J. Math. Biol. (1990) 28: 83–98

Journal of
Mathematical
Biology

Convergence to spatial-temporal clines in the Fisher equation with time-periodic fitnesses

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Abstract. The asymptotic behavior as $t \to \infty$ of the solutions with values in the interval $(0, 1)$ of a reaction-diffusion equation of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} - \Delta u = m(x, t, u)u(1-u) & \text{in } \Omega \times (0, \infty) \\ \dfrac{\partial u}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

is studied. Conditions on m which are satisfied when m is nonincreasing in u and which imply that every solution converges to some periodic limit function are found. Except in some very special and well-defined circumstances, the limit is the same for all solutions, so that it is a global attractor. This global attractor may be one of the trivial solutions 0 or 1, or it may be a spatial-temporal cline. The linear stability properties of the trivial states serve to distinguish between these cases.

Key words: Fisher's equation — Cline — Periodic solution — Global attractor — Linearized stability

1. Introduction

In this paper we study the behavior as t approaches infinity of solutions of the partial differential equation with no-flux boundary conditions

$$\begin{aligned} \frac{\partial u}{\partial t} - \Delta u &= m(x, t, u)h(u) \quad \text{in } \Omega \times (0, \infty) \\ \frac{\partial u}{\partial n} &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{$*$}$$

We shall assume that $\Omega \subset \mathbb{R}^n$ is a bounded domain, and that the function h satisfies the conditions

$$h(a) = h(b) = 0,$$
$$h > 0 \quad \text{in } (a, b)$$
$$h'(a) > 0, \quad h'(b) < 0.$$

The function $m(x, t, u)$ is Hölder continuous in all its variables and periodic of period T in t, and it may change sign.

We observe that $(*)$ admits the trivial constant solutions $u \equiv a$ and $u \equiv b$. We shall only be concerned with nontrivial solutions whose initial values lie in the interval $[a, b]$:

$$a \leqslant u(x, 0) \leqslant b \quad \text{in } \Omega; \qquad u(x, 0) \not\equiv a, \qquad u(x, 0) \not\equiv b.$$

It is well known [9] that such a solution exists for all t, that it is unique, and that $a < u(x, t) < b$ for $x \in \bar{\Omega}$ and $t > 0$.

We are motivated by the Fisher model [6] of population genetics. In this model, the fraction $u(x, t)$ of one of two alleles at a particular gene locus in the local population of a migrating diploid species evolves according to the equation

$$\frac{\partial u}{\partial t} - \Delta u = [(f_1 + f_2)u - f_2]u(1 - u), \tag{1.2}$$

where the ratios of the fitnesses of the three genotypes are $1 + f_1(x, t) : 1 : 1 + f_2(x, t)$. Our results give information when the functions f_1 and f_2 may vary in both space and time, but the temporal variation is seasonal, so that the f_i are periodic in t.

We shall present some conditions on the functions m and h which imply that every solution of $(*)$ with values in (a, b) converges to a periodic solution of period T. Our principal result is Theorem 1, which is stated and proved in Sect. 2. This theorem states that when $m(x, t, u)$ and $h'(u)$ are nonincreasing in u, every solution of $(*)$ with values in (a, b) converges to a periodic solution. Unless the functions m and h satisfy some easily verified and rather unlikely conditions, Theorem 1 yields the existence of a periodic solution which is a global attractor, and we show that this attractor is different from one of the trivial solutions if and only if both trivial solutions are linearly unstable.

A nonconstant stationary solution of the Fisher equation with fitnesses which depend only on x was called a cline by J. S. Huxley. By extension, we call any nonconstant time-periodic solution of (1.2) a spatial-temporal cline. Then Theorem 1 gives sufficient conditions for the existence of a spatial-temporal cline which is a global attractor. This existence implies that both types of alleles will persist in the population for all time.

We note that the function $u(1 - u)$ in Fisher's equation is concave. Thus Theorem 1 can be applied as long as

$$f_1(x, t) + f_2(x, t) \leqslant 0,$$

so that the fitness of the heterozygote is at least the mean of the fitnesses of the homozygotes. Moreover, if $\delta > -1$, the function $h = u(1-u)/(1+\delta u)$ is also concave on the interval [0, 1]. Therefore Theorem 1 can be applied if for some $\delta > -1$ and all (x, t) the function $m = ((f_1 + f_2)u - f_2)(1 + \delta u)$ is nonincreasing in u on [0, 1]. The condition for this is that for all (x, t) the point (f_1, f_2) lie in the sector

$$(1+\delta)f_1 + f_2 \leqslant -|\delta|\,|f_1 + f_2|.$$

Theorem 2 in Sect. 3 shows that the condition $m(x, t, u) \leqslant p(t)$ with the integral of p from 0 to T nonpositive also implies that every solution in (a, b) converges to a periodic solution. However, except for some unusual situations, a is found to be a global attractor, so that one only obtains the case of extinction of one of the alleles.

For the Fisher equation the condition of Theorem 2 is that there exist a function $p(t)$ such that

$$f_1(x, t) \leqslant p(t), \qquad f_2(x, t) \geqslant -p(t), \qquad \int_0^T p(t)\,dt \leqslant 0.$$

The interchange of f_1 and f_2 makes 1, rather than 0, the global attractor.

