DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS
Volume **6**, Number **1**, January **2000** pp.

MUTATION, SELECTION, AND RECOMBINATION IN A MODEL OF PHENOTYPE EVOLUTION

P. Magal

Faculte des Sciences et Techniques
25, rue Philippe Lebon, B.P. 540, 76058 Le Havre, France

G.F. Webb*

Department of Mathematics, Vanderbilt University, Nashville, TN 37240

Abstract. A model of phenotype evolution incorporating mutation, selection, and recombination is investigated. The model consists of a partial differential equation for population density with respect to a continuous variable representing phenotype diversity. Mutation is modeled by diffusion, selection is modeled by differential phenotype fitness, and genetic recombination is modeled by an averaging process. It is proved that if the recombination process is sufficiently weak, then there is a unique globally asymptotically stable attractor.

1. **Introduction.** We investigate the following model for the evolution of a population with a continuously varying phenotype structure:

$$\begin{cases} u_t = \alpha^2 u_{yy} + [\beta(y) - \mathcal{F}(u)]u + \tau[H(u) - u], \\ u_y(0,t) = u_y(1,t) = 0, \; t > 0, \\ u(y,0) = \varphi(y), 0 \leq y \leq 1, \end{cases} \tag{1.1}$$

where $\alpha \geq 0, \tau \geq 0$, $\beta \in L^\infty(0,1)$, and $\mathcal{F} \in L^1_+(0,1)^*$ is the linear form defined by $\mathcal{F}(\varphi) = \gamma \int_0^1 \varphi(\widehat{y}) d\widehat{y}, \forall \varphi \in L^1(0,1)$ with $\gamma \geq 0$, and

$$H(\varphi)(y) = \begin{cases} \frac{\int_0^1 k(y,y)\varphi(2y-y)\varphi(y)dy}{\int_0^1 \varphi(y)dy}, \forall \varphi \in L^1_+(0,1) \setminus \{0\}, \\ 0, \text{if } \varphi = 0 \end{cases}$$

with

$$k(y,\widehat{y}) = \begin{cases} 2 \text{ if } 0 \leq y \leq \frac{1}{2} \text{ and } 0 \leq \widehat{y} \leq 2y \\ 2 \text{ if } \frac{1}{2} \leq y \leq 1 \text{ and } 2y-1 \leq \widehat{y} \leq 1 \\ 0 \text{ elsewhere.} \end{cases}$$

In (1) $u = u(y,t)$ is the density of a population with respect to a phenotype variable $y \in (0,1)$ at time t. The subpopulation of phenotypes at time t in the range $[y_1, y_2] \subseteq [0,1]$ is given by $\int_{y_1}^{y_2} u(y,t)dy$. The population is viewed as evolving over time due to the three separate processes of mutation, selection, and recombination. In (1) the mutation process is represented by the diffusion term $\alpha^2 u_{yy}$, where α is a parameter corresponding to the average rate of movement in y per mutation per unit time. The boundary conditions at $y = 0$ and $y = 1$ in (1) mean that no individuals are lost through the boundary as a direct result of mutation. In (1) the selection process for the population depends on the fitness of individuals with

1991 *Mathematics Subject Classification.* 35K55, 47H20, 58F11, 92D15.

Key words and phrases. Semigroups, asymptotic behavior, evolution, mutation, recombination.

*Research partially supported by NSF grant DMS-9805515.

respect to phenotype represented by the function $\beta(y)$. Fitness is variable in y and the sign of $\beta(y)$ may be positive or negative. In (1) there is also a density dependent mortality independent of phenotype represented by the crowding term $\mathcal{F}(u)$. The problem (1) also incorporates DNA exchange in phenotype evolution represented by the term $\tau(H(u)-u)$. The recombination operator H corresponds to the average rate at which two parent phenotypes y_1 and y_2 hybridize to yield offspring with phenotype $\frac{y_1+y_2}{2}$. This form of recombination inheritance is an idealization and other genetic recombination processes could be treated in a similar way. Problem (1) thus models the evolution of phenotype structure from the initial phenotype distribution $\phi \in X = L^1(0,1)$ at time 0 subject to these processes.

Our analysis of (1) proceeds as follows: In Section 2 we will analyze problem (1) with mutation ($\alpha > 0$) and recombination ($\tau > 0$), but without selection ($\beta \equiv 0$) and crowding ($\gamma = 0$). We will establish that the recombination operator H is Lipschitz continuous in $X_+ = L^1_+(0,1)$, positive homogeneous in X_+, norm preserving in X_+, and mean preserving in X_+. Further, we will prove that $lim_{n\to\infty} H^n\phi$ is a delta function concentrated at the mean of ϕ for each ϕ in X_+. If only recombination acts on phenotype evolution ($\alpha = 0$, $\beta \equiv 0$, $\gamma = 0$, $\tau > 0$), then the population would evolve to a delta function. If only mutation acts on phenotype evolution ($\alpha > 0$, $\beta \equiv 0$, $\gamma = 0$, $\tau = 0$), then the population would evolve to a uniformly constant phenotype density. Thus, mutation and recombination can be viewed as having opposite effect, although each can result in increased phenotypic variability. We will prove that if both mutation and recombination are present and $\tau > 0$ is sufficiently small, then all solutions evolve to a nontrivial equilibrium phenotype distribution dependent on the norm of the initial distribution ϕ.

In Section 3 we will analyze problem (1) with mutation ($\alpha > 0$), selection ($\beta \not\equiv 0$), and crowding ($\gamma > 0$), but without hybridization ($\tau = 0$). In this case we will establish that the behavior of the solutions depends on the sign of the dominant eigenvalue $\tilde{\lambda}_0$ of the linear problem ($\alpha > 0$, $\beta \not\equiv 0$, $\gamma = 0$, $\tau = 0$). If $\tilde{\lambda}_0 \leq 0$ then the population goes extinct, and if $\tilde{\lambda}_0 > 0$ then the population evolves to a unique nontrivial equilibrium independent of the initial distribution ϕ.

