $x = \xi$ where one or more of these inequalities is violated. Since $\phi' > 0$ whenever $\rho_1 > 0$ and $\rho_2 < 0$, we must have $\rho_1(\xi) = 0$ or $\rho_2(\xi) = 0$. If $\rho_1(\xi) = 0$, then $\sigma\rho_1'(\xi) = \phi(\xi) > 0$. Thus $p^{(1)} \equiv 0$, which is not the case. A similar contradiction results if $\rho_2(\xi) = 0$. This proves the lemma in the case where the $\nu_i > 0$.

Now suppose that there are ψ_i and ν_i such that the lemma is false. This means that there is an $x^* \in \Omega$ where either $\rho_1 < 0, \rho_2 > 0$ or $\phi < 0$. Consider the problem with functions $\nu_i + \delta$ in place of the ν_i, for small $\delta > 0$. The solution $p^{(1)}$ is a continuous function of δ, so for small enough δ one of the inequalities is violated at x^*. This contradicts what was already shown when $\nu_i > 0$.

Similar remarks hold for $p^{(2)}$. This proves the lemma. □

Lemma 3.2. *For $p^{(1)}$ we have that $\rho_1 > 0$ on Ω and for $p^{(2)}$ we have that $\rho_2 > 0$ on Ω.*

Proof. For $p^{(1)}$, if $\rho_1(\xi) = 0$ for some $\xi \in (0, 1]$, then $\rho_1'(\xi) = 0$ since we know already that $\rho_1 \geqq 0$ on $\overline{\Omega}$. But $\phi' \geqq 0$ and hence, since $\phi(0) = 0, \phi \equiv 0$ on $[0, \xi]$, a contradiction, since this would imply $\rho_1 > 0$ on $[0, \xi]$. Similar remarks apply to $p^{(2)}$. □

Proof of theorem. Since each of the ν_i is positive somewhere in Ω, for $p^{(1)},\ \phi(1) > 0$ and for $p^{(2)},\ \phi(1) < 0$. Therefore there is a unique $c > 0$ such that

$$p = cp^{(1)} + p^{(2)}$$

satisfies

$$\begin{aligned}\phi(0) &= \phi(1) = 0\\ \rho_2(0) &= 1 \ \text{ and}\\ \rho_1(0) &= c > 0.\end{aligned}$$

We claim that for this p, $\rho_1 > 0$ and $\rho_2 > 0$. We argue by inspection of (3.23), although we could simply invoke the existence portion of the previous theorem at this point. Let ξ be the first point such that $\rho_1(\xi) = 0$. Then

$$\frac{\mathrm{d}\rho_1}{\mathrm{d}x}(\xi) \leqq 0.$$

If $\rho_2(\xi) = 0$ as well, then

$$\frac{\mathrm{d}\rho_2}{\mathrm{d}x}(\xi) \leqq 0$$

and hence $\pm\phi(\xi) \leqq 0$, so $\phi(\xi) = 0$. Thus we have that $\rho_1 = \rho_2 = \phi = 0$ at ξ, so $\rho_1 \equiv \rho_2 \equiv \phi \equiv 0$, a contradiction (to the ODE existence and uniqueness theorem). Hence $\rho_2(\xi) > 0$.

We now apply the boundary point version of Proposition 2.3 to ρ_1, which is a positive solution of (2.9) on the interval $[0, \xi]$. Thus $\phi(\xi) = \sigma\rho_1' + \psi_1'\rho_1 < 0$, from the equation, while $\mathrm{d}\phi(\xi)/\mathrm{d}x \leqq 0$, also from the equation. So $\rho_1 < 0,\ \rho_2 > 0$ and $\phi < 0$ in an interval $(\xi, \xi + \delta)$ while also $\mathrm{d}\phi/\mathrm{d}x \leqq 0$. As long as $\rho_1 < 0,\ \rho_2 > 0$, we have that $\phi < 0$ and $\mathrm{d}\phi/\mathrm{d}x \leqq 0$. Suppose that $\rho_1(\xi') = 0,\ \xi < \xi'$. We still have that $\phi(\xi') < 0$, since otherwise the decreasing function ϕ is identically zero on the interval (and thus ρ_1 cannot vanish from the equation). But

$$0 \leqq \frac{\mathrm{d}\rho_1}{\mathrm{d}x}(\xi') = \phi(\xi')$$

which is a contradiction. The same conclusion holds if $\rho_2(\xi') = 0$. Therefore, these inequalities are maintained until $x = 1$, whence $\phi(1) < 0$, which is a contradiction. If $\rho_1(1) = 0$, then by the boundary point lemma, we have again that $\phi(1) < 0$, but $\phi(1) = 0$. So $\rho_1 > 0$ in $\overline{\Omega}$. Similarly, $\rho_2 > 0$ in $\overline{\Omega}$. □

4. Transport: asymptotic behavior of the solution for small σ

In this section we show that our system exhibits transport, more precisely, that the mass of the stationary solution found in Theorem 2.1 decays exponentially away from one endpoint of the interval Ω. The demonstration has two parts. First we show that $\rho_1 + \rho_2$ decreases exponentially between successive maxima of the potentials. This involves a detailed study of the fundamental solution matrix of the first order system (3.23). To give a brief oversimplified idea, the solution of (3.23) may, locally, decrease exponentially, remain bounded, or increase exponentially as $x \to 1$ depending on the eigenvalues of the system. These depend on the ψ_i' and the support of the ν_i. To impede exponential increase, the potentials cannot be simultaneously decreasing and to have exponential decrease, there must be intervals where both potentials are increasing. This gives rise to the conditions below. Indeed, if we think of ψ_1 as the translate by half a period of ψ_2, the role of asymmetry is now obvious, since the interval in which a ψ_i is increasing must be longer than the one in which it is decreasing. The second part of the proof is to apply a scaling argument to obtain the conclusion at all points between the maxima. The main estimate here is based on our usual maximum principle applied in a different context to a specially chosen solution of (1.4), (1.5).

Let us impose these general conditions on the data:

(1) ψ_i and $\nu_i, i = 1, 2$, are in $C^2(\overline{\Omega})$ of period $1/N$;
(2) $\psi_i \geqq 0$ and $\nu_i \geqq 0, i = 1, 2$.

Theorem 4.1. *Assume that*

(1) in each period ψ_i has exactly one maximum and one minimum with $\psi_i'' < 0$ at the maximum and $\psi_i' \neq 0$ between the maxima and minima of $\psi_i, i = 1, 2$;
(2) $\psi_1' > 0$ on each interval where $\psi_2' \leqq 0$ and $\psi_2' > 0$ on each interval where $\psi_1' \leqq 0$;
(3) there are $c_0 > 0$ and $\delta > 0$ and a positive integer m such that for a minimum a_i of $\psi_i, \nu_i(x) \geqq c_0(x-a_i)^m$ on $(a_i, a_i + \delta)$.

Let ξ_0 denote the first maximum of ψ_2 and let $x_j = \xi_0 + \frac{j}{N}, 1 \leqq j \leqq N-1$ and $x_N = 1$. Then there are $c > 0$, independent of σ sufficiently small, and $K > 0$, which may depend on σ, but not j or N, such that the solution of (1.4), (1.5) satisfies

$$\max_{x_j \leqq x \leqq x_{j+1}} (\rho_1(x) + \rho_2(x)) \leqq K e^{-\frac{jc}{\sigma}}, \quad 1 \leqq j \leqq N. \tag{4.24}$$

With some trivial manipulation, (4.24) may be expressed as: there are constants K_0, c such that

$$\rho_1(x) + \rho_2(x) \leqq K_0 e^{-\frac{cN}{\sigma}(x-\xi_0)}, \quad x \geqq \xi_0. \tag{4.25}$$

Note that 3 above implies the asymmetric location of the minima of the ψ_i in their potential wells.

