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The Influence of a Geographical Barrier on the Balance of Selection and Migration

J. J. E. van der Meer, Amsterdam

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In biology, a cline is defined as a usually gradual change in gene frequency or phenotype of a population in equilibrium, from one place to another.

We define a cline as a nonconstant stable steady state solution. However, for the model studied in this paper, these two definitions coincide: a nonconstant stable steady state solution is necessarily monotone. It is proved that for small values of the penetrability of the barrier, exactly two clines exist.

Since we prove that the ω-limit set of any initial condition is a steady state solution, the information thus obtained yields a rather complete understanding of the qualitative behaviour of the solutions of the evolution problem under consideration.

0 Introduction

The joint effect of selection and migration on the genetic composition of a population is frequently described by a one-dimensional reaction-diffusion equation

$$u_t = u_{xx} + f(u) \quad \text{in } [-L, L] \tag{0.1}$$

$$u_x(-L) = u_x(L) = 0 .$$

For some background on this one gene – two alleles problem we refer to Nagylaki [15], Fife [5], and Fife and Peletier [6].

It has been proved by Chafee [2] that (0.1) does not admit *stable nonconstant* steady states (clines). This result has been extended to higher dimensional but *convex* domains by Casten and Holland [1] and Matano [12].

A complementary result of Matano, also in [12], shows that for a class of dumb-bell shaped domains (i.e. ○═○) clines do exist. The work of Hale [7] and Hale and Vegas [8] is concerned with the bifurcation of these nonconstant solutions from constants as the domain is perturbed.

In Fife and Peletier [6], one can find a one dimensional reaction diffusion equation on an interval, with homogeneous Neumann-boundary conditions, which *has* stable nonconstant steady state solutions, due to nonhomogeneous diffusion and/or space-dependent selection. In fact, work in this direction was strongly motivated by earlier results of Levin (see e.g. [11]).

In 1976 Nagylaki [14] adapted the model (0.1) to the situation in which the habitat is intersected by a geographical barrier. Under the assumption that the habitat is homogeneous, except for one geographical barrier which is situated at exactly the middle of the habitat, this adaptation takes the form of a transmission condition in 0:

$$u_x(0+,t) = u_x(0-,t) = \frac{1}{\mu}(u(0+,t) - u(0-,t)),$$

for $1/\mu \in \mathbf{R}^+$, which measures the penetrability of the barrier.

In 1979 ten Eikelder [4] analysed the effect of this transmission condition in an unbounded domain, in which selection is space-dependent. He proved the existence of a cline under some restrictions on the reaction function f.

Motivated by these observations we shall analyse the following evolution problem:

$$\text{E.P.}\qquad \begin{aligned} & u_t = u_{xx} + f(u), \qquad x \in [-L, 0) \cup (0, L] \\ & u_x(-L, t) = 0 \\ & u_x(L, t) = 0 \\ & u_x(0-,t) = u_x(0+,t) = \frac{1}{\mu}(u(0+,t) - u(0-,t)), \qquad \mu \in \mathbf{R}^+ \\ & u(x, 0) = \psi(x), \qquad x \in [-L, 0) \cup (0, L). \end{aligned}$$

In the present paper f will be the rather special cubic

$$f(u) = u(1-u)\left(u - \frac{1}{2}\right).$$

However, it should be clear that our results can serve as the starting point of a perturbation analysis for "nearby" functions f, for instance

$$f(u) = u(1-u)(u-a)$$

with

$$\left|a - \frac{1}{2}\right| \ll 1 \quad [10].$$

The operator A in $C[-L,0] \times C[0,L]$, defined by

$$\mathscr{D}(A) = \Big\{ w \in C^2[-L,0] \times C^2[0,L] \,|\, w'(-L) = w'(L) = 0$$
$$w'(0-) = w'(0+)$$
$$= \frac{1}{\mu}(w(0+) - w(0-)) \Big\}$$

and for $w \in \mathscr{D}(A)$

$$Aw = -w''$$

is a sectorial operator (see [9]), which has compact resolvent. Define $F(w) = \int_0^w f(\xi)\,d\xi$. The functional V on $\mathscr{D}(A)$, defined by