In Section 4 we will analyze the full problem (1) ($\alpha > 0$, $\beta \not\equiv 0$, $\gamma > 0$, $\tau > 0$). We will use a result of Smith and Waltman [13] to establish that if $\tau > 0$ is sufficiently small, then the population evolves to a unique nontrivial equilibrium phenotype distribution independent of the initial distribution ϕ. Thus, the ultimate fate of phenotype evolution depends on the relative strength of recombination. The combined effects of mutation, selection, and recombination yield stabilization to a unique equilibrium independent of the initial phenotype structure if the effect of recombination is sufficiently weak. We remark that numerical simulations indicate that if the effect of recombination is sufficiently strong, then the phenotype population again stabilizes to equilibrium, but that the phenotype structure of the equilibrium depends on the initial population structure.

An example of phenotype evolution in a continuously varying property is the colonization of *Helicobacter pylori*, a bacteria inhabiting the human stomach. This bacteria displays phenotype diversity in its expression of Lewis type antigen, which varies continuously through a range of optical density measurements. Experiments in [12] and [15] demonstrate that during the colonization of *Helicobacter pylori* the phenotype population migrates and stabilizes through successive generations subject to selection, mutation, and recombination processes in the host. In future work model (1) will be used to analyze and interpret these experimental data.

2. **Mutation and Recombination.** In this section we analyze (1) with $\alpha > 0$, $\beta \equiv 0$, $\gamma = 0$, and $\tau > 0$:

$$\begin{cases} u_t = \alpha^2 u_{yy} + \tau[H(u) - u], \\ u_y(0,t) = u_y(1,t) = 0,\, t > 0, \\ u(y,0) = \varphi(y), 0 \le y \le 1. \end{cases} \tag{2.2}$$

We first establish some properties of the recombination operator H.

Theorem 2.1. *H is a (nonlinear) operator from X_+ to X_+ satisfying the following properties:*

i) H is positive homogeneous, i.e., $H(c\phi) = cH(\phi)\,\forall\phi \in X_+$ and $c \ge 0$;
ii) H is Lipschitz continuous in X_+;
iii) H preserves norm in X_+, i.e., $\int_0^1 H(\phi)(y)dy = \int_0^1 \phi(y)dy \forall\phi \in X_+$;
iv) $supp(H(\phi))$ is contained in the closed convex hull of $supp(\phi)\,\forall\phi \in X_+$;
v) H preserves mean in X_+, i.e., if $\phi \in X_+ \setminus \{0\}$ and we define $y_m(\phi) := \int_0^1 y\,\phi(y)\,dy/\|\phi\|$, then $y_m(\phi) = y_m(H(\phi))$;
vi) if $\phi \in L^2_+(0,1) \setminus \{0\}$, then

$$lim_{n\to\infty}\,(H^n\phi)(y) \;=\; \begin{cases} 0,\; if\, y \ne\, y_m(\phi), \\ \infty,\; if\, y \,=\, y_m(\phi). \end{cases}$$

Proof: The proofs of i) - iv) are straightforward. To prove v) let $\phi \in X_+ \setminus \{0\}$. Then, using iii),

$$\begin{aligned} &\int_0^1 y\,(H\phi)(y)\,/\,\|H(\phi)\|\,dy \\ &= \int_0^1 y\,(\int_0^1 k(y,\tilde y)\,\phi(2y-\tilde y)\phi(\tilde y)\,d\tilde y)\,/\,\|\phi\|^2\,dy \\ &= \int_0^1 \phi(\tilde y)\,(\int_0^1 y\,k(y,\tilde y)\,\phi(2y-\tilde y)\,dy)\,/\,\|\phi\|^2\,d\tilde y \\ &= \int_0^1 \phi(\tilde y)\,(\int_{\tilde y/2}^{(\tilde y+1)/2} y\,2\,\phi(2y-\tilde y)\,dy)\,/\|\phi\|^2\,d\tilde y \\ &= \int_0^1 \phi(\tilde y)\,(2\int_0^1 (\frac{z+\tilde y}{2})\phi(z)\,\frac{dz}{2})\,d\tilde y/\|\phi\|^2 \\ &= \frac{1}{2}\int_0^1 \phi(\tilde y)\,(\int_0^1 z\,\phi(z)\,dz \,+\, \int_0^1 \tilde y\,\phi(z)\,)\,d\tilde y/\|\phi\|^2 \\ &= \frac{1}{2}\int_0^1 \phi(\tilde y)\,(y_m(\phi) \,+\, \tilde y\,)\,d\tilde y/\,\|\phi\| = y_m(\phi). \end{aligned}$$

To prove vi) let $\phi \in L^2_+(0,1) \setminus \{0\}$ such that $\|\phi\|_X = 1$ and extend ϕ to $(-\infty,\infty)$ by $\phi(y) = 0$ if $y < 0$ or $y > 1$. Let $\mu = y_m(\phi)$ and $\sigma^2 = variance(\phi)$. Then $H(\phi)(y) = 2(\phi * \phi)(2y)$ and consequently, $(H^n\phi)(y) = 2^n\phi^{*2^n}(2^n y)$. From the local central limit theorem [8]

$$lim_{n\to\infty}\,sup_{y\in(-\infty,\infty)}|\,\sigma\sqrt{n}\phi^{*n}(y\sigma\sqrt{n} + nm) \,-\, \frac{e^{-y^2/2}}{\sqrt{2\pi}}\,| \,=\, 0.$$

It follows that

$$lim_{n\to\infty}\,sup_{y\in(-\infty,\infty)}|\,n\phi^{*n}(ny) \,-\, \frac{\sqrt{n}}{\sqrt{2\pi}\sigma}\,e^{\frac{-n(y-m)^2}{2\sigma^2}}\,| \,=\, 0.$$

Thus,

$$lim_{n\to\infty}\, sup_{y\in(-\infty,\infty)} |\, H^n\phi(y) \; - \; \frac{\sqrt{2^n}}{\sqrt{2\pi}\sigma}\, e^{\frac{-2^n(y-m)^2}{2\sigma^2}} \; | \; = \; 0$$

and vi) follows.

Remark 2.1 The proof of vi) in Theorem 2.1 is due to R. Rudnicki and M. Kimmel.