We now discuss exponential decay between potential maxima, the first part described at the beginning of the section. For convenience, we assume that the coefficients ψ_i and ν_i have period 1 and the problem is defined on the interval $(0, N)$, where $N > 1$. To review,

$$\begin{aligned} \sigma\frac{d\rho_1}{dx} &= \phi - \psi_1'\rho_1 \\ \sigma\frac{d\rho_2}{dx} &= -\phi - \psi_2'\rho_2 \qquad \text{in } [0,N] \\ \frac{d\phi}{dx} &= \nu_1\rho_1 - \nu_2\rho_2 \\ \phi(0) &= \phi(N) = 0. \end{aligned} \tag{4.26}$$

Theorem 4.2. *With the assumptions of Theorem 4.1, scaled to $[0, N]$, let y_0 denote the first maximum of ψ_2 and let $y_j = y_0 + j, 1 \leqq j \leqq N-1$. Then there are $c > 0$ and $K > 0$, independent of σ sufficiently small, such that the solution of (4.26) satisfies*

$$\rho_1(y_j) + \rho_2(y_j) \leqq K e^{-\frac{c}{\sigma}} (\rho_1(y_{j-1}) + \rho_2(y_{j-1})), \quad j = 1...N-1. \tag{4.27}$$

Proof. To start, consider $R(\xi, x)$ a fundamental solution of (4.26), $\xi \leqq x$, with $R(\xi, \xi) = \mathbf{1}$, the 3×3 identity matrix. So

$$p(x) = R(\xi, x)p(\xi).$$

Write

$$R = \begin{pmatrix} \rho_{11} & \rho_{12} & \rho_{13} \\ \rho_{21} & \rho_{22} & \rho_{23} \\ \phi_1 & \phi_2 & \phi_3 \end{pmatrix}.$$

The same comparison technique used in the proof of the Lemma 3.1 shows that

$$\begin{aligned} &\rho_{11} > 0 \;\; \rho_{12} \leqq 0 \;\; \rho_{13} > 0 \\ &\rho_{21} \leqq 0 \;\; \rho_{22} > 0 \;\; \rho_{23} < 0 \quad \textit{for } x \in (\xi_1, \xi_2] \\ &\phi_1 \geqq 0 \;\; \phi_2 \leqq 0 \;\; \phi_3 \geqq 1. \end{aligned}$$

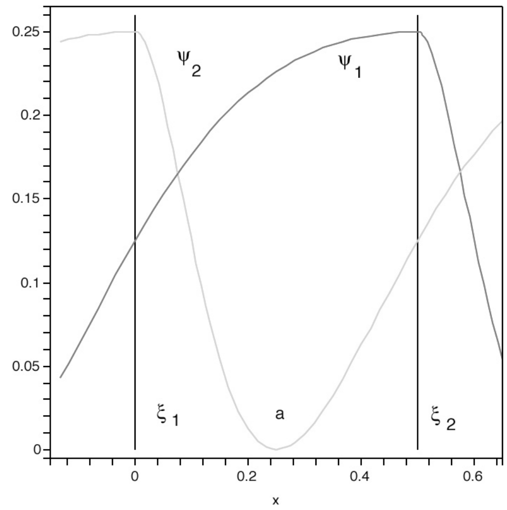

FIGURE 2. Setup for the proof of Theorem 4.2.

This gives us the convenient sign map

$$sign(R) = \begin{pmatrix} + & - & + \\ - & + & - \\ + & - & + \end{pmatrix}.$$

Let $[\xi_1, \xi_1 + 1]$ be a period interval of ψ_2 with $\psi_2(\xi_1) = \psi_2(\xi_1 + 1) = max\ \psi_2$ and let $a,\ \xi_1 < a < \xi_1 + 1$ be the minimum of ψ_2 in $[\xi_1, \xi_1 + 1]$. Say $\psi_2(a) = 0$. According to the hypothesis, there is a ξ_2 with $\psi_1(\xi_2) = \max\ \psi_1$, and

$$\xi_1 < a < \xi_2 < \xi_1 + 1.$$

We have, for example,

$$p(a) = R(\xi_1, a)p(\xi_1) \quad \text{and} \quad p(\xi_2) = R(\xi_1, \xi_2)p(\xi_1).$$

Since $\rho_i > 0$, the additional function ϕ can be eliminated from the equation (4.26) in favor of an inequality. Indeed,

$$0 < \rho_1(x) = \rho_{11}\rho_1(\xi) + \rho_{12}\rho_2(\xi) + \rho_{13}\phi(\xi), \quad x > \xi \tag{4.28}$$

$$0 < \rho_2(x) = \rho_{21}\rho_1(\xi) + \rho_{22}\rho_2(\xi) + \rho_{23}\phi(\xi), \quad x > \xi \tag{4.29}$$

where the ρ_{ij} are evaluated at x. Hence, checking the sign map,

$$\phi(\xi) > -\frac{\rho_{11}}{\rho_{13}}\rho_1(\xi) - \frac{\rho_{12}}{\rho_{13}}\rho_2(\xi) \ \text{ and} \tag{4.30}$$

$$\phi(\xi) < -\frac{\rho_{21}}{\rho_{23}}\rho_1(\xi) - \frac{\rho_{22}}{\rho_{23}}\rho_2(\xi). \tag{4.31}$$

Combining this with (4.28), (4.29) and reconfiguring gives that

$$\rho_1(x) < \frac{\rho_{13}\rho_{21} - \rho_{11}\rho_{23}}{-\rho_{23}}\rho_1(\xi) + \frac{\rho_{22}\rho_{13} - \rho_{12}\rho_{23}}{-\rho_{23}}\rho_2(\xi)$$

$$\rho_2(x) < \frac{\rho_{13}\rho_{21} - \rho_{11}\rho_{23}}{\rho_{13}}\rho_1(\xi) + \frac{\rho_{22}\rho_{13} - \rho_{12}\rho_{23}}{\rho_{13}}\rho_2(\xi).$$

A first thought here is that when a typical ρ_{ij} varies with $\exp(c/\sigma)$, the fraction varies like $\exp(c/\sigma)^2/\exp(c/\sigma) = \exp(c/\sigma)$, that is, exponential in $1/\sigma$. Interesting here is that the numerators in the fractions are the terms $(adj\ R)_{23}$ and $(adj\ R)_{13}$ and the adjugate itself satisfies an equation (a variation of Abel's formula), *cf.* [14, 25],

$$\frac{\mathrm{d}}{\mathrm{d}x} adj\ R = adj\ R\ M, \quad M = (trace\ A)\mathbf{1} - A \tag{4.32}$$

where we are taking the adjugate to be

$$adj(R) = det(R)R^{-1}:$$

which means that the numerator and the denominator are typically of the same order. This is the starting point of the proof.