$$V(w) = \int_{-L}^{0} \left\{ \frac{1}{2} w_x^2 - F(w) \right\} dx + \int_0^L \left\{ \frac{1}{2} w_x^2 - F(w) \right\} dx + \frac{\mu}{2} w_x^2(0)$$

is a strict Lyapunov functional for (E.P.). Moreover, $\dot{V}(w) = 0$ if and only if w is an element of the discrete set of steady state solutions and for $\mu > 0$, $K > 0$, the set

$$\{ w \in \mathscr{D}(A) \,|\, V(w) < K \}$$

is bounded in $C[-L,0] \times C(0,L]$.

All together, we have "proved" by these remarks:

1) existence and uniqueness of solutions of (E.P.).
2) the justification of identifying stability in (E.P.) and linearized stability.
3) that the ω-limit set of any initial condition is a steady state solution.

For the backgrounds of these techniques we refer to [9], for the specific details in case of (E.P.) to [13].

The analysis of (E.P.) is therefore restricted to the steady state problem

$$q_{xx} + f(q) \qquad q \in \mathscr{D}(A)$$

and an analysis of the spectrum of the operator $(-A + f'(q))$, for q a steady state solution.

We shall use in this paper the following

0.1 Definition. *A steady state solution q is called trivial when q is a constant function of x. A* nontrivial *steady state is called symmetric when $q(x) = q(-x)$ and anti-symmetric when $q(x) = 1 - q(-x)$ for $x \in (0,L]$; it is called a-symmetric when it is not symmetric, anti-symmetric or trivial. A cline is a nontrivial* stable *steady state solution.*

With respect to (E.P.) we prove the following results:

1) a cline is strictly monotone on $(-L,L)$.
2) a number $0 < \hat{\mu}(L) < \infty$ exists, such that
   - for $0 < \mu < \hat{\mu}(L)$ no anti-symmetric clines exist,
   - for $\mu > \hat{\mu}(L)$ exactly two such clines exist.

3) a number $\hat{\mu}(L) < \infty$ exists such that for $\mu > \hat{\mu}(L)$ every cline is anti-symmetric.

We conjecture that $\hat{\mu}(L) = 0$, i.e., every cline is anti-symmetric.

The phase portrait of

$$q_{xx} + f(q) = 0$$

is most easily obtained by introducing formally $p(\zeta) = \zeta_x(\zeta)$ to find $pp_\zeta + f(\zeta) = 0$ and subsequently, by integration

$$p^2(w) - p^2(v) + 2\int_v^w f(\xi)\,d\xi = 0.$$

It can be found in Figure 1.

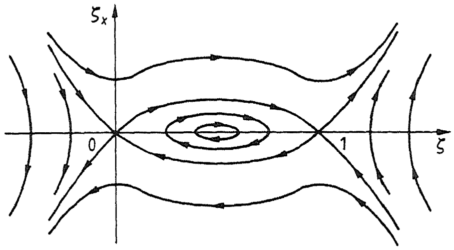

Fig. 1

A natural technical tool in both the steady state and the stability problem connected to (E.P.) is the L-curve. We shall introduce this curve in Section 1 and subsequently derive some general properties of the phase portrait. In Section 2 we present various results concerning the set of steady state solutions and in Section 3 we discuss their stability.

In Section 4 we turn to a second evolution problem

$$u_t = (D(x)u_x)_x + f(u), \qquad x \in [-L-\delta, L+\delta]$$

E.P.2 $$u_x(-L-\delta, t) = 0$$

$$u_x(L+\delta, t) = 0$$

$$u(x,0) = \psi(x), \qquad x \in [-L-\delta, L+\delta].$$

We shall show that the L-curve is useful in this context too, by presenting a description of the sets of trivial, symmetric and anti-symmetric steady state solutions for the special choice

$$f(u) = u(1-u)\left(u - \frac{1}{2}\right)$$

$$D(x) = \varepsilon > 0 \quad \text{when } |x| < \delta$$

$$= 1 \quad \text{otherwise,}$$

whereas $D \cdot u_x \in C[-L-\delta, L+\delta]$ (see [14]).