Our analysis will use the theory of semigroups of linear operators and view (2) as a semilinear perturbation of a linear problem. Define the unbounded operator $A : D(A) \to X$ by $A\varphi = \alpha^2\varphi''$, where $D(A) = \{\varphi \in X : \varphi'$ is absolutely continuous and $\varphi'(0) = \varphi'(1) = 0\}$. We state the following results concerning the linear strongly continuous semigroup $\{T(t)\}_{t\geq 0}$ with infinitesimal generator A (see Brezis [1], Clement *et al.* [6], Pazy [11], and Wu [16]):

i) $T(t)X_+ \subset X_+, \forall t \geq 0;$

ii) $\int_0^1 T(t)(\varphi)(y)dy = \int_0^1 \varphi(y)dy, \forall t \geq 0;$

iii) $T(t)$ is compact for $t > 0$;

iv) $\sigma(A) = P\sigma(A) = \{\lambda_n = -(n\pi\alpha)^2 : n = 0, 1, ...\}$ with $A\varphi_0 = \lambda_0\varphi_0$, where $\varphi_0 \equiv 1$ ($\sigma(A)$ denotes the spectrum of A and $P\sigma(A)$ denotes the point spectrum of A).

v) $X = X_0 \oplus X_1$ where $X_0 = \{c\varphi_0 : c \in \mathbf{R}\}$, and $X_1 = R(I - P_0)$, where $P_0(\varphi)(y) = (\int_0^1 \varphi(\widehat{y})d\widehat{y})\varphi_0(y)$, $T(t)X_i \subset X_i, \forall t \geq 0, \forall i = 0, 1.$

vi) $T(t)P_0\varphi = P_0\varphi$ and there exists $M > 0$ and $\delta \in (0, (\pi\alpha)^2)$ such that

$$||T(t)P_1\varphi|| \leq Me^{-\delta t}||P_1\varphi||,$$

where $P_1 = I - P_0$.

We note that properties v) and vi) above imply that $\{T(t)\}_{t\geq 0}$ has the property of *asynchronous exponential growth*, that is, $lim_{t\to\infty} e^{-\lambda_0 t}T(t)\phi = P_0\phi\,\forall\phi \in X$. The global existence, uniqueness, and positivity of weak solutions to (2) is a direct consequence of the properties of $\{T(t)\}_{t\geq 0}$ and the fact that H is Lipschitz continuous (see Pazy [11]). To investigate the asymptotic behavior of these solutions we first prove the following result:

Theorem 2.2. *If $\tau > 0$ is sufficiently small, then for each $\xi > 0$ there exists a unique $\widehat{\varphi}_\xi \in X_+$ such that $||\widehat{\varphi}_\xi|| = \xi$, $\widehat{\varphi}''_\xi(y) + \tau((H(\widehat{\varphi}_\xi))(y) - \widehat{\varphi}_\xi(y)) = 0$, and $\widehat{\varphi}'_\xi(0) = \widehat{\varphi}'_\xi(1) = 0$. Moreover, $\forall\xi > 0$, $\widehat{\varphi}_\xi = \xi\widehat{\varphi}_1$.*

Proof: Let $\xi > 0$ and consider the fixed point problem

$$\varphi'' + \tau(H(\varphi) - \varphi) = 0 \Leftrightarrow \varphi = \tau(\tau I - A)^{-1}H(\varphi) = K(\varphi).$$

Then we have $K : S_\xi = \{\varphi \in X_+ : ||\varphi|| = \xi\} \to S_\xi$, (since $\tau(\tau I - A)^{-1}$ and H are norm preserving on X_+), and for all $\varphi_1, \varphi_2 \in S_\xi$, we have

$$||K(\varphi_1) - K(\varphi_2)|| \leq \tau\frac{M}{\tau + \delta}||H||_{Lip},$$

because $(\tau I - A)^{-1}\,|_{X_1}\, P_1\phi = \int_0^{+\infty} e^{-\tau t}T(t)P_1\phi dt$. Thus,

$$||(\tau I - A)^{-1}\,|_{X_1}\, P_1\phi|| \leq \frac{M}{\tau + \delta}||P_1\phi||.$$

Choose $\tau > 0$, sufficiently small such that $||K||_{Lip} < 1$, and then we know that there exists a unique $\widehat{\varphi}_\xi \in S_\xi$ such that $K(\widehat{\varphi}_\xi) = \widehat{\varphi}_\xi$. To prove that $\forall \xi > 0$, $\varphi_\xi = \xi\varphi_1$, it is sufficient to remark that K is homogenous, and the property follows by uniqueness of the fixed point on the sphere S_ξ.

Theorem 2.3. *If u is a weak solution of equation (2.2), and $||\varphi|| = \xi > 0$, then $||u(t)|| = \xi$, $\forall t \geq 0$. Moreover, if $u_{\lambda\varphi}(t)$ is the weak solution of equation (2.2) with initial value $\lambda\varphi$, then $u_{\lambda\varphi}(t) = \lambda u_\varphi(t), \forall t \geq 0, \lambda \geq 0$.*

Proof: Let us recall that u is a weak solution of equation (2.2) if

$$u(t) = T(t)\varphi + \int_0^1 T(t-s)\tau[H(u(s)) - u(s)]ds.$$

Now using the property $ii)$ for $T(t)$, and denoting $x^*(\varphi) = \int_0^1 \varphi(y)dy$, one deduces that

$$\begin{aligned} x^*(u(t)) &= x^*(T(t)\varphi) + x^*(\textstyle\int_0^1 T(t-s)\tau[H(u(s)) - u(s)]ds), \\ &= x^*(\varphi) + \textstyle\int_0^1 x^*(\tau[H(u(s)) - u(s)])ds = x^*(\varphi), \end{aligned}$$

since $x^*(H(\varphi)) = x^*(\varphi)$. The last assertion is a direct consequence of the homogeneity of the mapping H.

Theorem 2.4. *If $\tau > 0$ is sufficiently small, $\varphi_1, \varphi_2 \in X_+$, and $||\varphi_i|| = 1, \forall i = 1, 2$, then* $\lim_{t\to\infty} ||u_1(t) - u_2(t)|| = 0$.