Our objective is to show that

$$\lim_{\sigma\to 0^+} \frac{\rho_{13}\rho_{21} - \rho_{11}\rho_{23}}{-\rho_{23}} = 0, \quad \lim_{\sigma\to 0^+} \frac{\rho_{22}\rho_{13} - \rho_{12}\rho_{23}}{-\rho_{23}} = 0,$$

and

$$\lim_{\sigma\to 0^+} \frac{\rho_{13}\rho_{21} - \rho_{11}\rho_{23}}{\rho_{13}} = 0, \quad \lim_{\sigma\to 0^+} \frac{\rho_{22}\rho_{13} - \rho_{12}\rho_{23}}{\rho_{13}} = 0$$

with an exponential rate of decay in each case. Consider first

$$\frac{\rho_{13}\rho_{21} - \rho_{11}\rho_{23}}{-\rho_{23}}. \tag{4.33}$$

Let

$$W = adj(R) = (w_{ij}) = \begin{pmatrix} \rho_{22}\phi_3 - \rho_{23}\phi_2 & \rho_{13}\phi_2 - \rho_{12}\phi_3 & \rho_{12}\rho_{23} - \rho_{13}\rho_{22} \\ \rho_{23}\phi_1 - \rho_{21}\phi_3 & \rho_{11}\phi_3 - \rho_{13}\phi_1 & \rho_{13}\rho_{21} - \rho_{11}\rho_{23} \\ \rho_{21}\phi_2 - \rho_{22}\phi_1 & \rho_{12}\phi_1 - \rho_{11}\phi_2 & \rho_{11}\rho_{12} - \rho_{21}\rho_{22} \end{pmatrix}.$$

For this way of writing, the rows of W satisfy the system (4.32) determined by M.

Note that

$$M = \begin{pmatrix} -\frac{1}{\sigma}\psi_2' & 0 & -\frac{1}{\sigma} \\ 0 & -\frac{1}{\sigma}\psi_1' & \frac{1}{\sigma} \\ -\nu_1 & \nu_2 & -\frac{1}{\sigma}(\psi_1' + \psi_2') \end{pmatrix}.$$

Now the term in (4.33) that we are considering is w_{23} in the second row of W. Dropping the subscript 2, let

$$w = (w_1, w_2, w_3)$$

denote this second row. Then our usual comparison methods, and what we already know from the sign matrix, tell us that

$$w_1 \leqq 0, \quad w_2 \geqq 0, \quad w_3 > 0 \quad \text{and} \quad w(\xi_1) = (0, 1, 0).$$

Lemma 4.3. *There are $K > 0$ and $c > 0$ independent of σ so that*

$$|w(a)| \leqq K\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)} \tag{4.34}$$

and

$$|w(\xi_2)| \leqq K\mathrm{e}^{\frac{1}{\sigma}(\psi_2(\xi_1) - c)} \tag{4.35}$$

as $\sigma \to 0$.

Proof. Let

$$v(x) = \mathrm{e}^{\frac{1}{\sigma}\psi_2(x)} w(x), \quad x \geqq \xi_1$$

so that

$$\frac{\mathrm{d}v}{\mathrm{d}x} = v(M + \frac{1}{\sigma}\psi_2' \mathbf{1}), \quad M + \frac{1}{\sigma}\psi_2' \mathbf{1} = \begin{pmatrix} 0 & 0 & -\frac{1}{\sigma} \\ 0 & \frac{1}{\sigma}(\psi_2' - \psi_1') & \frac{1}{\sigma} \\ -\nu_1 & \nu_2 & -\frac{1}{\sigma}\psi_1' \end{pmatrix}.$$

We prove the first part of the lemma by estimating v. Note that $\psi_1' \geqq \alpha$ and $\psi_2' \leqq 0$ on $[\xi_1, a]$. This means that we can compare v with q, where

$$\frac{\mathrm{d}q}{\mathrm{d}x} = qP, \quad \text{with} \quad P = \begin{pmatrix} 0 & 0 & \frac{1}{\sigma} \\ 0 & -\frac{\alpha}{\sigma} & \frac{1}{\sigma} \\ \overline{\nu} & \overline{\nu} & -\frac{\alpha}{\sigma} \end{pmatrix} \tag{4.36}$$

$$q(\xi_1) = \left(0, \mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}, 0\right) \tag{4.37}$$

where $\overline{\nu} = \max_i\{\nu_i(x)\}$. Namely, simple comparison methods show that $0 \leqq -v_1 \leqq q_1, 0 \leqq v_2 \leqq q_2$ and $0 \leqq v_3 \leqq q_3$. To see this, note that $q(\xi_1) = v(\xi_1)$ and let q_δ be the solution of

$$\frac{\mathrm{d}q_\delta}{\mathrm{d}x} = q_\delta P + \delta(1,1,1), \quad q_\delta(\xi_1) = q(\xi_1).$$

Now $q_{i\ \delta}'(x) > v_i'(x)$ for $x \in [\xi_1, a]$ and also $q_{i\ \delta}(x) > v_i(x)$ for $x \in [\xi_1, \xi_1 + \epsilon]$. If there is an initial point x_1 where $q_{i\ \delta}(x_1) = v_i(x_1)$, then $q_{i\ \delta}'(x_1) \leqq v_i'(x_1)$, a contradiction. Now let $\delta \to 0$.

The eigenvalues of P are of the form

$$-\frac{\alpha}{\sigma} + O(1), -\frac{\alpha}{\sigma} + O(1), O(1) \quad \textit{as } \sigma \to 0.$$

This implies that $|q(a)| \leqq K|q(\xi_1)| = K\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}$ for some $K > 0$ independent of σ.

We now wish to extend the estimate to $x = \xi_2$, which is the maximum point of ψ_1. Note that

$$\psi_1' \geqq 0, \ \psi_2' \geqq 0, \quad \text{and} \quad \psi_1' + \psi_2' \geqq \alpha > 0, \quad \text{in } [a, \xi_2] \text{ independent of } \sigma$$

for some α. We must separate the interval $[a, \xi_2]$ into three subintervals $[a, a+\delta], [a+\delta, \xi_2-\delta]$ and $[\xi_2-\delta, \xi_2]$. On the first and last intervals w is bounded while in the middle $|w|$ decreases with $|w(\xi_2-\delta)/w(a+\delta)|$ exponentially small.

Suppose that $\psi_1' \geqq \beta$ on $[a, a+\delta]$. We compare w with q where

$$\frac{\mathrm{d}q}{\mathrm{d}x} = qP, \quad \text{with} \quad P = \begin{pmatrix} 0 & 0 & \frac{1}{\sigma} \\ 0 & -\frac{\beta}{\sigma} & \frac{1}{\sigma} \\ \overline{\nu}_1 & \overline{\nu}_2 & -\frac{\alpha}{\sigma} \end{pmatrix} \tag{4.38}$$

$$q(a) = (-w_1(a), w_2(a), w_3(a)) \tag{4.39}$$

where $\overline{\nu}_i = \max_x \nu_i(x)$. Then $-w_1 \leqq q_1, w_2 \leqq q_2$ and $w_3 \leqq q_3$ on $[a, a+\delta]$. The eigenvalues of P are of the form

$$-\frac{\alpha}{\sigma} + O(1), -\frac{\beta}{\sigma} + O(1), O(1) \quad \text{as } \sigma \to 0,$$

from which it follows that $|v| \leqq K|w(a)|$ for some K independent of σ on $[a, a+\delta]$.