If the function $m(x, t, u)$ is independent of t, it is, of course, periodic of all periods. Thus our results immediately lead to the existence of clines which are global attractors.

The problem of the existence of clines has been studied by many authors (e.g., [3, 5, 7, 8, 10, 13, 15]) for a special case of the Fisher equation. If the ratio of the functions f_1 and f_2 in the Fisher equation remains constant, and these functions are independent of t, one obtains an equation of the form

$$\frac{\partial u}{\partial t} - \Delta u = \lambda s(x)[(1-\alpha)u + \alpha(1-u)]u(1-u).$$

Most of the above studies deal with this equation in one space dimension and on the whole real line. However, Fleming [8] applied variational considerations to this equation with no-flux boundary conditions in an N-dimensional domain. For the one-dimensional case he showed that if $1/3 < \alpha < 2/3$, then there is a nonnegative critical value λ_1 such that one of the trivial solutions is a global attractor if $0 < \lambda < \lambda_1$, and there exists a stable cline for λ above λ_1. The condition $1/3 < \alpha < 2/3$ is just the condition that the function $h(u) = [(1-\alpha)u + \alpha(1-u)]u(1-u)$ is strictly concave, and our Theorem 1 shows that for all $\lambda > \lambda_1$ there is a cline which is a global attractor.

For $\alpha < 1/3$ we can apply Theorem 2 if and only if $s(x) \leqslant 0$ to show that 0 is a global attractor, but we are not able to treat the case when s changes sign. In fact, Fleming showed that in one dimension when $0 < \alpha < 1/3$ an unstable periodic solution appears, so that our results cannot hold in this case.

Our results serve to strengthen a number of other results in the literature. Henry [11], chap. 10.1, has used bifurcation theory to study the nontrivial solutions which can occur in the autonomous problem where m is independent of t and u. The existence of at least one stable periodic solution of the problem (*) was proved in [4], but there seem to be no results about the asymptotic behavior of solutions even in the special case where m depends only on t. The results of [1] on discrete order-preserving semigroups cannot be applied in this case, because one does not have the orbital stability which is assumed there.

While we have confined our results to convergence in the maximum norm, convergence in stronger norms then follows from standard parabolic estimates.

We remark that the Laplace operator on the left of (*) can easily be replaced by any uniformly elliptic operator of the form

$$\sum_{i,j} \frac{\partial}{\partial x_i} a_{ij}(x) \frac{\partial}{\partial x_j}$$

in all our results.

We are grateful to a referee, whose suggestions have led us to a simpler and clearer presentation of the statement and proof of Theorem 1.

2. Sufficient conditions for convergence

In this section we shall show that when $m(x, t, u)$ and $h'(u)$ are nonincreasing in u, every solution of (*) with values in (a, b) converges to some periodic solution.

In order to make more precise statements about the convergence, we look at the linearization

$$\begin{aligned} &\frac{\partial \phi}{\partial t} - \Delta\phi = m(x, t, a)h'(a)\phi \quad \text{in } \Omega \times (0, \infty) \\ &\frac{\partial \phi}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \tag{2.1}$$

of the equation (*) about the constant solution a. We define the period map Q_a of this equation as

$$Q_a[\phi(\cdot, 0)] := \phi(\cdot, T).$$

This operator is the Frechet derivative at $u \equiv a$ of the period map of (*).

The maximum principle [9, 14] and the regularity theory for parabolic equations show that this map is a compact positive operator on the space of continuous functions of x. The Krein–Rutman Theorem then states that Q_a has a positive eigenvalue μ, the principal eigenvalue, with a positive eigenfunction $\phi(x, 0)$. The corresponding solution $\phi(x, t)$ of (2.1) is positive and satisfies the relation $\phi(x, t + T) = \mu\phi(x, t)$.

We say that the solution a of (*) is linearly stable if $\mu < 1$, linearly unstable if $\mu > 1$, and neutrally stable if $\mu = 1$. Analogous concepts are defined for the solution b.

We shall prove the following result:

Theorem 1. *If $h(u)$ is concave, and $m(x, t, u)$ is nonincreasing in u, then as t approaches infinity every solution of (*) with values in (a, b) converges, uniformly in x, to a solution which is periodic in t of period T. Moreover,* (*a*) *if a is linearly stable, then every solution of* (∗) *with values in* (a, b) *converges to a, so that a is a global attractor*;

(*b*) *if a is neutrally stable, then either a is a global attractor or the set of limits of such solutions is a uniformly continuous one-parameter family* $U(x, t; L)$ *of distinct periodic solutions of* (∗) *which converges to a uniformly as* $L \to -\infty$; *the latter case occurs if and only if there is a one-sided neighborhood of a in which either both* h' *and m are independent of u, or m is independent of both u and x and its integral form* 0 *to T is zero*;

(*c*) *the analogues of* (*a*) *and* (*b*) *are valid for the trivial solution b*;

(*d*) *if a and b are linearly unstable, then either there exists a unique periodic solution* v^* *of* (∗) *with values in* (a, b) *which is a global attractor, or there is a continuous one-parameter family* $U(x, t; L)$ *of distinct periodic solutions which is bounded away from a and b, and every solution with values in* (a, b) *converges to a member of this family. If the latter case occurs, then for each value* t_1 *of t either* $U(x, t_1; L)$ *is independent of x for all L and* $m(x, t_1, U(x, t_1; L))$ *is independent of both x and L, or* $m(x, t_1, U(x, t_1; L))$ *and* $h'(U(x, t_1; L))$ *are independent of L for all x.*

Proof. We shall obtain these results in a series of lemmas.