Proof: Let $u_i(t) = T(t)\varphi_i + \int_0^1 T(t-s)\tau[H(u_i(s)) - u_i(s)]ds$ and observe that

$$\begin{aligned} ||u_1(t) - u_2(t)|| &\leq ||T(t)P_0(\varphi_1 - \varphi_2)|| + ||T(t)P_1(\varphi_1 - \varphi_2)|| \\ &+\tau \textstyle\int_0^t ||T(t-s)P_0([H(u_1(s)) - H(u_2(s))] - [u_1(s) - u_2(s)])||ds \\ &+\tau \textstyle\int_0^t ||T(t-s)P_1([H(u_1(s)) - H(u_2(s))] - [u_1(s) - u_2(s)])||ds. \end{aligned}$$

Thus, $||u_1(t) - u_2(t)|| \leq$

$$0 + Me^{-\delta t}||\varphi_1 - \varphi_2|| + 0 + \int_0^t Me^{-\delta(t-s)}C||u_1(s) - u_2(s)||ds,$$

where $C = \tau||H - I||_{Lip}$. Setting $w(t) = ||u_1(s) - u_2(s)||$, one has

$$e^{\delta t}w(t) \leq C_1 + CM\int_0^t e^{\delta s}w(s)ds,$$

where $C_1 = M||\varphi_1 - \varphi_2||$. Setting $v(t) = e^{\delta t}w(t)$, one has

$$v(t) \leq C_1 + CM\int_0^t v(s)ds,$$

so that by Gronwall's lemma (see lemma 3.1 p:15 in Hale ([9]) $v(t) \leq C_1e^{CMt}$. Thus, $w(t) \leq C_1e^{(CM-\delta)t}$, so that for $\tau > 0$ sufficiently small, we have $\tau||H - I||_{Lip}M < \delta$, and the result follows.

Theorem 2.5. *If $\tau > 0$ is sufficiently small, then for every $\varphi \in X_+ \setminus \{0\}$ one has* $\lim_{t\to\infty} u(t) = \widehat{\varphi}_{||\phi||}$, *where $\widehat{\varphi}_{||\phi||}$ is the unique equilibrium solution given by theorem 2.2.*

Proof: The result is a direct consequence of theorem 2.2 and theorem 2.4.

3. **Mutation and Selection.** In this section we investigate the global asymptotic behavior of (1) in the case that mutation and selection determine phenotype evolution without recombination ($\alpha > 0$, $\beta \not\equiv 0$, $\gamma > 0$, and $\tau = 0$):

$$\begin{cases} u_t = \alpha^2 u_{yy} + [\beta(y) - \mathcal{F}(u)]u \\ u_y(0,t) = u_y(1,t) = 0,\, t > 0, \\ u(y,0) = \varphi(y), 0 \leq y \leq 1, \end{cases} \tag{3.3}$$

The formulation (3) allows us to use the method developed in [14]. Let $\beta \in L^\infty(0,1)$ and denote by $B : D(B) \to X$ the unbounded linear operator defined by $B\varphi = \alpha^2\varphi'' + \beta\varphi$, where $D(B) = D(A)$. Since B is a perturbation of A obtained by addition of a bounded operator, we know (see Pazy [11] p:76-77) that B generates a linear semigroup $\{S(t)\}_{t\geq 0}$ which satisfies the variation of constants formula

$$S(t)\varphi \,=\, T(t)\varphi \,+\, \int_0^t T(t-s)(\beta S(s)\varphi)ds, t \geq 0. \tag{3.4}$$

We also know that for all $\xi \in \mathbf{R}$, equation (3.4) is equivalent to the following equation

$$S(t)\varphi = e^{-\xi t}T(t)\varphi + \int_0^t e^{-\xi(t-s)}T(t-s)(\beta S(s)\varphi + \xi S(s)\varphi)ds,\ \forall t \geq 0. \tag{3.5}$$

So by taking $\xi > \max(0, -\underline{\beta})$, where $\underline{\beta} = \inf ess_{\sigma\in(0,1)}\beta(\sigma)$, we deduce that *i)* $S(t)X_+ \subset X_+, \forall t \geq 0$. Moreover, we deduce from lemma 1.6 p:42 in Wu [16] that, *ii)* $S(t)$ is compact for $t > 0$. Finally, we remark that by using equation (3.5) one has for $\xi \geq \max(0, -\underline{\beta})$,

$$S(t)\varphi \geq e^{-\xi t}T(t)\varphi,\ \forall t \geq 0, \forall \varphi \in X_+. \tag{3.6}$$

From equation (3.6) and the properties of $\{T(t)\}_{t\geq 0}$ it is not difficult to deduce that $\{S(t)\}_{t\geq 0}$ is irreducible, that is, $\forall \varphi \in X_+ \setminus \{0\}, \forall \varphi^* \in X_+^* \setminus \{0\}$

$$\exists t_0 = t_0(\varphi, \varphi^*) > 0, \text{ such that } \varphi^*(S(t)\varphi) > 0,$$

where $X_+^* = \{\varphi^* \in X^* : \varphi^*(x) \geq 0, \forall x \in X_+\}$. From theorem 1 p:158 in Zerner [17], we know that there exists $\widetilde{\varphi}_0 \in X_+ \setminus \{0\}, \widetilde{\varphi}_0^* \in X_+^* \setminus \{0\}$, such that if

$$\widetilde{P}_0(\varphi)(y) = (\int_0^1 \widetilde{\varphi}_0^*(\widehat{y})\varphi(\widehat{y})d\widehat{y})\widetilde{\varphi}_0(y),$$

then the following hold: *iii)* if $X = \widetilde{X}_0 \oplus \widetilde{X}_1$, where $\widetilde{X}_0 = \{c\widetilde{\varphi}_0 : c \in \mathbf{R}\}$ and $\widetilde{X}_1 = R(I - \widetilde{P}_0)$, then $S(t)\widetilde{X}_i \subset \widetilde{X}_i, \forall t \geq 0, \forall i = 0,1$; and *iv)* if $\widetilde{\lambda}_0 = s(B)$, the spectral bound of B, then $S(t)\widetilde{P}_0\varphi = e^{\lambda_0 t}\widetilde{P}_0\varphi$ and there exists some $\widetilde{M} > 0$ and $\widetilde{\delta} > 0$ such that

$$||S(t)\widetilde{P}_1\varphi|| \leq Me^{(\lambda_0-\delta)t}||\widetilde{P}_1\varphi||, \text{ where } \widetilde{P}_1 = I - \widetilde{P}_0.$$