Prof. J. K. Hale informed me that C. Rocha has independently obtained similar results using similar techniques.

We end this introduction by showing a certain relation between (E. P.) and (E. P.2), the last one modelling a domain, in which diffusion is relatively hard in a middle part of it.

By the transformation $\hat{x} = x/\varepsilon$ *for* $|x| < \delta$, $\hat{x} = x + \operatorname{sgn}(x)\delta\left(\frac{1}{\varepsilon} - 1\right)$ otherwise, one replaces the condition

$$D \cdot u_x \in C[-L-\delta, L+\delta]$$

by the condition

$$u_x \in C\left[-L - \frac{\delta}{\varepsilon},\quad L + \frac{\delta}{\varepsilon}\right].$$

In the interval $[-\delta/\varepsilon, \delta/\varepsilon]$, (E. P. 2) becomes

$$u_t = \frac{1}{\varepsilon} u_{xx} + f(u)$$

and hence, for $\varepsilon \downarrow 0$, $u_{xx}(x, t) = 0$. Let $\delta = \delta(\varepsilon)$ such that $\lim_{\varepsilon \downarrow 0} 2\delta(\varepsilon)/\varepsilon = \mu \in (0, \infty)$, then it follows in the limit that

$$u_x\left(-\frac{\mu}{2}, t\right) = u_x\left(\frac{\mu}{2}, t\right)$$

and

$$u\left(\frac{\mu}{2}, t\right) = u\left(-\frac{\mu}{2}, t\right) + \mu u_x\left(\frac{\mu}{2}, t\right).$$

So after the deletion of the uninteresting interval $[-\mu/2, \mu/2]$ (cf. the untransformed problem (E. P. 2)!), we end up exactly with (E. P.).

1 The *L*-Curve

A connected piece of one of the trajectories in the phase plane represents a function with a well-defined length of its domain of definition (for periodic orbits we have to keep track of the number of times an orbit is completed or, in other words, of a winding number). We shall call this length the length of that piece of that trajectory.

Clearly, steady state solutions consist of two parts of length L starting or ending at the line $\zeta_x = 0$. This observation motivates the introduction of the L-curve, which is obtained by pacing a length L along such trajectories. Exploiting the symmetry, we can restrict our attention to the half line $\zeta \in$

[1/2, ∞); exploiting the specific applications we have in mind, we can even restrict it to trajectories *ending* at the interval [1/2, 1].

1.1 Definition *Let* $\varrho\colon (-\infty,\infty)\times[1/2,1]\to[0,1]$ *be the solution of:*

$$\frac{\partial^2\varrho}{\partial x^2}(x,w)+f(\varrho(x,w))=0 \qquad \frac{\partial\varrho}{\partial x}(L,w)=0 \qquad \varrho(L,w)=w.$$

The L-curve is the set $\Gamma_L=\left\{\left((\varrho(0,w),\frac{\partial\varrho}{\partial x}(0,w)\right)\middle|\, w\in\left[\frac{1}{2},1\right]\right\}$.

In order to state the main result about Γ_L, proved in [13], we state, using the subscript w to denote a derivative with respect to the second argument,

1.2 Definition. *For* $w\in[1/2,1]$, *let*

$$S(w)=\frac{\frac{\partial\varrho_w}{\partial x}(0,w)}{\varrho_w(0,w)}.$$

The angle function $\theta(w)$ *is defined by*

i) $S(w) = \tan\theta(w)$,
ii) θ *is continuous,*
iii) $\theta(1) = \operatorname{Arctan} S(1)$.

Note that $S(w)$ is the slope of Γ_L at the point $\left(\varrho(0,w),\frac{\partial\varrho}{\partial x}(0,w)\right)$. The following result states, roughly speaking, that Γ_L is a "convex" curve — where we put "convex" within quotes, since Γ_L will spiral around the point (1/2, 0) for L sufficiently large.

1.3 Theorem. $\theta'(w)<0$ *for* $w\in(1/2,1)$.

The lines $\zeta_x = 0$ and $\zeta = 1/2$ devide the phase plane in four quadrants which we shall number counterclockwise as usual. A component of the intersection of Γ_L and a quadrant, without the point (1/2, 0), will be called a quadrant component (of Γ_L).