It is easily seen that if u_1 and u_2 are any solutions of (∗) with values in (a, b), then the nonnegative function

$$z(x, t) = \left\{ \int_{u_1(x,t)}^{u_2(x,t)} \frac{\partial \eta}{h(\eta)} \right\}^2 \tag{2.2}$$

satisfies the equation

$$\begin{aligned} &\frac{\partial z}{\partial t} - \Delta z - h'(u_1)\left(\frac{\nabla u_2}{h(u_2)} + \frac{\nabla u_1}{h(u_1)}\right) \cdot \nabla z \\ &\quad = 2[m(x, t, u_2) - m(x, t, u_1)] \int_{u_1}^{u_2} \frac{d\eta}{h(\eta)} \\ &\quad\quad + 2\left|\frac{\nabla u_2}{h(u_2)}\right|^2 [h'(u_2) - h'(u_1)] \int_{u_1}^{u_2} \frac{d\eta}{h(\eta)} - 2\left|\nabla \int_{u_1}^{u_2} \frac{d\eta}{h(\eta)}\right|^2. \end{aligned} \tag{2.3}$$

Clearly, the conditions that m and h' be nonincreasing in u imply that the right-hand side is nonpositive. Since the normal derivative of z vanishes on the boundary, the maximum principle then shows that z remains bounded as t goes to infinity. This fact has three immediate consequences.

Lemma 2.1. *If* $m(x, t, u)$ *is nonincreasing in u and* $h(u)$ *is concave and if not all solutions of* (∗) *with values in* (a, b) *are bounded away from a and b, then as* $t \to \infty$ *either every such solution converges to a, uniformly in x, or every such solution converges uniformly to b.*

Proof. If $u(x, t)$ is a solution with values in (a, b) and u is not bounded away from a, then there is a sequence (x_j, t_j) such that $u(x_j, t_j)$ approaches a while t_j increases to infinity. We then define the sequence n_j such that $n_j \leqslant t_j/T < n_j + 1$.

It easily follows from simple a priori bounds for the heat equation that the sequence of translates $u(x, n_j T + t)$ is equicontinuous and bounded. Therefore it has a subsequence $u(x, n'_j T + t)$ which converges, uniformly in bounded t-intervals, to a limit function $v(x, t)$, which is easily seen to be a solution of $(*)$. Because of our construction of the sequence n_j, v must be equal to a somewhere on the set $\bar{\Omega} \times [0, T]$. Because a is a solution of $(*)$, it follows from the comparison theorem for parabolic equations ([9], §3.6) that $v \equiv a$. Since the comparison theorem also shows that $u(x, T)$ is bounded away from a, and since $u(x, n'_j T + t)$ converges to a uniformly for $0 \leqslant t \leqslant T$, there is an integer J such that $u(x, T) \geqslant u(x, n'_J T + T)$ for all $x \in \bar{\Omega}$. We then see from the comparison theorem that

$$u(x, n'_J T + t) \leqslant u(x, t)$$

for all $t \geqslant T$. Because the sequence $u(x, n'_j T + t)$ converges to a uniformly on bounded t-intervals, there is for any preassigned $\varepsilon > 0$ an integer K such that $u(x, n'_K T + t) \leqslant a + \varepsilon$ for $0 \leqslant t \leqslant n'_J T$. This together with the above inequality $u(x, n'_J T + t) \leqslant u(x, t)$ implies that $u(x, t) \leqslant a + \varepsilon$ for $t \geqslant n'_K T$. Thus, if the solution u is not bounded away from a, it converges to a, uniformly in x, as $t \to \infty$.

Similarly, if u is not bounded away from b, it converges to b uniformly in x.

Now if there is a solution u_1 which converges to a uniformly in x, then because the function z defined by (2.2) is bounded, all other solutions u_2 with values in (a, b) must also converge to a uniformly. A similar statement holds for b. Since the only other possibility is that every solution is bounded away from a and b, the lemma is proved.

Lemma 2.2. *If $m(x, t, u)$ and $h'(u)$ are nonincreasing in u, and if the solution $u(x, t)$ of $(*)$ is bounded away from a and b, then there is a solution $\hat{u}$ of $(*)$ which is periodic of period T in t and such that $u(x, t) - \hat{u}(x, t)$ converges to zero as $t \to \infty$, uniformly in x.*

Proof. Let u be a solution of $(*)$ with values in (a, b) which is bounded away from a and b.

As in the proof of Lemma 2.1, the sequence $u(x, nT + t)$ is bounded and equicontinuous. Therefore there is a subsequence $u(x, n_j T + t)$ which converges to a solution $\hat{u}(x, t)$ of $(*)$, uniformly on bounded sets.