Remark 3.1: In the references [2], [3], and [4] sufficient conditions are given to assure that the dominant eigenvalue $\widetilde{\lambda}_0$ of B is strictly positive. We remark that a sufficient, but not necessary, condition that $\widetilde{\lambda}_0 > 0$ is that the average value $\int_0^1 \beta(y)dy$ of β on $(0,1)$ is positive.

Theorem 3.1. *Let $\widetilde{\lambda}_0 > 0$, let $\varphi \in X_+\setminus\{0\}$, and denote by $\{W_0(t)\}_{t\geq 0}$ the strongly continuous semigroup associated with (3.3). Then*

$$W_0(t)\varphi = u(t) \to u^* = \frac{\widetilde{\lambda}_0\widetilde{P}_0\varphi}{\mathcal{F}(\widetilde{P}_0\varphi)} = \frac{\widetilde{\lambda}_0\widetilde{\varphi}_0}{\mathcal{F}(\widetilde{\varphi}_0)},\ \textit{as } t \to \infty.$$

Moreover, u^* is an exponentially asymptotically stable equilibrium solution.

Proof: Let $\varphi \in X_+ \setminus \{0\}$. It is straightforward to verify that the weak solution of equation (3.3) is given by

$$u(t) = W_0(t)\varphi = \frac{S(t)\varphi}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds},$$

and by using l'Hospital's rule, we have $u(t) \to \frac{\lambda_0 P_0 \varphi}{\mathcal{F}(P_0\varphi)} = u^*,$ as $t \to \infty$. It remains to prove that u^* is exponentially asymptotically stable. In order to do this we now show that

$$\frac{S(t)\varphi}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0 \widetilde{P}_0\varphi}{\mathcal{F}(\widetilde{P}_0\varphi)} \to 0, \text{ as } t \to \infty$$

exponentially on bounded sets of $X_+ \setminus \{0\}$. Consider the following expression:

$$\begin{aligned} \|\frac{S(t)\varphi}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0 \widetilde{P}_0\varphi}{\mathcal{F}(\widetilde{P}_0\varphi)}\| &\le \|\frac{S(t)\varphi}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0 S(t)\varphi}{e^{\lambda_0 t}\mathcal{F}(\widetilde{P}_0\varphi)}\| \\ &+ \|\frac{\widetilde{\lambda}_0 S(t)\varphi}{e^{\lambda_0 t}\mathcal{F}(\widetilde{P}_0\varphi)} - \frac{\widetilde{\lambda}_0 \widetilde{P}_0\varphi}{\mathcal{F}(\widetilde{P}_0\varphi)}\| \\ &\le \|\frac{S(t)\varphi}{e^{\lambda_0 t}}\| |\frac{e^{\lambda_0 t}}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0}{\mathcal{F}(\widetilde{P}_0\varphi)}| \\ &+ |\frac{\widetilde{\lambda}_0}{\mathcal{F}(\widetilde{P}_0\varphi)}| \|\frac{S(t)\varphi}{e^{\lambda_0 t}} - \widetilde{P}_0\varphi\|. \end{aligned}$$

It remains to prove that $|\frac{e^{\lambda_0 t}}{1+ \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\lambda_0}{\mathcal{F}(P_0\varphi)}| \to 0, \, as\, t \to \infty$ exponentially on bounded sets of $X_+ \setminus \{0\}$. But

$$|\frac{e^{\lambda_0 t}}{1 + \int_0^t \mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0}{\mathcal{F}(\widetilde{P}_0\varphi)}| = |\frac{e^{\lambda_0 t}}{e^{-\lambda_0 t} + \int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds} - \frac{\widetilde{\lambda}_0}{\mathcal{F}(\widetilde{P}_0\varphi)}|,$$

so it only remains to show that $|\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \frac{\mathcal{F}(P_0\varphi)}{\lambda_0}| \to 0$, as $t \to \infty$ exponentially on bounded sets of $X_+ \setminus \{0\}$. Since

$$\begin{aligned} &|\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \frac{\mathcal{F}(\widetilde{P}_0\varphi)}{\widetilde{\lambda}_0}| \\ &\le |\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \mathcal{F}(\int_0^t e^{-\lambda_0 s}\widetilde{P}_0\varphi ds)| + |\frac{\mathcal{F}(e^{-\lambda_0 t}\widetilde{P}_0\varphi)}{\widetilde{\lambda}_0}|, \end{aligned}$$

it is sufficient to consider the term

$$\begin{aligned} &|\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \mathcal{F}(\int_0^t e^{-\lambda_0 s}\widetilde{P}_0\varphi ds)| \\ &= |\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \mathcal{F}(\int_0^t e^{-\lambda_0 s}\widetilde{P}_0\varphi ds)|. \end{aligned}$$