A careful look at the points of intersection of Γ_L and the lines $\zeta_x=0$ and $\zeta = 1/2$, combined with the foregoing theorem, yields

1.4 Corollary. *Each quadrant component contains exactly one critical point. For the first quadrant, it is a maximum of* ζ_x, *for the second, a minimum of* ζ, *for the third, a minimum of* ζ_x *and for the fourth, a maximum of* ζ *along* Γ_L.

The next result is a minor modification of theorem (1.4) in [13].

1.5 Theorem. *For a part T of a trajectory let*

$$\mathrm{d}(T) = \inf\left\{\left(\zeta - \frac{1}{2}\right)^2 + \zeta_x^2 \mid (\zeta, \zeta_x) \in T\right\}.$$

For any two different lines through the point $(1/2, 0)$ *within each sector separated by those lines, the length of a trajectory partT between those lines, and completely in the strip*

$$\{(\zeta, \zeta_x) \mid \zeta \in [0, 1]\}$$

is a strictly increasing function of $\mathrm{d}(T)$.

Theorem (1.5) will be useful in Section 4. We end this section by a sketch of Γ_L, for $L = 9\pi/2$.

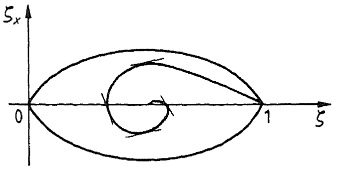

Fig. 2

2 The Steady State Solutions of (E.P.)

In this section we shall take into account Proposition (3.4), which proves that the non-trivial, non-monotone (i.e. not *strictly* monotone on $(-L, L)$) steady state solutions of (E. P.) are unstable. However, this restriction has not been made in Section 2 of [13], in which much more detailed information on the set of steady state solutions can be found.

2.1 Proposition. *For* $\mu > 0$, *the range of a steady state solution* q *is in the interval* $[0, 1]$.

Proof. When both $q(-L)$ and $q(L)$ are in the interval $[0, 1]$, clearly $\mathscr{R}(q) \subset [0, 1]$. See Fig. 1.
Suppose $q(-L) < 0$, then $q(0) < q(-L)$ and $q_x(0-) < 0$. Hence, by the transmission condition $q_x(0+) = q_x(0-)$ and $q(0+) = q(0-) + \frac{1}{\mu} \cdot q_x(0-) < 0$. But this implies $q_x(L) < 0$. By the symmetry of the problem, this proves the proposition. □

The first goal of this section is to characterize the set of monotone anti-symmetric steady state solutions; note that every symmetric steady state solution q is non-monotone, since $q_x(0) = 0$. The proof of the following proposition is trivial.

2.2 Proposition. *An anti-symmetric steady state solution is completely determined by a function $q \in C^2[0, L]$ satisfying*

$$q_{xx} + f(q) = 0$$

$$q_x(0) = \frac{2}{\mu}\left(q(0) - \frac{1}{2}\right)$$

$$q_x(L) = 0.$$

By the symmetry of the problem, we restricted our attention to Γ_L: since we are looking for monotone solutions we can further restrict it to the essential part of Γ_L, i.e., that part of Γ_L indicating functions ϱ which are strictly monotone on $[0, L]$. The convexity of Γ_L guarantees that the essential part is connected; it clearly consists of the outer first and second quadrant component minus the points of intersection with the line $\zeta_x = 0$.

By Proposition (2.2) an increasing monotone anti-symmetric steady state solution is determined by a point of intersection of the line $\zeta_x = \frac{2}{\mu}\left(\zeta - \frac{1}{2}\right)$ and the essential part of Γ_L. So the convexity of Γ_L implies the uniqueness of such a solution.

The following proposition results from the observation that

$$\varrho_w\left(x, \frac{1}{2}\right) = \cos\frac{1}{2}(L - x).$$

2.3 Proposition. *When $L \geq \pi$, a unique increasing monotone anti-symmetric steady state solution exists for all $\mu \geq 0$. When $L < \pi$ such a solution exists for all $\mu > 4/\tan\frac{1}{2}L$.*

2.4 Remark. Note that for $\mu \to \infty$, the solution mentioned in Proposition (2.3) converges to 0, uniformly on $[-L, 0-]$, to 1, uniformly on $[0+, L]$.