So far we have used that ψ_1 is increasing to maintain the boundedness of w. Now we use that both are increasing on $[a+\delta, \xi_2 - \delta]$ to show that w is exponentially decreasing. Say

$$\psi_1' \geqq \kappa \text{ and } \psi_2' \geqq \kappa, \quad \text{in } [a+\delta, \xi_2-\delta] \text{ independent of } \sigma.$$

The relevant comparison system here is

$$\frac{\mathrm{d}q}{\mathrm{d}x} = qP, \quad \text{with } P = \begin{pmatrix} -\frac{\kappa}{\sigma} & 0 & \frac{1}{\sigma} \\ 0 & -\frac{\kappa}{\sigma} & \frac{1}{\sigma} \\ \overline{\nu}_1 & \overline{\nu}_2 & -\frac{2\kappa}{\sigma} \end{pmatrix} \tag{4.40}$$

$$q(a+\delta) = (-w_1(a+\delta), w_2(a+\delta), w_3(a+\delta)). \tag{4.41}$$

For this P, the eigenvalues are of the form

$$-\frac{\kappa}{\sigma} + O(1), -\frac{\kappa}{\sigma} + O(1), -\frac{2\kappa}{\sigma} + O(1) \quad \text{as } \sigma \to 0.$$

From this it follows that

$$|w(\xi_2 - \delta)| \leqq K\mathrm{e}^{-\frac{c}{\sigma}}|w(a+\delta)|.$$

Finally, we may check that $|w(\xi_2)|/|w(\xi_2-\delta)|$ remains bounded using the same technique as for the interval $[a, a+\delta]$.

Putting together all these estimates shows that

$$|w(\xi_2)| \leqq K\mathrm{e}^{\frac{1}{\sigma}(\psi_2(\xi_1)-c)} \quad \text{as } \sigma \to 0. \tag{4.42}$$

This proves the lemma. □

Maintaining our interest in the minimum point a and the maximum point ξ_1, we look for an upper bound on ρ_{23}.

Lemma 4.4. *There is are $\epsilon > 0, K > 0$, and k, all independent of σ, such that*

$$\rho_{23}(a) \leqq -K\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)} \tag{4.43}$$

and

$$\rho_{23}(\xi_2) \leqq -K\sigma^k \mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}. \tag{4.44}$$

Proof. From the equation, we have that

$$\frac{\mathrm{d}}{\mathrm{d}x}\rho_{23} = -\frac{\phi_3}{\sigma} - \frac{\psi_2'}{\sigma}\rho_{23} \leqq -\frac{1}{\sigma} - \frac{\psi_2'}{\sigma}\rho_{23}, \quad x \geqq \xi_1$$

since $\phi_3(\xi_1) = 1$ and $\phi_3' = \nu_1\rho_{13} - \nu_2\rho_{23} \geqq 0$. Therefore,

$$\frac{\mathrm{d}}{\mathrm{d}x}\left(\rho_{23}(x)\mathrm{e}^{\frac{1}{\sigma}\psi_2(x)}\right) \leqq -\frac{1}{\sigma}\mathrm{e}^{\frac{1}{\sigma}\psi_2(x)}, \quad \text{with } \rho_{23}(\xi_1) = 0.$$

So we find that

$$\rho_{23}(a) \leqq -\frac{1}{\sigma}\mathrm{e}^{-\frac{1}{\sigma}\psi_2(a)}\int_{\xi_1}^{a}\mathrm{e}^{\frac{1}{\sigma}\psi_2(x)}\mathrm{d}x.$$

Now we have assumed that $\psi_2(a)=0$ and ψ_2' is bounded. There are $\gamma_1>0, \delta>0$ such that

$$\psi_2(x) \geqq \psi_2(\xi_1) - \gamma_1(x-\xi_1) \text{ in } \xi_1 \leqq x \leqq \xi_1+\delta.$$

Consequently

$$\rho_{23}(a) \leqq -\frac{1}{\sigma}\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}\int_{\xi_1}^{\xi_1+\delta}\mathrm{e}^{-\frac{\gamma_1}{\sigma}(x-\xi_1)}\mathrm{d}x.$$

Hence we obtain that for σ sufficiently small,

$$\rho_{23}(a) \leqq -K\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)} \tag{4.45}$$

which is the statement of the first part of the lemma.

We now proceed to the lower bound for $\rho_{23}(\xi_2)$. Integrating the equation satisfied by ρ_{23} over $[a,\xi_2]$, we obtain, using (4.45),

$$\rho_{23}(x) = \rho_{23}(a)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(a)-\psi_2(x))} - \frac{1}{\sigma}\int_a^x \phi_3(s)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(s)-\psi_2(x))}\mathrm{d}s. \tag{4.46}$$

We estimate ϕ_3 by noting that $\phi_3' \geqq -\nu_2\rho_{23} \geqq 0$; whence,

$$\phi_3(x)-\phi_3(a) \geqq -\int_a^x \nu_2(t)\rho_{23}(t)\mathrm{d}t \tag{4.47}$$

$$\geqq -\int_a^x \nu_2(t)\rho_{23}(a)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(a)-\psi_2(x))}\mathrm{d}t \tag{4.48}$$

by (4.46). Now $\phi_3 \geqq 0$, so

$$-\phi_3(x) \leqq \int_a^x \nu_2(t)\rho_{23}(a)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(a)-\psi_2(x))}\mathrm{d}t. \tag{4.49}$$

This resubstituted into (4.46) gives that (note: $\psi_2(a)=0$)

$$\rho_{23}(x) \leqq \mathrm{e}^{-\frac{1}{\sigma}\psi_2(x)}\frac{1}{\sigma}\int_a^x \mathrm{e}^{\frac{1}{\sigma}\psi_2(s)}\int_a^s \nu_2(t)\rho_{23}(a)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(a)-\psi_2(t))}\mathrm{d}t\mathrm{d}s \tag{4.50}$$

$$= -K\mathrm{e}^{\frac{1}{\sigma}(\psi_2(\xi_1)-\psi_2(x))}\int_a^x \frac{1}{\sigma}\mathrm{e}^{\frac{1}{\sigma}\psi_2(s)}\int_a^s \nu_2(t)\mathrm{e}^{-\frac{1}{\sigma}\psi_2(t)}\mathrm{d}t\mathrm{d}s \tag{4.51}$$

using (4.45). Therefore

$$\rho_{23}(\xi_2) \leqq -K\mathrm{e}^{\frac{1}{\sigma}(\psi_2(\xi_1)-\psi_2(\xi_2))}\int_{\xi_2-\delta}^{\xi_2}\frac{1}{\sigma}\mathrm{e}^{\frac{1}{\sigma}\psi_2(s)}\int_a^{a+\delta}\nu_2(t)\mathrm{e}^{-\frac{1}{\sigma}\psi_2(t)}\mathrm{d}t\mathrm{d}s. \tag{4.52}$$

To show that this leads to a nondegenerate estimate, that is, that the right hand side is less than zero, we employ here our hypothesis that $\nu_2(x) \geqq c_0(x-a)^m$ for $x \geqq a$. So

$$\int_a^{a+\delta}\nu_2(t)\mathrm{e}^{-\frac{1}{\sigma}\psi_2(t)}\mathrm{d}t \geqq C_1\sigma^k \tag{4.53}$$

for some k and $C_1 > 0$. Now let us do the accounting. (4.52) implies that for some $\epsilon > 0, K > 0$, and k, all independent of σ,

$$\rho_{23}(\xi_2) \leqq -K\mathrm{e}^{\frac{1}{\sigma}(\psi_2(\xi_1)-\psi_2(\xi_2))}\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_2)}\sigma^k \tag{4.54}$$

$$\leqq -K\sigma^k\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}. \tag{4.55}$$