Since $\int_0^t e^{-\lambda_0 s}ds = \int_0^t e^{-\lambda_0 (t-l)}dl$, we have

$$|\int_0^t e^{-\lambda_0 t}\mathcal{F}(S(s)\varphi)ds - \mathcal{F}(\int_0^t e^{-\lambda_0 s}\widetilde{P}_0\varphi ds)| = |\int_0^t e^{-\lambda_0(t-s)}\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)ds|$$

$$\leq |\int_{\frac{t}{2}}^t e^{-\lambda_0(t-s)}\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)ds| + |\int_0^{\frac{t}{2}} e^{-\lambda_0(t-s)}\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)ds|$$

$$\leq \frac{1}{\widetilde{\lambda}_0}\sup_{s\in[\frac{t}{2},t]}|\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)| + \frac{e^{-\lambda_0\frac{t}{2}}}{\widetilde{\lambda}_0}\sup_{s\in[0,\frac{t}{2}]}|\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)|$$

$$\leq \frac{1}{\widetilde{\lambda}_0}\sup_{s\in[\frac{t}{2},t]}|\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)| + \frac{e^{-\lambda_0\frac{t}{2}}}{\widetilde{\lambda}_0}\sup_{s\in[0,\frac{t}{2}]}|\mathcal{F}(e^{-\lambda_0 s}S(s)\varphi - \widetilde{P}_0\varphi)|$$

$$\leq \frac{1}{\widetilde{\lambda}_0}\sup_{s\in[\frac{t}{2},t]}Me^{-\delta s}\|\widetilde{P}_1\varphi\| + \frac{e^{-\lambda_0\frac{t}{2}}}{\widetilde{\lambda}_0}\sup_{s\in[0,\frac{t}{2}]}Me^{-\delta s}\|\widetilde{P}_1\varphi\|$$

$$\leq \frac{1}{\widetilde{\lambda}_0}Me^{-\delta\frac{t}{2}}\|\widetilde{P}_1\varphi\| + \frac{e^{-\lambda_0\frac{t}{2}}}{\widetilde{\lambda}_0}M\|\widetilde{P}_1\varphi\|,$$

and the result follows.

We recall that the *growth bound* of the linear semigroup $\{T(t)\}_{t\geq 0}$ is the real number given by

$$\omega = \inf\left\{w \in \mathbf{R} : \exists M \in \mathbf{R}_+ \text{ such that } \|T(t)\| \leq Me^{wt}\forall t \geq 0\right\}.$$

We now investigate the linearized semigroup of $W_0(t)\varphi$ at u^*. In order to define the linearized semigroup one has to be careful, because $W_0(t)\varphi$ is only globally defined for φ in X_+. Clearly for each $t \geq 0$, the mapping $\varphi \to W_0(t)\varphi$ is right differentiable with respect to the positive cone X_+ (see Deimling [7] p:225 for the definition). More precisely, for each $t \geq 0$, there exists a bounded linear operator $D_xW_0(t) \in \mathcal{L}(X)$, such that the limit as $\|h\| \to 0$ with $u^* + h \in X_+$ of

$$\frac{1}{\|h\|}[W_0(t)(u^*+h) - W_0(t)(u^*) - D_xW_0(t)(u^*)(h)] = 0,$$

where $D_xW_0(t)$ is defined for each $\varphi \in X$ by $D_xW_0(t)(u^*)\varphi =$

$$\frac{S(t)\varphi}{1+\int_0^t \mathcal{F}(S(s)u^*)ds} - \frac{S(t)u^*}{(1+\int_0^t \mathcal{F}(S(s)u^*)ds)^2}\int_0^t \mathcal{F}(S(s)\varphi)ds.$$

Moreover, since by construction $\frac{S(t)u^*}{1+\int_0^t \mathcal{F}(S(s)u^*)ds} = u^*$, we deduce that

$$D_xW_0(t)(u^*)\varphi = \frac{S(t)\varphi - u^*\int_0^t \mathcal{F}(S(s)\varphi)ds}{(1+\int_0^t \mathcal{F}(S(s)u^*)ds)}.$$

Moreover, since $u^* = \frac{\lambda_0}{\mathcal{F}(\varphi_0)}\widetilde{\varphi}_0$, and $S(t)u^* = e^{\lambda_0 t}u^*, \forall t \geq 0$, we deduce that $D_xW_0(t)(u^*)\varphi = e^{-\lambda_0 t}[S(t)\varphi - u^*\int_0^t \mathcal{F}(S(s)\varphi)ds]$. It is not difficult to see that $t \to D_xW_0(t)(u^*)\varphi$ is continuous. Then it is possible to prove by a direct computation (using again the fact that $u^* = \frac{\lambda_0}{\mathcal{F}(\varphi_0)}\widetilde{\varphi}_0$) that $D_xW_0(t)(u^*) \circ D_xW_0(s)(u^*) = D_xW_0(t+s)(u^*),\ \forall t, s \geq 0$. Thus, the family of linear operators $\{D_xW_0(t)(u^*)\}_{t\geq 0}$ is a C_0-semigroup.

Lemma 3.2. *Let $\widetilde{\lambda}_0 > 0$. The linear C_0-semigroup $\{D_xW_0(t)(u^*)\}_{t\geq 0}$ has a strictly negative growth bound.*

Proof: Since X is reproducing (*i.e.*, $X = \{u - v : u, v \in X_+\}$), it is sufficient to prove that there exists a constant $\delta > 0$, such that for all $\varphi \in X_+ \setminus \{0\}$, $\|D_x W_0(t)(u^*)\varphi\| \leq M e^{-\delta t}\|\varphi\|, \forall t \geq 0$. Let $\varphi \in X_+ \setminus \{0\}$, be fixed. Thus

$$D_x W_0(t)(u^*)\varphi = \frac{S(t)\varphi - u^* \int_0^t \mathcal{F}(S(s)\varphi)ds}{(1+\mathcal{F}(u^*)\int_0^t e^{\lambda_0 s}ds)} = \frac{S(t)\varphi - u^* \int_0^t \mathcal{F}(S(s)\varphi)ds}{(1+\mathcal{F}(u^*)(\frac{e^{\lambda_0 t}-1}{\lambda_0}))}$$
$$= \frac{S(t)P_0\varphi - u^* \int_0^t \mathcal{F}(S(s)P_0\varphi)ds}{(1+\mathcal{F}(u^*)(\frac{e^{\lambda_0 t}-1}{\lambda_0}))} + \frac{S(t)P_1\varphi - u^* \int_0^t \mathcal{F}(S(s)P_1\varphi)ds}{(1+\mathcal{F}(u^*)(\frac{e^{\lambda_0 t}-1}{\lambda_0}))}.$$