The next proposition deals with monotone a-symmetric steady state solutions. Let w_0 be defined by $\varrho_x(0, w_0) = \max\{\zeta_x \mid (\zeta, \zeta_x) \in \Gamma_L\}$, i.e. $(\varrho(0, w_0), \varrho_x(0, w_0))$ is the first quadrant critical point of the essential part of Γ_L.

2.5 Proposition. *For $\mu > 2\varrho(0, w_0)/\frac{\partial\varrho}{\partial x}(0, w_0)$ exactly two increasing monotone a-symmetric steady state solutions exist.*

Proof. Let $\left\{\left(\varrho(0, w), \frac{\partial\varrho}{\partial x}(0, w)\right) \mid w \in (\underline{w}, 1)\right\}$ be the essential part of Γ_L. For $\mu > 0$, let $J\ \mathbf{R}^2 \to \mathbf{R}^2$ be defined by

$$J(\xi_1, \xi_2) = \left(\xi_1 - \frac{\mu}{2}\xi_2, \xi_2\right)$$

and consider the set

$$Q = \left\{ J\left(\varrho(0,w), \frac{\partial \varrho}{\partial x}(0,w) \right) \mid w \in (\underline{w}, 1) \right\}$$

as well as its mirror image MQ in the line $\zeta = 1/2$. One can easily see that a point of intersection of Q and MQ on $\zeta = 1/2$ represents an increasing monotone anti-symmetric steady state solution, a point of intersection not on $\zeta = 1/2$, an a-symmetric one.

Since the slope $JS(w)$ of Q at the point $J\left(\varrho(0,w), \frac{\partial \varrho}{\partial x}(0,w) \right)$ satisfies

$$JS(w) = \frac{S(w)}{1 - \frac{\mu}{2} S(w)},$$

it follows, under the restriction $w \in (\underline{w}, 1)$, that $JS(w) = 0$ if and only if $w = w_0$, and

$$JS'(w) = \frac{S'(w)}{\left(1 - \frac{\mu}{2} S(w)\right)^2}$$

and hence, also Q is convex.

When $\varrho(0,w_0) - \frac{\mu}{2}\varrho_x(0,w_0) < 0$, Q and MQ intersect exactly once on both sides of the line $\zeta = 1/2$, as can easily be seen. □

3 The Stability of Steady State Solutions of (E.P.)

Let $X = C[-L,0] \times C[0,L]$, and let $X_{\mathbf{C}}$ be its complexification. For $c \in X$ and $\mu \in \mathbf{R}$, one can prove that $(-A+c)$ is a symmetric linear operator on $\mathscr{D}(A)_{\mathbf{C}}$, the complexification of $\mathscr{D}(A)$. Here we used the same symbol c for the operator on $X_{\mathbf{C}}$ defined by

$$(c(u))(x) = c(x) \cdot u(x).$$

In [13], it is proved that $(-A+c)$ has compact resolvent; the proof is based on the existence of Green's functions for both $[-L,0]$ and $[0,L]$. The following implication of these results is proved in [18], and it strongly facilitated the proof that A is a sectorial operator in [13].

3.1 Proposition. *For $c \in X$, $\mu \in \mathbf{R}$, $P_\sigma(-A+c) = \sigma(-A+c) \subset \mathbf{R}$.*

For q an increasing steady state solution, let $w = q(L)$ and $\alpha = 1 - q(-L)$. Let η: $[0,L] \times [1/2,1] \times (-\infty,\infty)$ be the solution of

$$\frac{\partial^2 \eta}{\partial x^2}(x,w,\lambda) + f'(\varrho(x,w))\eta(x,w,\lambda) = \lambda\eta(x,w,\lambda)$$

$$\frac{\partial \eta}{\partial x}(L,w,\lambda) = 0$$

$$\eta(L,w,\lambda) = 1\,.$$

Then it follows that $\lambda \in \sigma(-A + f'(q))$ if and only if

$$\mu = \frac{\eta(0,w,\lambda)}{\frac{\partial \eta}{\partial x}(0,w,\lambda)} + \frac{\eta(0,\alpha,\lambda)}{\frac{\partial \eta}{\partial x}(0,\alpha,\lambda)}$$

or

$$\frac{\partial \eta}{\partial x}(0,w,\lambda) = \frac{\partial \eta}{\partial x}(0,\alpha,\lambda) = 0\,.$$

Further, by uniqueness it follows that $\eta(x,w,0) = \varrho_w(x,w)$.