This proves the lemma. □

Combining (4.42) with this, (4.44), with shows that

$$\frac{\rho_{13}\rho_{21}-\rho_{11}\rho_{23}}{-\rho_{23}} = O\left(\mathrm{e}^{-\frac{c}{\sigma}}\right) \quad as \quad \sigma \to 0^+.$$

To estimate

$$\frac{\rho_{13}\rho_{21}-\rho_{11}\rho_{23}}{\rho_{13}} \tag{4.56}$$

we compute a lower bound for ρ_{13}, known to be nonnegative and to vanish at ξ_1. One difference between this estimate and the preceding one for ρ_{23} is that it involves both ψ_1 and ψ_2. Since the estimate follows by direct integration, we do not isolate it as a separate lemma. The equation for ρ_{13} is

$$\frac{\mathrm{d}}{\mathrm{d}x}\rho_{13} = \frac{1}{\sigma}\left(-\frac{\mathrm{d}}{\mathrm{d}x}\psi_1\rho_{13}+\phi_3\right)$$

so, since $\phi_3 \geqq 0$,

$$\rho_{13}(x) = \frac{1}{\sigma}\mathrm{e}^{-\frac{1}{\sigma}\psi_1(x)}\int_{\xi_1}^{x}\mathrm{e}^{\frac{1}{\sigma}\psi_1(s)}\phi_3(s)\mathrm{d}s \tag{4.57}$$

$$\geqq \frac{1}{\sigma}\mathrm{e}^{-\frac{1}{\sigma}\psi_1(x)}\int_{a}^{x}\mathrm{e}^{\frac{1}{\sigma}\psi_1(s)}\phi_3(s)\mathrm{d}s \tag{4.58}$$

and using (4.49), (4.53), for some k, K, which are independent of σ but which may change from line to line,

$$\rho_{13}(\xi_2) \geqq -\frac{1}{\sigma}\mathrm{e}^{-\frac{1}{\sigma}\psi_1(\xi_2)}\int_{a}^{\xi_2}\mathrm{e}^{\frac{1}{\sigma}\psi_1(s)}\int_{a}^{s}\nu_2(t)\rho_{23}(a)\mathrm{e}^{\frac{1}{\sigma}(\psi_2(a)-\psi_2(t))}\mathrm{d}t\mathrm{d}s \tag{4.59}$$

$$\geqq K\sigma^k\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)}\int_{\xi_2-\delta}^{\xi_2}\mathrm{e}^{\frac{1}{\sigma}(\psi_1(s)-\psi_1(\xi_2))}\int_{a}^{a+\delta}\nu_2(t)\mathrm{e}^{-\frac{1}{\sigma}\psi_2(t)}\mathrm{d}t\mathrm{d}s \tag{4.60}$$

$$\geqq K\sigma^k\mathrm{e}^{\frac{1}{\sigma}\psi_2(\xi_1)} \tag{4.61}$$

for σ sufficiently small. Now combining this with (4.42) shows that

$$\frac{\rho_{13}\rho_{21}-\rho_{11}\rho_{23}}{\rho_{13}} = O\left(\mathrm{e}^{-\frac{c}{\sigma}}\right) \quad \text{as} \quad \sigma \to 0^+.$$

This establishes half of the estimates, but it is thankfully most of the work. To complete the proof, we must estimate terms involving

$$-w_{13} = \rho_{22}\rho_{13} - \rho_{12}\rho_{23}.$$

So we now let

$$w = (\rho_{22}\phi_3 - \rho_{23}\phi_2, \rho_{13}\phi_2 - \rho_{12}\phi_3, \rho_{12}\rho_{23} - \rho_{13}\rho_{22})$$

the first row of $adj(R)$, which satisfies

$$w(\xi_1) = (1, 0, 0).$$

The analysis is very similar to the previous case. Interchanging the roles of ψ_2 and ψ_1, we extend the result to $\xi_0 + 1$. This concludes the proof of Theorem 4.2. □

We now address the second part of the enterprise, the extension of the estimates to the entire interval. Recall we are thinking of the problem as defined on $(0, N)$ and, as usual, $\Omega = (0, 1)$.

Theorem 4.5. *Suppose that $\varphi_i \geqq 0$ and $\lambda_i \geqq 0$ are smooth, $\sigma > 0$, and $\lambda_i \not\equiv 0, i = 1, 2$. Let $\eta = (\eta_1, \eta_2)$ be a solution of*

$$L\eta = -\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}\eta}{\mathrm{d}x} + \eta\Phi'\right) - \eta\lambda = 0 \text{ in } \Omega$$

$$\eta|_{x=0} = \eta^{(0)}, \quad \eta|_{x=1} = \eta^{(1)}.$$

There is a constant $M > 0$ (independent of η) such that

$$\|\eta\|_{C(\overline{\Omega})} \leqq M\left(|\eta^{(0)}| + |\eta^{(1)}|\right).$$

Above we have written the equation in the obvious vector form with

$$\Phi' = \begin{pmatrix} \varphi_1' & 0 \\ 0 & \varphi_2' \end{pmatrix} \quad \text{and} \quad \lambda = \begin{pmatrix} -\lambda_1 & \lambda_1 \\ \lambda_2 & -\lambda_2 \end{pmatrix}.$$

Proof. For the proof, let f denote the solution of

$$Lf = 0 \quad \text{in } \Omega \tag{4.62}$$

$$\frac{\mathrm{d}f}{\mathrm{d}x} + f\Phi' = 0 \quad \text{on } \partial\Omega. \tag{4.63}$$

We know that this problem has a unique solution which may be also taken to satisfy

$$\int_\Omega (f_1 + f_2)\mathrm{d}x = 1.$$

It enjoys the additional property that $f_i > 0$ in Ω. Hence for $\epsilon > 0$ small enough,

$$f_i - \epsilon\eta_i > 0 \text{ in } \Omega.$$

Choose ϵ as large as possible:

$$f_i - \epsilon\eta_i > 0 \text{ in } \Omega, \quad i = 1, 2$$

$$f_j(x_0) - \epsilon\eta_j(x_0) = 0, \quad \text{for some } j = 1, 2, \text{ and } x_0 \in \overline{\Omega}.$$

Say $j = 1$. Let $v = f - \epsilon\eta$. Then

$$-\frac{\mathrm{d}}{\mathrm{d}x}\left(\sigma\frac{\mathrm{d}v_1}{\mathrm{d}x} + \varphi_1' v_1\right) + \lambda_1 v_1 = \lambda_2 v_2 \geqq 0 \quad \text{in } \Omega.$$

So if the minimum of v_1 is attained in Ω, it is positive. Thus, by our choice of ϵ, it must be attained at $x = 0$ or $x = 1$ according to Proposition 2.3, the elementary maximum principle redux. Say $v_1(0) = \min\ v_1$. Then we compute that

$$\frac{1}{\epsilon} = \frac{\eta_1(0)}{f_1(0)} \quad \text{and} \quad \eta_1(x) \leqq \frac{\eta_1(0)}{f_1(0)} f_1(x)$$