Let us consider the first term of the last sum. We have $u^* = \frac{\lambda_0 P_0 \varphi}{\mathcal{F}(P_0\varphi)}$, and

$$S(t)\widetilde{P}_0\varphi - u^* \int_0^t \mathcal{F}(S(s)\widetilde{P}_0\varphi)ds = e^{\lambda_0 t}\widetilde{P}_0\varphi - \frac{\lambda_0 P_0\varphi}{\mathcal{F}(P_0\varphi)}\int_0^t \mathcal{F}(e^{\lambda_0 s}\widetilde{P}_0\varphi)ds$$
$$= e^{\lambda_0 t}\widetilde{P}_0\varphi - \frac{\lambda_0 P_0\varphi}{\mathcal{F}(P_0\varphi)}\mathcal{F}(\widetilde{P}_0\varphi)(\frac{e^{\lambda_0 t}-1}{\lambda_0}) = \widetilde{P}_0\varphi.$$

On the other hand, we have by construction $\|S(t)\widetilde{P}_1\varphi\| \leq M e^{(\lambda_0-\delta)t}\|\widetilde{P}_1\varphi\|$, so

$$\|S(t)\widetilde{P}_1\varphi - u^* \int_0^t \mathcal{F}(S(s)\widetilde{P}_1\varphi)ds\|$$
$$\leq [M e^{(\lambda_0-\delta)t} + \|u^*\| \int_0^t M e^{(\lambda_0-\delta)s}ds]\|\widetilde{P}_1\varphi\|.$$

Finally we deduce that $\|D_x W_0(t)(u^*)\varphi\| \leq$

$$\frac{\|\widetilde{P}_0\varphi\|}{(1+\mathcal{F}(u^*)(\frac{e^{\lambda_0 t}-1}{\lambda_0}))} + \frac{[M e^{(\lambda_0-\delta)t} + \|u^*\| \int_0^t M e^{(\lambda_0-\delta)s}ds]\|\widetilde{P}_1\varphi\|}{(1+\mathcal{F}(u^*)(\frac{e^{\lambda_0 t}-1}{\lambda_0}))}.$$

The result directly follows from this last inequality.

Lemma 3.3. *Let $\widetilde{\lambda}_0 > 0$. There exists a constant $c_0 > 0$ such that*

$$\|\widetilde{P}_0\varphi\| \geq c_0\|\varphi\| \, \forall \varphi \in X_+.$$

Proof: From the definition of $\widetilde{P}_0$ it is clear that it is sufficient to prove the existence of a constant $c_0 > 0$, such that $\widetilde{\varphi}_0^*(\varphi) \geq c_0\|\varphi\|, \forall \varphi \in X_+$. By using equation (3.6) we know that for $c \geq \max(0, -\underline{\beta})$, $e^{\lambda_0 t}\widetilde{\varphi}_0^*(\varphi) = \widetilde{\varphi}_0^*(S(t)\varphi) \geq \widetilde{\varphi}_0^*(e^{-ct}T(t)\varphi) = \widetilde{\varphi}_0^*(e^{-ct}T(t)P_0\varphi) + \widetilde{\varphi}_0^*(e^{-ct}T(t)P_1\varphi)$, so that

$$\widetilde{\varphi}_0^*(\varphi) \geq e^{-(\lambda_0+c)t}\widetilde{\varphi}_0^*(\varphi_0)\|\varphi\| - \|\widetilde{\varphi}_0^*\|e^{-(\lambda_0+c)t}Me^{-\delta t}\|\varphi\|.$$

Thus, for $t > 0$ large enough we have $\widetilde{\varphi}_0^*(\varphi_0) > \|\widetilde{\varphi}_0^*\|Me^{-\delta t}$, and the result follows.

4. Mutation, Selection, and Recombination.

We now turn to the full problem (1.1) with $\alpha > 0$, $\beta \in L^\infty(0,1)$, $\beta \not\equiv 0$, $\gamma > 0$, and $\tau > 0$.

Theorem 4.1. *(Existence and Uniqueness) For each $\varphi \in X_+$ the problem (1.1) has a unique global weak solution in X_+.*

Proof: Consider the problem (1.1) with $\gamma = 0$:

$$\begin{cases} u_t = \alpha^2 u_{yy} + \beta u + \tau[H(u) - u], \ \text{a.e.} y \in (0,1), \\ u_y(0,t) = u_y(1,t) = 0, \\ u(y,0) = \varphi(y), \ \text{a.e.} y \in (0,1) \end{cases} \tag{4.7}$$

Since H is a Lipschitzian mapping, we know by using classical arguments that problem (4.7) has a unique global weak solution (see theorem 1.2 p:184 in Pazy

[11]). Further, the solution is positive for positive initial values, because the solution of (4.7) must satisfy

$$u(t) = e^{-\tau t} S(t)\varphi + \tau \int_0^t e^{-\tau(t-s)} S(t-s) H(u(s)) ds$$

and $H(X_+) \subset X_+$. Let $\{\widetilde{S}_\tau(t)\}_{t \geq 0}$ be the nonlinear semigroup associated with (4.7). Since H is positive homogeneous, the weak solution of (1.1) is given for every $\varphi \in X_+$ by

$$u(t) = \frac{\widetilde{S}(t)\varphi}{1 + \int_0^t \mathcal{F}(\widetilde{S}(s)\varphi) ds}, \; t \geq 0. \tag{4.8}$$

We now investigate the existence of a global attractor for (1.1). Here we use the definition of global attractor due to Hale [10] p:17, that is, a maximal compact invariant set which attracts each bounded set in X_+. We restrict ourselves to the metric space X_+, because we are only interested in the asymptotic behavior of nonnegative solutions.

Theorem 4.2. *(Boundedness) Denote by $u(t)$ the solution of the problem (1.1). There are two cases:*

i) if $\int_0^1 \varphi(y)dy \geq \frac{\overline{\beta}}{\gamma}$ (where $\overline{\beta} = \sup ess_{\sigma \in (0,1)} \beta(\sigma)$), then there exists $t_0 > 0$, such that $\int_0^1 u(t)(y)dy \leq \frac{\overline{\beta}}{\gamma}, \forall t \geq t_0$,

ii) if $\int_0^1 \varphi(y)dy \leq \frac{\overline{\beta}}{\gamma}$, then $\int_0^1 u(t)(y)dy \leq \frac{\overline{\beta}}{\gamma}, \forall t \geq 0$.