This method can be extended to the whole set of steady state solutions. The only difference is that one has to take care to define α and w properly.

The following proposition is proved in [3].

3.2 Proposition. *For* $w \in [1/2, 1]$

1) $\eta(0,w,\lambda)/\frac{\partial \eta}{\partial x}(0,w,\lambda)$ *is strictly increasing in* λ, *jumps from infinity to minus infinity for* λ, *such that* $\frac{\partial \eta}{\partial x}(0,w,\lambda) = 0$, *and tends to* 0 *for* $\lambda \to \infty$.

2) *the number of zeros of* $\eta(x,w,\lambda)$ *for* $x \in [0,L]$ *is non-increasing in* λ.

By some technicalities, which can be found in [13], we can apply proposition (3.2) in the following way:

3.3 Corollary. *An eigenfunction which belongs to the largest element of* $\sigma(-A + f'(q))$ *is non-zero* $x \in [-L, L]$.

3.4 Proposition. *Every non-trivial, non-monotone steady state solution* q *is unstable.*

Proof. Since $\mu > 0$, $q(0+) > q(0-)$ if and only if $q_x(0) > 0$. So when q is non-monotone, we can assume $q_x(x_0) = 0$ for some $x_0 \in [0, L]$, and $w = q(L) \in (1/2, 1)$. Note that one can achieve this, by considering the four related steady state solutions $q(x)$, $1 - q(x)$, $q(-x)$ and $1 - q(-x)$. Since both q_x and $\varrho_w(\cdot, w)$ satisfy

$$\eta_{xx} + f'(q)\eta = 0$$

and $q_w(x_0) = q_x(L) = 0, \varrho_w(x,w) = 0$ for some $x \in [x_0, L]$ by the Sturmian oscillation theorem. Now Proposition (3.4) is proved by Proposition (3.2)2) and Corollary (3.3), since $\eta(x,w,0) = \varrho_w(x,w)$. □

3.5 Proposition. *Let q be an increasing monotone anti-symmetric steady state solution and $w = q(L)$, then $0 \in \sigma(-A + f'(q))$ if and only if* $\frac{\partial \varrho_w}{\partial x}(0, w) = 0$.

Proof. For q as stated, $q(L) = 1 - q(-L)$, i.e. $\alpha = w \in (1/2, 1)$ and it follows $0 \in \sigma(-A + f'(q))$ if and only if

$$\mu = 2 \frac{\varrho_w(0, w)}{\frac{\partial \varrho_w}{\partial x}(0, w)}$$

or

$$\frac{\partial \varrho_w}{\partial x}(0, w) = 0.$$

However, the first condition gives $S(w) = 2/\mu$, which implies by Proposition (2.2) that the line $\zeta_w = \frac{2}{\mu}\left(\zeta - \frac{1}{2}\right)$ is *tangent* on Γ_L at $(\varrho(0, w), \frac{\partial \varrho}{\partial x} \cdot (0, w))$. This clearly contradicts theorem (1.3). □

3.6 Proposition. *The trivial steady state solutions* 0, 1/2, 1 *are stable, unstable and stable, respectively (for all $\mu > 0$).*

Proof. Since $\lambda \in \sigma(-A + f'(0)) \cap (-1/2, \infty) = \sigma(-A + f'(1)) \cap (-1/2, \infty)$ if and only if

$$\mu = \frac{-2}{\sqrt{\lambda + 1/2} \tanh \sqrt{\lambda + 1/2}\, L} < 0,$$

and since $1/4 \in \sigma(-A + f'(1/2))$, $\eta(x, 1/2, 1/4) \equiv 1$, the proposition follows. □

3.7 Theorem. *The increasing, monotone, anti-symmetric steady state solution q is stable for*

$$\mu > \frac{2\left(\varrho(0, w_0) - \frac{1}{2}\right)}{\frac{\partial \varrho}{\partial x}(0, w_0)},$$

and unstable for other (positive) values of μ.