We now define the function

$$z(x, t) = \left\{ \int_{u(x, t)}^{u(x, T + t)} \frac{d\eta}{h(\eta)} \right\}^2$$

by (2.2) with $u_1(x, t) = u(x, t)$ and $u_2(x, t) = u(x, t + T)$. As we have already observed, z satisfies the equation (2.3) with the right-hand side nonpositive. It follows from the maximum principle that the quantity

$$\max_{x \in \bar{\Omega}} z(x, t)$$

is nonincreasing, so that it has a limit K^2 as $t \to \infty$.

Because u is bounded away from a and b, the function $1/h(\eta)$ in the definition of z is uniformly bounded. Therefore the sequence of translates $z(x, n_j T + t)$ converges to the function

$$\hat{z}(x, t) = \left\{ \int_{\hat{u}(x, t)}^{\hat{u}(x, T+t)} \frac{d\eta}{h(\eta)} \right\}^2,$$

uniformly on bounded sets. This function satisfies the equation (2.3) with u_1 and u_2 replaced by $\hat{u}(x, t)$ and $\hat{u}(x, T+t)$, and we again see that the right-hand side is nonpositive.

Moreover, since $\max_x z(x, t)$ converges to K^2, we see from our construction that $\max_x \hat{z}(x, t) = K^2$ for all t. The strong maximum principle then implies that $\hat{z} \equiv K^2$. Thus the function $\hat{u}$ satisfies the equation

$$\int_{\hat{u}(x, t)}^{\hat{u}(x, T+t)} \frac{d\eta}{h(\eta)} = K,$$

where K is a suitable square root of K^2. Therefore

$$\int_{\hat{u}(x, t)}^{\hat{u}(x, nT+t)} \frac{d\eta}{h(\eta)} = nK$$

for every positive integer n. Because $\hat{u}$ is bounded away from a and b, the left-hand side of this equation is uniformly bounded. We conclude that $K = 0$. This implies that $\hat{u}(x, T+t) = \hat{u}(x, t)$, so that $\hat{u}$ is a periodic solution of $(*)$.

We now define the function

$$z^*(x, t) = \left\{ \int_{\hat{u}(x, t)}^{u(x, t)} \frac{d\eta}{h(\eta)} \right\}^2.$$

This function again satisfies an equation of the form (2.3) with u_1 replaced by $\hat{u}$ and u_2 by u. The right-hand side is again nonpositive so that z^* satisfies a maximum principle. Because the function $1/h(\eta)$ in the definition of z^* is uniformly bounded on the range of integration, we see that $z^*(x, n_j T)$ approaches zero uniformly. It follows from the maximum principle that $z^*(x, t)$ approaches zero uniformly in x as $t \to \infty$. Since $1/h$ is uniformly positive, u converges to the periodic solution $\hat{u}$ uniformly in x, and the lemma is established.

While it is possible to have more than one nontrivial periodic solution of $(*)$, the following lemma shows that this can only happen under special circumstances.

Lemma 2.3. *Suppose that $m(x, t, u)$ and $h'(u)$ are nonincreasing in u. If there are two distinct solutions u_1 and u_2 of period T of $(*)$ with values in (a, b), then*

(a) $u_1 - u_2$ is bounded away from zero;

(b) u_1 and u_2 are members of a uniformly continuous one-parameter family $U(x, t; L)$ of distinct periodic solutions;

(c) for each value t_1 of t either $U(x, t_1; L)$ is independent of x for all L and $m(x, t_1, U(x, t_1; L))$ is independent of x and L, or the functions $m(x, t_1; U(x, t_1; L))$ and $h'(U(x, t_1; L))$ are independent of L for all x.

Proof. The proof of Lemma 2.2 shows that there is a constant $K \neq 0$ such that

$$\int_{u_1}^{u_2} \frac{d\eta}{h(\eta)} = K.$$

This immediately yields statement (a). Moreover, it shows that the function z defined by (2.2) is constant, so that the right-hand side of (2.3) is zero. Because the first two terms are nonpositive, they must both be zero. Since m is nonincreasing in u, this implies that $m(x, t, u)$ must be independent of u for u between $u_1(x, t)$ and $u_2(x, t)$.

We also see from the vanishing of the right-hand side of (2.3) that if $h'(u_1(x, t_1)) \neq h'(u_2(x, t_1))$, then the gradient of u_2 must vanish at (x, t_1). The above integral equation shows that the gradient of u_1 must also vanish there. A simple continuity argument then shows that $u_1(x, t_1)$ and $u_2(x, t_1)$ must be independent of x. Thus at those values of t where u_1 and u_2 are not independent of x, $h'(u)$ must have the same value for all u between $u_1(x, t)$ and $u_2(x, t)$.

We now define the function $U(x, t; L)$ by the equation

$$\int_{u_1}^{U} \frac{d\eta}{h(\eta)} = L.$$

Suppose without loss of generality that $u_1 < u_2$ so that $K > 0$, and let $0 \leqslant L \leqslant K$. Because this equation implies that $\nabla U/h(U) = \nabla u_1/h(u_1)$ and because $u_1 \leqslant U \leqslant u_2$, the above conditions satisfied by m and h show that the function $U(x, t; L)$ is a periodic solution of $(*)$. We also see from the above conditions that the function $m(x, t, U(x, t; L))$ is independent of L, and that the same is true of $h'(U(x, t; L))$ at those t at which u_1, and hence U, is not independent of x. If $U(x, t_1; L)$ is independent of x, the equation $(*)$ shows that the same is true of $m(x, t_1, U(x, t_1; L))$. Thus we have established all parts of the lemma.