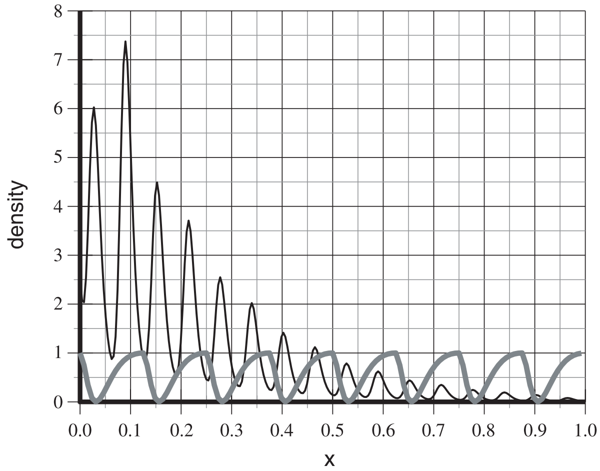

FIGURE 3. Transport realized in an eight well system. The upper curve is $\rho_1(x) + \rho_2(x)$. The lower gray curve is $\psi_1(x)$ and ψ_2 is ψ_1 translated by half a period. The conformational change coefficients ν_i have their maxima at the bottoms of the potential wells.

so in general,

$$\eta_i(x) \leqq \frac{|\eta^{(0)}| + |\eta^{(1)}|}{\min(f_1(0), f_2(0), f_1(1), f_2(1))} f_i(x)$$

and the theorem is proved with

$$M = \frac{1}{\min(f_1(0), f_2(0), f_1(1), f_2(1))} \max_{i=1,2} \max_{\Omega} f_i(x).$$

To complete the proof of Theorem 4.1, still retaining the stretched coordinates $(0, N)$, we determine M by solving the problem (4.63) in a period interval, say $\Omega = (\xi_0, \xi_0 + 1)$. We take $\eta = \rho$ in this interval and compare it with f. Then

$$\begin{aligned}\max_{y_j \leqq x \leqq y_{j+1}} (\rho_1 + \rho_2) &\leqq M(\rho_1(y_j) + \rho_2(y_j) + \rho_1(y_{j+1}) + \rho_2(y_{j+1})) \\ &\leqq MK\mathrm{e}^{-\frac{c}{\sigma}}(\rho_1(y_{j-1}) + \rho_2(y_{j-1}) + \rho_1(y_j) + \rho_2(y_j)) \\ &= \hat{K}\mathrm{e}^{-\frac{cj}{\sigma}}.\end{aligned}$$

The final detail is that there may be an unaccounted for interval (y_{N-1}, N) in this induction. For this interval, the $\eta = \rho$ on (y_{N-1}, N) satisfies a mixed problem, Dirichlet on the left and natural boundary conditions on the right. This may be compared with a second choice of f, the solution of (4.62), (4.63) on (y_{N-1}, N).

The result in Theorem 4.1 may be extended to piecewise continuous potentials. We observe that the scaling estimate argument of Theorem 4.5 may serve as the basis of an existence theory for the Dirichlet Problem for this system. □

5. LONG TIME BEHAVIOR: TREND TO STATIONARITY

The free energy associated to (1.1), (1.2) is

$$F(\rho) = \sum_i \int_\Omega (\psi_i \rho_i + \sigma \rho_i \ log \ \rho_i)\mathrm{d}x.$$

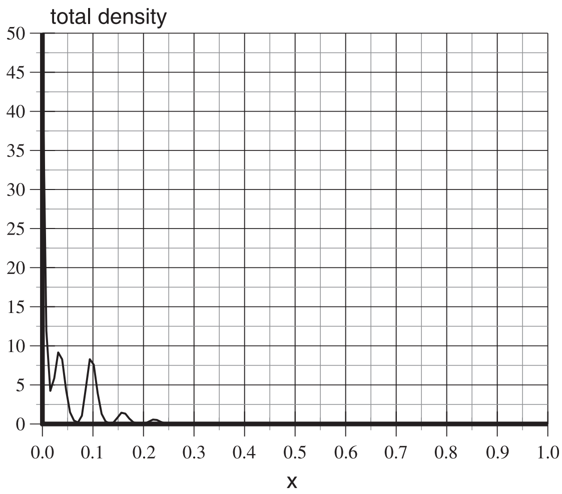

FIGURE 4. This simulation is identical to Figure 3 except that ψ_1 and ψ_2 have been replaced by $2\psi_1$ and $2\psi_2$. This is approximately the same as halving the diffusion coefficient.

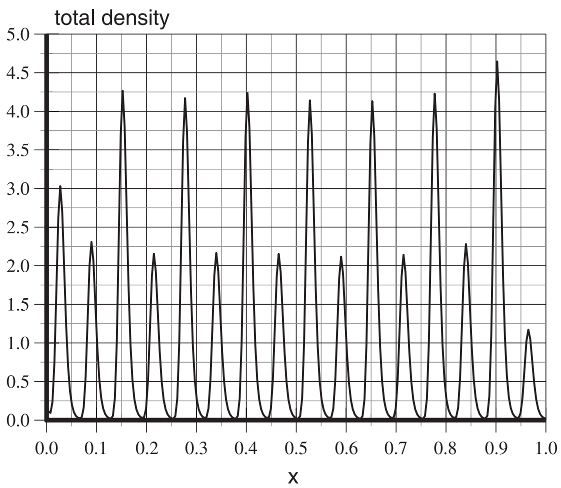

FIGURE 5. This simulation is identical to Figure 3 except that the conformational change coefficients ν_i have been translated so their maxima occur at the maxima of the potential wells.

The solution $\rho^\sharp$ of the stationary equations (1.4), (1.5) is not a minimum of F and, in fact, there does not seem to be a natural Lyapunov function or H-function for this system. Moreover, $F(\rho)$ is not decreasing along a trajectory of (1.1), (1.2). This complicates the search for a proof of asymptotic behavior of the system. However, the analytical structure is simple enough that we may appeal to a variant of the Krein-Rutman Theorem to understand this issue, *cf.* for example [29] for an extensive discussion. The main tool is the standard maximum principle for weakly coupled parabolic systems, the version of Proposition 2.3, *the elementary maximum principle redux*, we introduced earlier for stationary systems, also found in Protter and Weinberger, [22], p. 188. Throughout we assume some simple properties of the data:

$\psi_i \in C^3(\overline{\Omega}), \psi_i \geqq 0, i = 1, 2;$
$\nu_i \in C^3(\overline{\Omega}), \nu_i \geqq 0$ and $\nu_i \not\equiv 0$ for each $i = 1, 2;$
$\sigma > 0$ constant.

It may be convenient to write the system in vector form, with

$$\Psi' = \begin{pmatrix} \psi_1' & 0 \\ 0 & \psi_2' \end{pmatrix} \quad \text{and} \quad \nu = \begin{pmatrix} -\nu_1 & \nu_1 \\ \nu_2 & -\nu_2 \end{pmatrix}$$

as

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial x}\left(\sigma \frac{\partial \rho}{\partial x} + \rho \Psi'\right) + \rho\nu \ \text{ in } \Omega,\ t > 0 \tag{5.64}$$

$$\sigma \frac{\partial \rho}{\partial x} + \rho \Psi' = 0 \ \text{ on } \partial\Omega,\ t > 0. \tag{5.65}$$

For

$$u_i = \mathrm{e}^{\frac{1}{\sigma}\psi_i}\rho_i \quad \alpha_i = \mathrm{e}^{-\frac{1}{\sigma}\psi_i}, \quad \mu_i = \mathrm{e}^{-\frac{1}{\sigma}\psi_i}\nu_i, i = 1, 2$$

we have a divergence form, actually the adjoint system, where to retain conventional notions, we express u as a column vector, and set

$$\alpha = \begin{pmatrix} \alpha_1 & 0 \\ 0 & \alpha_2 \end{pmatrix} \quad \text{and} \quad \mu = \begin{pmatrix} -\mu_1 & \mu_2 \\ \mu_1 & -\mu_2 \end{pmatrix}.$$

Then

$$\alpha \frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(\sigma\alpha \frac{\partial u}{\partial x}\right) + \mu u \ \text{ in } \Omega,\ t > 0 \tag{5.66}$$

$$\frac{\partial u}{\partial x} = 0 \ \text{ on } \partial\Omega,\ t > 0. \tag{5.67}$$

We denote by $\rho^\sharp$ the solution of the stationary equations (1.4), (1.5), whose components we know to be positive.