Proof. Note that q is unstable, when, using $w = q(L)$,

$$\frac{\eta(0, w, 0)}{\frac{\partial \eta}{\partial x}(0, w, 0)} = \frac{\varrho_w(0, w)}{\frac{\partial \varrho_w}{\partial w}(0, w)} = \frac{1}{S(w)} > 0,$$

since then Proposition (3.2)1) gives a value $\lambda > 0$, such that $\frac{\partial \eta}{\partial x}(0, w, \lambda) = 0$. By the knowledge of Γ_L, this proves the last statement, since for $w < w_0$, $S(w) < 0$ or $\varrho_w(x, w)$ is zero somewhere in the interval $[0, L]$, in which case we use Proposition (3.2)2). To prove the first, note that the stability of q can not change for

$$\mu > \frac{2\left(\varrho(0, w_0) - \frac{1}{2}\right)}{\frac{\partial \eta}{\partial x}(0, w_0)},$$

by Proposition (3.5). Since $\varrho(x, w)$ converges uniformly on $[0, L]$ to 1, for $w \uparrow 1$, one can complete this proof by that of Proposition (3.6) (cf. remark (2.4)). □

Like Theorem (3.7), Theorem (3.8) is proved by showing first, for a very large value of μ, the instability of an increasing monotone a-symmetric steady state q: this proves the instability of any other steady state q' on the same branch as q, when no bifurcation has occurred between q and q'. For the reason, and to avoid some lengthy technicalities, we refer to [13] – and Proposition (2.5) – for the proof of

3.8 Theorem (*a sufficient condition*): *The increasing monotone a-symmetric steady state solutions are unstable for*

$$\mu > 2\frac{\varrho(0, w_0)}{\frac{\partial \eta}{\partial x}(0, w_0)}.$$

If the branch of monotone a-symmetric steady state solutions does not contain any turning points at all it would follow that a cline is *necessarily* anti-symmetric. However, in view of the proof of Proposition (2.5) we note that this takes much more information of Γ_L than derived so far.

3.9 Remark. For a steady state solution q_1, one can obtain, as already mentioned in Proposition (3.4), three other – not necessarily different – solutions by defining

$$q_2(x) = 1 - q_1(x),$$

$$q_3(x) = q_1(-x),$$

$$q_4(x) = 1 - q_1(-x).$$

One can easily verify that $\sigma(-A + f'(q_i))$ is independent of $i \in \{1, 2, 3, 4\}$, and that we obtain all monotone steady states by taking q_1 an increasing one.

In Fig. 3, one finds a bifurcation diagram, restricted to the monotone and trivial steady state solutions, for some $L > \pi$. We want to emphasize that the analysis and presentation in [13] are much less restricted to monotone steady state solutions and $\mu > 0$, and for that reason [13] contains a more clarifying "overall" picture of (E. P.)

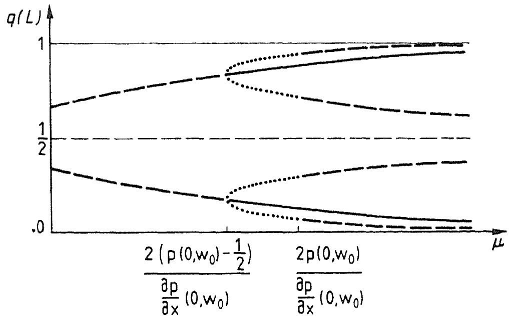

Fig. 3 ———: stable; - - -: unstable;
.......: conjectured to be like drawn (and hence unstable)

4 The Steady State Solutions of (E.P. 2)

In this section we study (E.P. 2) after the transformation $x \to \hat{x}$, given at the end of Section 0.