The following example shows that the statement of Lemma 2.3 is sharp in the sense that for any positive concave function $h(u)$ with $h(a) = h(b) = 0$ there is a function m which depends only on t such that the equation $(*)$ has a one-parameter family of disjoint solutions which depend only on t, and that if h is linear on an open interval, one can choose an $m(x, t)$ in such a way that the equation $(*)$ has a one-parameter family of disjoint periodic solutions which depend on x as well as t.

Example. Choose any smooth function $v(x, t)$ with values in (a, b) and period T which satisfies the condition $\partial v/\partial n = 0$, and which has the following property: If the given concave function h is linear in some open subinterval (r, s) of (a, b), v is independent of x except for a finite set of t-intervals, in which the values of v lie in (r, s). If h is strictly concave, let v be a function of t only. Define

$$m(x, t) := \left[\frac{\partial v}{\partial t} - \Delta v\right] \Big/ h(v),$$

so that v is a solution of $(*)$. Define the function U by

$$\int_{v(x, t)}^{U(x, t)} \frac{d\eta}{h(\eta)} = L.$$

Because $\nabla U/h(U) = \nabla v/h(v)$ and because h' is constant in (r, s), it is easily verified that U is a periodic solution of $(*)$ for all sufficiently small values of the parameter L.

Lemma 2.4. *If $m(x, t, u)$ and $h'(u)$ are nonincreasing in u and if a is linearly stable, then all solutions of $(*)$ with values in (a, b) converge uniformly to a as $t \to \infty$.*

If m and h' are nonincreasing in u and a is neutrally stable, then either all solutions with values in (a, b) converge uniformly to a or every such solution converges uniformly to a member of a uniformly continuous one-parameter family $U(x, t; L)$ of distinct periodic solutions which converge uniformly to a as $L \to -\infty$.

The latter case occurs if and only if there is a constant $\gamma > a$ such that either $m(x, t, u)$ and $h'(u)$ are independent of u for $a \leqslant u \leqslant \gamma$, or the function $m(x, t, u)$ is independent of x and u for $a \leqslant u \leqslant \gamma$ and the integral of $m(x, t, a)$ from 0 to T is zero.

Proof. Let ϕ be the solution of (2.1) with initial value equal to the positive eigenfunction of Q_a. Choose a d in (a, b) and a constant K, and define the function $\hat{u}$ by the equation

$$\int_d^{\hat{u}(x,t;K)} \frac{d\eta}{h(\eta)} = \frac{1}{h'(a)} \log \phi(x, t) + K. \tag{2.4}$$

An easy computation shows that

$$\frac{\partial \hat{u}}{\partial t} - \Delta \hat{u} - m(x, t, \hat{u})h(\hat{u}) = [m(x, t, a) - m(x, t, \hat{u})]h(\hat{u}) + \frac{|\nabla \phi|^2}{h'(a)^2 \phi^2}[h'(a) - h'(\hat{u})]h(\hat{u}).$$

Because m and h' are nonincreasing in u, the right-hand side is nonnegative. We see from the comparison theorem that if $u(x, t; K)$ is the solution of $(*)$ such that $u(x, 0; K) = \hat{u}(x, 0; K)$ then $u(x, t; K) \leqslant \hat{u}(x, t; K)$.

Since $\phi(x, t + T) = \mu\phi(x, t)$, we see that if a is linearly stable so that $\mu < 1$, then ϕ goes to zero uniformly in x as $t \to \infty$. Therefore $\hat{u}$ approaches a uniformly in x, and it follows that $u(x, t; K)$ also goes to a uniformly in x. Lemma 2.1 now shows that every solution with values in (a, b) goes to a, uniformly in x.

If $\mu = 1$, then the function ϕ, and hence also $\hat{u}$, is periodic of period T, and hence $\hat{u}$ is bounded away from a and b. Since we have shown that the solution $u(x, t; K)$ with the initial values $\hat{u}(x, 0; K)$ is bounded above by $\hat{u}$, it is bounded away from b. If for some $K = K_1$ the function $u(x, t; K_1)$ converges to a, we again see from Lemma 2.1 that all solutions of $(*)$ with values in (a, b) converge to a, uniformly in x.

If, on the other hand, $u(x, t; K_1)$ does not converge to a, we see from Lemmas 2.1 and 2.2 that it converges to a T-periodic function $u_1(x, t)$, and that every solution of $(*)$ with values in (a, b) is bounded away from a and b and converges to some T-periodic solution, uniformly in x. In particular, if we choose $K_2 < K_1$ so small that $\hat{u}(x, t; K_2) < u_1(x, t)$, we see that $u(x, t; K_2)$ converges to a

T-periodic function $u_2 < u_1$. We see from the proof of Lemma 2.3 that the equation

$$\int_{u_1(x,t)}^{U(x,t;L)} \frac{d\eta}{h(\eta)} = L$$

defines a continuous one-parameter family $U(x, t; L)$ of T-periodic solutions of $(*)$ for $L_2 \leqslant L \leqslant 0$, where $U(x, t; L_2) = u_2(x, t)$.