Lemma 5.1. *Let $f \in C(\overline{\Omega}) \times C(\overline{\Omega})$. There is a unique solution ρ of the evolution system (5.64), (5.65) with*

$$\rho|_{t=0} = f.$$

Moreover,

(1) $\rho \in L^\infty(\Omega \times (0, \infty)) \cap L^\infty(\epsilon, \infty; H^1(\Omega))$, *for* $\epsilon > 0$, *and there are* $M > 0, C_\tau > 0$ *depending on the problem data such that*

$$|\rho_i(x,t)| \leqq M\|f\|_{C(\overline{\Omega})},\ i = 1, 2, \mathit{and} \tag{5.68}$$

$$\|\rho(\cdot,\tau)\|_{H^1(\Omega)} \leqq C_\tau \|f\|_{C(\overline{\Omega})} \quad \mathit{for}\ \tau > 0; \tag{5.69}$$

(2) *if* $f_i \geqq 0$ *in* $\Omega, i = 1, 2$ *then* $\rho_i > 0$ *in* $\Omega, i = 1, 2$.

Proof.

Step 1. Let $\rho_i^\sharp(x) \geqq 1/C_0$ in Ω and choose M so that $C_0\rho_i^\sharp(x) \leqq M, x \in \Omega,\ i = 1, 2$.

Assume initial data η^0 smooth, not necessarily positive, for the parabolic system (5.64), (5.65). According to classical results, there is a solution $\eta \in C^2(\overline{\Omega} \times (0, \infty))$ and $u(x, 0) = u^0(x)$. Now

$$-C_0\|\eta^0\|\rho_i^\sharp \leqq \eta_i^0 \leqq C_0\|\eta^0\|\rho_i^\sharp,\ i = 1, 2$$

implies, by the maximum principle for weakly coupled systems, that

$$|\eta(x,t)| \leqq C_0\|\eta^0\|\rho_i^\sharp(x),\ i = 1, 2,$$

and hence

$$\|\eta\|_{C(\overline{\Omega}\times(0,\infty))} \leqq M\|\eta^0\|_{C(\overline{\Omega})}.$$

From this we conclude that we can extend the class of initial data to $\rho^0 \in C(\overline{\Omega})$, and second, that the solution of (5.64), (5.65) satisfies

$$|\rho_i(x,t)| \leqq M\|f\|_{C(\overline{\Omega})},\ i=1,2.$$

and if $f_i \geqq 0$,

$$0 \leqq \rho_i(x,t) \leqq M\|f\|_{C(\overline{\Omega})},\ i=1,2.$$

Step 2. The integral estimates are routine. The main feature, as suggested in the conclusion above, is that the boundedness of ρ permits us uniform H^1 estimates at each time. Note that it suffices to prove some estimate for u in view of the boundedness of ρ from Step 1. The argument has two parts, a and b.
Part a. Multiply the equation, for example, divergence form equation for u at a fixed time t, by u and integrate over Ω. After integration by parts,

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega \frac{1}{2}(\alpha_1 u_1^2 + \alpha_2 u_2^2)\mathrm{d}x = -\sigma\int_\Omega(\alpha_1(u_{1x})^2 + \alpha_2(u_{2x})^2)\mathrm{d}x + \int_\Omega u\cdot\mu u\ \mathrm{d}x.$$

Since the α_i are bounded away from 0, we obtain after rearranging that for a constants $C, \delta > 0$,

$$\delta\int_\Omega |u_x|^2\mathrm{d}x \leqq C\int_\Omega |u|^2\mathrm{d}x - \frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\frac{1}{2}(\alpha_1u_1^2+\alpha_2u_2^2)\mathrm{d}x.$$

Integrating this over $T_1 \leqq t \leqq T_2$ and using the bound for u from step 1 and positiveness of the α_i gives the estimate

$$\int_{T_1}^{T_2}\int_\Omega |u_x|^2\mathrm{d}x\mathrm{d}t \leqq C((T_2-T_1)+2)\max|u^0|^2, \tag{5.70}$$

for some constant C, where u^0 denotes the initial values of u.

Part b. We repeat the previous argument for the differentiated equation. Here, by employing the divergence form system, the boundary integrals vanish when integrating by parts. Differentiating the equation, we obtain

$$\alpha u_{xt} + \alpha_x u_t = (\sigma\alpha u_x)_{xx} + (\mu u)_x \ \text{ in } \Omega, t>0$$

and substituting the equation for $\frac{\partial u}{\partial t}$ on the left gives

$$\alpha u_{xt} + \alpha_x\alpha^{-1}(\sigma(\alpha u_x)_x + \mu u) = (\sigma\alpha u_x)_{xx} + (\mu u)_x \ \text{ in } \Omega, t>0.$$

Multiply this expression by $\frac{\partial u}{\partial x}$ and integrate over Ω. Integrate by parts in the first term on the right.

$$\begin{aligned}\frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}&\int_\Omega\left(\sum\alpha_i(u_{ix})^2\right)\mathrm{d}x\\ &+\int_\Omega(\alpha_x\alpha^{-1}(\sigma(\alpha u_x)_x+\mu u)\cdot u_x\mathrm{d}x = -\int_\Omega(\sigma\alpha u_x)_x\cdot u_{xx}\mathrm{d}x + \int_\Omega(\mu u)_x\cdot u_x\mathrm{d}x\\ &\qquad= -\int_\Omega\sigma\alpha u_{xx}\cdot u_{xx}\mathrm{d}x - \int_\Omega\sigma\alpha_x u_x\cdot u_{xx}\mathrm{d}x + \int_\Omega(\mu u)_x\cdot u_x\mathrm{d}x\\ &\qquad\leqq -c_0\int_\Omega|u_{xx}|^2\mathrm{d}x - \int_\Omega\sigma\alpha_x u_x\cdot u_{xx}\mathrm{d}x + \int_\Omega(\mu u)_x\cdot u_x\mathrm{d}x.\end{aligned}$$

Employing "Young Inequality" $ab \leqq \epsilon a^2 + C_\epsilon b^2$ with ϵ small in the usual fashion, we estimate the second integral on the right:

$$\left|\int_\Omega \sigma\alpha_x u_x \cdot u_{xx}\mathrm{d}x\right| \leqq \epsilon \int_\Omega |u_{xx}|^2\mathrm{d}x + C\int_\Omega |u_x|^2\mathrm{d}x.$$

All second derivative terms may be absorbed into the leading term on the right side of the equation, which is negative. These are then discarded. We then obtain the estimate

$$\frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega \left(\sum \alpha_i (u_{ix})^2\right)\mathrm{d}x \leqq C\int_\Omega (|u_x|^2 + |u|^2)\mathrm{d}x.$$