We restrict our attention to the steady state problem, and moreover to the sets of trivial, symmetric and anti-symmetric solution only. For the background of the techniques we use, we refer to [16]. For the problems concerning the asymptotic behaviour of solutions of (E.P. 2), the stability of steady state solutions (and in particular the a-symmetric steady state solutions), according to Prof. J. K. Hale, these have been solved by C. Rocha. Just as we proved proposition (2.1), one proves

4.1 Proposition. *The range of a steady state solution q of* (E.P. 2) *is in the interval* $[0, 1]$.

By a symmetry argument, we can restrict our attention to steady states q with $q(L) \in [1/2, 1]$. Therefore, we place $\Gamma_L, \tilde{\Gamma}_L$, the mirror-image of Γ_L in the line $\zeta = 1/2$ and $\tilde{\tilde{\Gamma}}_L$, the mirror-image of Γ_L is the line $\zeta_x = 0$, in the phase plane with the phase portrait derived from $\frac{1}{\varepsilon} q_{xx} + f(q) = 0$.

By looking for (orientated!) orbit pieces of the $1/\varepsilon$ phase portrait connecting $\tilde{\Gamma}_L$ to Γ_L, having length $2\delta/\varepsilon$, one finds anti-symmetric steady states and possible a-symmetric ones. Doing the same for $\tilde{\tilde{\Gamma}}_L$ instead of $\tilde{\Gamma}_L$, one finds symmetric steady states and possibly a-symmetric ones.

Using the convexity of Γ_L (Theorem (1.3)) and theorem (1.5), and taking $L < \pi$, just for convenience, we can prove

4.2 Proposition. *For $L < \pi$, $\delta > 0$ and $i \in \mathbf{N}_0$ there exists $\varepsilon_i > 0$ such that for $\varepsilon > \varepsilon_i$ no symmetric (in case i is odd) or anti-symmetric (in case i is even) steady state solutions q exist, for which $\partial q/\partial x$ has i zeroes in the interval $(-\delta, \delta)$; for $\varepsilon < \varepsilon_i$ exactly one such solution does exist, for which $q(L) \in (\frac{1}{2}, 1)$.*

Moreover, one can prove that $\varepsilon_{i+1} < \varepsilon_i$ for all $i \in \mathbf{N}_0$, that every branch of (anti-)symmetric steady state solutions bifurcates from the constant steady state $q = 1/2$ (here we use $L < \pi$), and that, for $\varepsilon \downarrow 0$, the steady state solutions, mentioned in Proposition (4.2) converge to the simple step functions, depicted in Fig. 4.

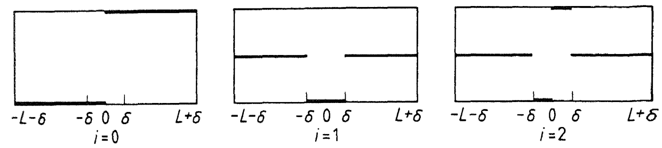

Fig. 4

Further, it is only little harder to prove that along the branch of monotone increasing (anti-symmetric) steady state solutions ($i = 0$), $q(L)$ is a strictly decreasing function of $\varepsilon < \varepsilon_0$.

The trivial steady state solutions are again the constant functions 0, 1/2 and 1. It is very easy, using the ideas mentioned before, to indicate some a-symmetric steady states, and moreover a branch of such solutions bifurcating from an anti-symmetric one, for which $i = 0$, and for which the connecting $1/\varepsilon$ orbit piece is tangent to Γ_L.

In Fig. 5, we depicted our results with respect to (anti-)symmetric and trivial steady states.

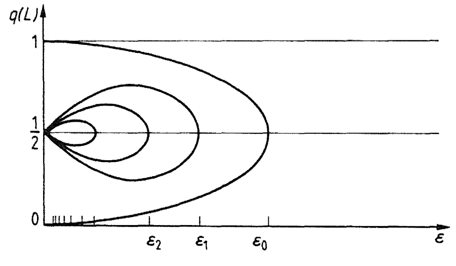

Fig. 5

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Reference [13] can be obtained directly from the author.

J. J. E. van der Meer
Centre for Mathematics
and Computer Science
P.O. Box 4079,
1009 AB Amsterdam,
The Netherlands

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