We observe that as $K_2 \to -\infty$, $\hat{u}(x, t; K_2)$, and hence also $u_2(x, t)$ decreases to a uniformly. Therefore the family $U(x, t; L)$ of periodic solutions is defined for all nonpositive L and approaches a uniformly as $L \to -\infty$. (The set of L-values for which $U(x, t; L)$ is a periodic solution is easily seen to be an open interval, so that it also contains some positive values of L.)

We now see from Lemma 2.3 that if we define

$$\gamma = \min_{x \in \Omega,\, 0 \leqslant t \leqslant T} u_1(x, t),$$

and if $h'(u)$ is not constant for $a \leqslant u \leqslant \gamma$, then $m(x, t, u)$ must be independent of x and u for $x \in \Omega$ and $a \leqslant u \leqslant \gamma$. In this case it is easily seen that the condition $\mu = 1$ is equivalent to the vanishing of the t-integral of $m(x, t, a)$ from 0 to T, and that the formula

$$\int_\gamma^U \frac{d\eta}{h(\eta)} = \int_0^t m\, dt + L$$

defines a one-parameter family of periodic solutions for all sufficiently negative L.

Alternatively, both $h'(u)$ and $m(x, t, u)$ are independent of u for $a \leqslant u \leqslant \gamma$. In this case the family U is defined for sufficiently small L by the formula

$$U(x, t; L) = a + e^{Lh'(a)}\phi(x, t)$$

where ϕ is a periodic solution of (2.1) which corresponds to the eigenvalue $\mu = 1$ of Q_a.

Thus Lemma 2.4 is established.

We now turn our attention to what happens when the linear problem (2.1) is unstable.

Lemma 2.5. *Suppose that m and h' are nonincreasing in u. Also suppose that the principal eigenvalue of the operator Q_a is greater than one. Then every solution of $(*)$ with values in (a, b) is bounded away from a.*

Proof. Let ϕ be a positive solution of (2.1) whose initial value is an eigenfunction of Q_a corresponding to the eigenvalue $\mu > 1$. Then $\phi(x, t + T) = \mu\phi(x, t)$. Define the function

$$v(x, t) := a + \varepsilon\phi(x, t)\mu^{-t/T},$$

which is positive and periodic of period T. If ε is small, we find that

$$\frac{\partial v}{\partial t} - \Delta v - m(x, t, v)h(v) = -\frac{\varepsilon}{T}\phi\mu^{-t/T}\log\mu + O(\varepsilon^2).$$

Thus there is an $\varepsilon > 0$ such that $v(x, t) \in (a, b)$ and v is a subsolution of (*). The comparison theorem now shows that if $\hat{v}(x, t)$ is the solution of (*) with the initial conditions $v(x, 0)$, then $\hat{v}(x, t) > v(x, t)$, which is bounded away from a. The statement of the lemma now follows from Lemma 2.1.

We are now in a position to prove Theorem 1. Lemmas 2.1 and 2.2 show that every solution of (*) with values in (a, b) converges to a T-periodic solution.

Lemma 2.4 immediately yields statements (a) and (b).

To prove statement (c) we observe that the change of dependent variables $u \to a + b - u$ interchanges the end points a and b and replaces the equation (*) with an equation of the same form with $h(u)$ replaced by $h(a + b - u)$ and m replaced by $-m(x, t, a + b - u)$. These changes preserve the concavity of h and the monotonicity in u of m.

We obtain statement (d) by applying Lemma 2.5 to u and $a + b - u$ and using Lemmas 2.2 and 2.3, and the theorem is established.

Remarks. (1) By applying Lemmas 2.1, 2.2, and 2.3 to u and to $a + b - u$, we see that if there is a point (x, t) at which $m(x, t, u)$ is strictly decreasing, then there is a global attractor.

(2) We also see from Lemmas 2.1, 2.2, and 2.3 that if the function h is strictly concave, then there is a global attractor unless there is a one-parameter family of spatially homogeneous periodic solutions. Since such solutions satisfy a first-order ordinary differential equation, it is relatively easy to check whether or not this is the case.

We note that if ϕ is the solution of (2.1) with $\phi(x, 0)$ a positive eigenfunction of Q_a corresponding to the principal eigenvalue μ, then

$$\psi(x, t) = \phi(x, t)\mu^{-t/T}$$

is a periodic solution of the equation

$$\frac{\partial\psi}{\partial t} - \Delta\psi - m(x, t, a)h'(a)\psi = \lambda\psi \quad \text{in } \Omega,$$

$$\frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega,$$

where $\lambda = -\log \mu$. This is the form in which the eigenvalue problem was treated in [2] and [4].

Because the Theorem 1 assumes knowledge of the linear stability properties of a and b, it is useful to find some simple conditions under which these can be predicted.