Now integrating over $t \leqq s \leqq \tau$

$$\frac{1}{2}\int_\Omega \left(\sum \alpha_i (u_{ix})^2\right)\mathrm{d}x|_\tau \leqq C\int_t^\tau \int_\Omega (|u_x|^2 + |u|^2)\mathrm{d}x\mathrm{d}s + \frac{1}{2}\int_\Omega \left(\sum \alpha_i (u_{ix})^2\right)\mathrm{d}x|_t.$$

Integrate the above expression with respect to t over $[\tau/2, 3\tau/4]$. This gives

$$\frac{1}{2}\int_\Omega \left(\sum \alpha_i (u_{ix})^2\right)\mathrm{d}x|_\tau \leqq C\int_{\tau/2}^\tau \int_\Omega (|u_x|^2 + |u|^2)\mathrm{d}x\mathrm{d}s + \frac{C'}{\tau}\int_{\tau/2}^{3\tau/4} \int_\Omega \left(\sum \alpha_i (u_{ix})^2\right)\mathrm{d}x\mathrm{d}t.$$

Using now (5.70), and, as usual, that the $\alpha_i > 0$, and Part 1,we obtain the desired estimate that

$$\int_\Omega |u_x|^2\mathrm{d}x|_\tau \leqq C\ \max|u^0|^2, \quad for\ \tau > 0.$$

This translates into an estimate of the same form for ρ. □

We now discuss the exponential decay of the time dependent solution $\rho(x,t)$ to $\rho^\sharp(x)$. Let $\tau > 0$ and define the linear mapping on initial data

$$T_\tau : C(\overline{\Omega}) \times C(\overline{\Omega}) \to C(\overline{\Omega}) \times C(\overline{\Omega}) \tag{5.71}$$

$$f(x) \to \rho(x,\tau) \tag{5.72}$$

where $\rho(x,t)$ is the associated solution of (1.1), (1.2). So $T_\tau^k f(x) = \rho(x,t), t = k\tau$. We conclude from the Lemma, and the Ascoli-Arzela' Theorem, that

$T_\tau : C(\overline{\Omega}) \times C(\overline{\Omega}) \to C(\overline{\Omega}) \times C(\overline{\Omega})$ is a (linear) compact positive operator.

So T_τ has a discrete spectrum with eigenvalues $\lambda_i \to 0$. Let us adopt, for the purposes of brevity, the notation that for a vector α, $\alpha \geqq 0$ means each $\alpha_i \geqq 0$ and $\alpha > 0$ means each $\alpha_j > 0$. Then T_τ is positive in the sense that

$$f \geqq 0 \ \text{ in } \Omega \text{ and } f \not\equiv 0 \quad \Longrightarrow \quad T_\tau f > 0 \ \text{ in } \Omega.$$

Since $\rho^\sharp$ is a stationary solution of (1.1), (1.2) , we have that

$$T_\tau \rho^\sharp = \rho^\sharp$$

for any $\tau > 0$. So T_τ has a positive eigenvector with eigenvalue 1. Indeed, that $\rho^\sharp > 0$ implies that $\lambda = 1$ is the eigenvalue of maximum modulus and it has multiplicity one. We check this.

Suppose that η is an eigenfunction with real eigenvalue $\lambda, |\lambda| \geqq 1$ and $\eta \not\equiv \rho^\sharp$;

$$T_\tau \eta = \lambda\eta$$

say $\lambda \geqq 1$ for example. Then we can find an $\epsilon > 0$ such that

$$\rho_i^\sharp - \frac{\epsilon}{\lambda}\eta_i \geqq 0,\ i = 1,2, \quad \text{and} \quad \min_i \min_\Omega \left(\rho_i^\sharp - \frac{\epsilon}{\lambda}\eta_i\right) = 0.$$

Now

$$T_\tau\left(\rho^\sharp - \frac{\epsilon}{\lambda}\eta\right)_i > 0 \ \text{ in } \Omega$$

by positivity but

$$T_\tau\left(\rho^\sharp - \frac{\epsilon}{\lambda}\eta\right) = \rho^\sharp - \epsilon\eta$$

which is not strictly positive since $\lambda \geqq 1$ and ϵ has been carefully chosen. Similarly if $\lambda \leqq -1$. Thus $\lambda = 1$ is the largest real eigenvalue of T_τ and it has a unique (normalized) eigenfunction $\rho^\sharp$. An analogous argument prevails if λ is complex and $|\lambda| \geqq 1$.

So we have verified that $\lambda = 1$ is the eigenvalue of largest modulus of T_τ and that it has multiplicity 1. Now consider the space X of functions $f = (f_1, f_2) \in C(\overline{\Omega}) \times C(\overline{\Omega})$ with

$$\int_\Omega (f_1 + f_2)\mathrm{d}x = 0.$$

From the boundary conditions (5.65),

$$f \in X \ \text{ implies } \ T_\tau f \in X.$$

So

$$T_\tau : X \to X \ \text{ is compact, linear}$$

and 1 is not an eigenvalue; the largest eigenvalue is less than one. So there is a $\lambda_0 < 1$ in the resolvent of T_τ larger than any eigenvalue. Set $r_0 = 1/\lambda_0$. Then

$$(\lambda_0\mathbf{1} - T_\tau)^{-1} f = \frac{1}{\lambda_0}\left(\mathbf{1} - \frac{1}{\lambda_0}T_\tau\right)^{-1} f \tag{5.73}$$

$$= \frac{1}{\lambda_0}\sum T_\tau^k f(x)\left(\frac{1}{\lambda_0}\right)^k \tag{5.74}$$

$$= r_0 \sum T_\tau^k f(x) r_0^k, \quad f \in X. \tag{5.75}$$

So the series $\sum T_\tau^k f(x) z^k$ converges absolutely for $|z| \leqq r = r_0 - \epsilon, r > 1$, so in particular the terms are bounded. Consequently, for each $f \in X$ there is an M_τ such that

$$|T_\tau^k f(x)| \leqq M_\tau r^{-k} \to 0, as\ k \to \infty.$$

Consequently, choosing $f(x) = \rho(x,0) - \rho^\sharp(x)$ for a solution $\rho(x,t)$ of (1.1), (1.2), tells us that

$$|\rho(x,k\tau) - \rho^\sharp(x)| \leqq M_\tau r^{-k} \to 0, as\ k \to \infty$$

and using (5.68),

$$\sup_{t \geqq k\tau} |\rho(x,t) - \rho^\sharp(x)| \leqq M M_\tau r^{-k} \to 0, as\ k \to \infty.$$

This proves the convergence of the solution of the evolution equations to the stationary solution, indeed, with an exponential rate of convergence determined by the second eigenvalue of T_τ on $C(\overline{\Omega}) \times C(\overline{\Omega})$; namely, with $t = k\tau$,

$$r^{-k} = \mathrm{e}^{-\frac{\log\ r}{\tau}t}, \ \ \log\ r > 0.$$

To review, r above satisfies

$$\lambda_2 < \frac{1}{r} < 1$$

where λ_2 is the second eigenvalue of T_τ. We have shown

Theorem 5.2. *Under the hypotheses (5), let $\rho(x,t)$ denote the solution of (1.1), (1.2), (1.3) and $\rho^\sharp$ denote the solution of the stationary problem (1.4), (1.5), (1.6). Then there are $M_0 > 0, \gamma > 0$ such that*

$$\sup_\Omega |\rho(x,t) - \rho^\sharp(x)| \leqq M_0 e^{-\gamma t}. \tag{5.76}$$

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