Proposition 2.1. *If*

$$\int_0^T \int_\Omega m(x, t, a)\, dx\, dt > 0$$

or if

$$\int_0^T \int_\Omega m(x, t, a)\, dx\, dt = 0$$

and $m(x, t, a)$ is not independent of x, then a is linearly unstable. If the integral is zero and $m(x, t, a)$ is independent of x, then a is neutrally stable.

Proof. We see from (2.1) that if ϕ is positive,

$$\left(\frac{\partial}{\partial t} - \Delta\right) \log \phi = m(x, t, a)h'(a) + |\nabla \log \phi|^2.$$

Let $\phi(x, 0)$ be the eigenfunction of Q_a which corresponds to the principal eigenvalue μ, and integrate both sides to find that

$$|\Omega| \log \mu = h'(a) \int_0^T \int_\Omega m(x, t, a)\, dx\, dt + \int_0^T \int_\Omega |\nabla \log \phi|^2\, dx\, dt.$$

The integrals on the right are nonnegative. Thus, a is linearly unstable unless they are both zero. This can only happen if the first integral is zero and ϕ is independent of x. Then (2.1) shows that m is independent of x. If this is the case, we have

$$\phi = \exp\left[h'(a) \int_0^t m(\tau, a)\, d\tau\right],$$

which shows that $\mu = 1$.

Remark. This proposition implies that if a is linearly stable, then the period integral of $m(x, t, a)$ is negative. Since m is nonincreasing in u, and $h'(b) < 0$, it follows that the corresponding integral for b is positive, so that b is linearly unstable.

A partial complement to Proposition 2.1 is the following, which was proved in [2] and [4].

Proposition 2.2. *If $m(x, t, a) \leqslant p(t)$ and the integral of p from 0 to T is negative, or if this integral is zero and $m(x, t, a)$ is not independent of x, then a is linearly stable.*

If we apply standard perturbation theory to the eigenvalue μ, we find that if $m(x, t, u)$ is replaced by $\gamma m(x, t, u)$, and if the integral of $m(x, t, a)$ over $\Omega \times [0, T]$ is negative, then a is linearly stable when γ is positive and sufficiently small.

3. A second sufficient condition

The aim of this section is to prove the following result:

Theorem 2. *Suppose that the function*

$$p(t) = \max_{\substack{x \in \bar{\Omega} \\ u \in [a, b]}} m(x, t, u), \tag{3.1}$$

satisfies the inequality

$$\int_0^T p(t)\, dt \leqslant 0. \tag{3.2}$$

If $u(x, t)$ is any solution of $(*)$ with values in the interval (a, b), then as t approaches infinity, $u(t, \cdot)$ converges uniformly to a spatially homogeneous T-periodic solution $\tilde{c}(t)$ of $(*)$.

Unless equality holds in (3.2) and the maximum of $m(x, t, u)$ with respect to $u \in [a, b]$ is independent of x for all t, this limit is the constant a.

Proof. For fixed constants $\alpha > 0$ and $d \in (a, b)$ we define the new dependent variable

$$w(x, t) = \exp\left\{\alpha\left[\int_d^{u(x,t)} \frac{d\eta}{h(\eta)} - \int_0^t p(\tau)\, d\tau\right]\right\}. \tag{3.3}$$

An easy computation shows that if u is a solution of $(*)$, then

$$\frac{\partial w}{\partial t} - \Delta w = -\alpha\{p(t) - m(x, t, u) + [\alpha - h'(u)]h(u)^{-2}|\nabla u|^2\}w.$$

We choose α larger than the maximum of h' on the interval $[a, b]$. It then follows from the definition (3.1) of p that the right-hand side is nonpositive, so that

$$\frac{\partial w}{\partial t} - \Delta w \leqslant 0. \tag{3.4}$$

It is easily seen that the normal derivative of w vanishes on $\partial\Omega$.

If $u(x, t) \in (a, b)$ in $\Omega \times (0, \infty)$, then $u(x, 1)$ is bounded away from a and b, and hence $w(x, 1)$ is uniformly bounded. Because w satisfies the differential inequality (3.4) and homogeneous Neumann boundary conditions, we conclude from the maximum principle that it is uniformly bounded in $\bar{\Omega} \times [1, \infty)$.

We now consider two cases:

(i) If the inequality (3.2) is strict, then the indefinite integral of $p(t)$ approaches $-\infty$ as t goes to infinity. We then see from the definition (3.3) of w and the boundedness of w that the first integral in the exponent must approach $-\infty$ uniformly in x. We conclude that if the inequality (3.2) is strict, the solution $u \equiv a$ is a global attractor.

(ii) If equality holds in (3.2), we introduce the mean value

$$\bar{w}(t) = \frac{1}{|\Omega|}\int_\Omega w(x, t)\, dx.$$

We see from (3.4) and the Neumann boundary condition that $\bar{w}$ is nonincreasing. Since it is also nonnegative, it must decrease to a limit w^* as t goes to infinity. For an arbitrary positive ε choose t_ε so that

$$\bar{w}(t_\varepsilon) \leqslant w^* + \frac{\varepsilon}{5|\Omega|}.$$

Let $q(x, t)$ be the solution of the problem

$$\frac{\partial q}{\partial t} - \Delta q = 0 \quad \text{in } \Omega \times (t_\varepsilon, \infty)$$

$$\frac{\partial q}{\partial n} = 0 \quad \text{on } \partial\Omega \times (t_\varepsilon, \infty)$$

$$q(x, t_\varepsilon) = w(x, t_\varepsilon) \quad \text{in } \Omega.$$

By the comparison theorem $w(\cdot, t) \leqslant q(\cdot, t)$ for $t \geqslant t_\varepsilon$. It follows from separation of variables that q converges uniformly to the mean value $\bar{w}(t_\varepsilon)$ of its initial values as t goes to infinity. Thus there exists a $\tilde{t}_\varepsilon \geqslant t_\varepsilon$ such that

$$w(\cdot, t) \leqslant q(\cdot, t) \leqslant \bar{w}(t_\varepsilon) + \frac{\varepsilon}{5|\Omega|}$$

$$\leqslant \bar{w}(t) + \frac{2\varepsilon}{5|\Omega|} \quad \text{for } t \geqslant \tilde{t}_\varepsilon. \tag{3.5}$$

If $w^* = 0$, this argument shows that $w(x, t)$ approaches zero uniformly. Since the integral of p is bounded above, we conclude from the transformation (3.3) that in this case $u(x, t)$ converges uniformly to the constant solution a.

Suppose now that $w^* > 0$. Because $\bar{w}$ is the mean value of w, it follows from (3.5) that

$$\|w(\cdot, t) - w^*\|_{L_1} \leqslant |\Omega|(\bar{w} - w^*) + 2\int_\Omega [w - \bar{w}]_+ \, dx$$

$$\leqslant \varepsilon \quad \text{for } t \geqslant \tilde{t}_\varepsilon.$$

That is, w converges to w^* in L_1. This clearly implies that w converges to w^* in measure.

We now define the periodic function $\tilde{c}(t)$ implicitly by the formula

$$\int_d^{\tilde{c}(t)} \frac{d\eta}{h(\eta)} = \int_0^t p(\tau)\, dt + \frac{1}{\alpha} \log w^*. \tag{3.6}$$

We then see from the transformation (3.3) that the convergence in measure of w to w^* implies the convergence in measure of $u(\cdot, t) - \tilde{c}(t)$ to zero. Since both u and $\tilde{c}$ are bounded, this, in turn, implies that $u - \tilde{c}$ converges to zero in L_p for all p.

We note that $\tilde{c}$ satisfies the equation

$$\frac{\partial \tilde{c}}{\partial t} - \Delta \tilde{c} = p(t) h(\tilde{c}).$$

We define the translate

$$u_n(x, t) := u(x, t + nT)$$

for $t \geqslant 0$. If $\Gamma(x, y, t)$ is the Green's function for the Neumann problem of the heat equation on Ω, we easily obtain the integral equation

$$u_n(x, t) - \tilde{c}(t) = \int_\Omega \Gamma(x, y, t)[u(y, nT) - \tilde{c}(0)]\, dy$$

$$+ \int_0^t \int_\Omega \Gamma(x, y, t - s)[m(y, s, u_n) h(u_n(y, s)) - p(s) h(\tilde{c}(s))]\, dy\, ds. \tag{3.7}$$

We confine our attention to the interval $T \leqslant t \leqslant 2T$. As can be seen from the form of the fundamental solution of the heat equation, both $\|\Gamma(x, \cdot, t))\|_{L_q}$ and the integral

$$\int_0^{2T} \|\Gamma(x, \cdot, t)\|_{L_q} dt$$

are uniformly bounded when $q < n/(n-2)$. Since m and h are Hölder continuous, the convergence of $u - \tilde{c}$ in measure implies that as $n \to \infty$ the first integral goes to zero, while the limit of the second integral is obtained by replacing u_n by $\tilde{c}$. Thus

$$\lim_{n \to \infty} u_n(x, t) - \tilde{c}(t) = -\int_0^t \int_\Omega \Gamma(x, y, t-s)[p(s) - m(y, s, \tilde{c})]h(\tilde{c}(s))\, dy\, ds. \quad (3.8)$$

We see from the fact that $h(\tilde{c}) > 0$ and the definition of $p(t)$ that the right-hand side is nonpositive. If it is negative, (3.8) contradicts the fact that $u - \tilde{c}$ approaches zero in measure. We conclude that w^* can only be positive and hence the constant solution a can fail to be a global attractor only if the right-hand side is zero. Since the integrand is nonnegative, this can only happen if

$$m(x, t, \tilde{c}(t)) \equiv p(t). \quad (3.9)$$

In this case, the right-hand side of (3.8) is zero, so that $u_n - \tilde{c}$ converges to zero uniformly for $T \leqslant t \leqslant 2T$. This is equivalent to the statement that $u(x, t) - \tilde{c}(t)$ approaches zero uniformly in x as t approaches infinity, so that the theorem is established.

Since the change of dependent variable $u \to a + b - u$ takes (*) into an equation of the same form, we immediately obtain the following corollary:

Corollary. *If*

$$\int_0^T \min_{\substack{x \in \bar{\Omega} \\ u \in [a, b]}} m(x, t, u)\, dt \geqslant 0,$$

then the conclusion of Theorem 2, with the solution a replaced by the solution b, is valid.

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Received January 30, 1989; received in revised form May 15, 1989