Proof: We start by considering the following approximate problem:

$$u'_\lambda(t) = A_\lambda u_\lambda(t) + \beta u_\lambda(t) + \tau(H(u_\lambda(t)) - u_\lambda(t)) - \mathcal{F}(u_\lambda(t)) u_\lambda(t)$$

where $A_\lambda = \lambda A(\lambda I - A)^{-1}$ is the Yosida approximation. Let $V(\varphi) = \int_0^1 \varphi(y)dy$, and we then have $V(u'_\lambda(t)) = V(\beta u_\lambda(t)) - V(u_\lambda(t))\mathcal{F}(u_\lambda(t))$, which implies

$$V(u_\lambda(t)) - V(u_\lambda(0)) = \int_0^t V(\beta u_\lambda(s)) - V(u_\lambda(s))\mathcal{F}(u_\lambda(s)) ds.$$

Let $\lambda \to \infty$, to obtain

$$V(u(t)) - V(u(0)) = \int_0^t V(\beta u(s)) - V(u(s))\mathcal{F}(u(s)) ds,$$

so that

$$V(u(t))' = V(\beta u(s)) - V(u(s))\mathcal{F}(u(s)),$$

and thus

$$V(u(t))' = V(\beta u(s)) - \gamma V(u(s))^2,$$

and

$$V(u(t))' \leq V(u(t))[\overline{\beta} - \gamma V(u(t))]. \tag{4.9}$$

Assume first that $V(u(0)) > \frac{\overline{\beta}}{\gamma}$, then clearly from inequality (4.9) there exists $t_0 > 0$, such that $V(u(t_0)) \leq \frac{\overline{\beta}}{\gamma}$. Assume that $V(u(0)) \leq \frac{\overline{\beta}}{\gamma}$, and assume that there exists $t_1 > 0$, such that $V(u(t_1)) \geq \frac{\overline{\beta}}{\gamma} + \epsilon$, for some $\epsilon > 0$. Then there exists $t_2 \in (0, t_1)$, such that $V(u(t_2)) \geq \frac{\overline{\beta}}{\gamma} + \frac{\epsilon}{2}$, and $V(u(t)) \geq \frac{\overline{\beta}}{\gamma} + \frac{\epsilon}{2}$, for all $t \in [t_2, t_1]$. By (4.9) $V(u(t))$ must be strictly decreasing on $[t_2, t_1]$, which gives us a contradiction. From the contradiction, we deduce that we must have $V(u(t)) < \frac{\overline{\beta}}{\gamma} + \epsilon$, for each $\epsilon > 0$.

Theorem 4.3. *(Compactness of the Nonlinear Semigroup) Denote by* $\{W_\tau(t)\}_{t\geq 0}$ *the nonlinear semigroup in* X_+ *associated with problem (1.1) given by formula (4.8). Then for* $t>0$, $W_\tau(t)$ *is compact, i.e., maps bounded sets into relatively compact sets.*

Proof: The result follows from (4.8) and the fact that $\widetilde{S}_\tau(t)$ is compact for $t>0$, because $\widetilde{S}_\tau(t)_{t\geq 0}$ arises from a Lipschitz perturbation of a compact linear semigroup (it is a direct consequence of lemma 1.6 p:42 in Wu [16]).

Lemma 4.4. *Let* $c_1 > c_0 > 0$ *such that* $c_0\|\varphi\| \leq \|\widetilde{P}_0\varphi\| \leq c_1\|\varphi\|, \forall\varphi\in X_+$. *Let* $\eta > 0$ *and* $\tau^* > 0$ *(small enough) such that* $C = \frac{\lambda_0}{2}c_0 + \tau^* c_0 - \tau^* c_1 - c_1\eta > 0$. *If* $u(t)$ *is a weak solution of equation (1.1) satisfying* $V(u(t)) \leq \eta, \forall t\in[0,T]$, *then we have for all* $0 \leq \tau \leq \tau^*$,

$$V(u(t)) \geq e^{\frac{\lambda_0}{2}t}\frac{c_0}{c_1}V(u(0)) + \int_0^t e^{\frac{\lambda_0}{2}(t-s)}\frac{C}{c_1}V(u(s))ds, \forall t\in[0,T].$$

Proof: The solution $u(t)$ of equation (1.1) can be expressed as

$$u(t) = e^{-\frac{\lambda_0}{2}t}S(t)\varphi + \int_0^t e^{-\frac{\lambda_0}{2}(t-s)}S(t-s)[\frac{\widetilde{\lambda}_0}{2}u(s) + \tau[H(u(s)) - u(s)] - \mathcal{F}(u(s))u(s)]ds,$$

so

$$V(\widetilde{P}_0(u(t))) = e^{\frac{\lambda_0}{2}t}V(\widetilde{P}_0(\varphi)) + \int_0^t e^{\frac{\lambda_0}{2}(t-s)}V(\widetilde{P}_0[\frac{\widetilde{\lambda}_0}{2}u(s) + \tau[H(u(s)) - u(s)] - \mathcal{F}(u(s))u(s)])ds.$$

Now using lemma 3.3, we know that there exists $0 < c_0 < c_1$ such that

$$c_0\|\varphi\| \leq \|\widetilde{P}_0\varphi\| \leq c_1\|\varphi\|, \forall\varphi\in X_+,$$

where c_1 is the norm of the operator $\widetilde{P}_0$. From the previous inequalities we have

$$c_1 e^{-\frac{\lambda_0}{2}t}V(u(t)) \geq c_0 V(u(0)) + \int_0^t e^{-\frac{\lambda_0}{2}s}[\frac{\widetilde{\lambda}_0}{2}c_0 + \tau c_0 - \tau c_1 - c_1 V(u(s))]V(u(s))ds$$

and the result follows.

Theorem 4.5. *Let* $0 < \eta_1 < \eta, \epsilon > 0$, *let*

$$D_{\eta_1,\frac{\overline{\beta}}{\gamma}+\epsilon} = \left\{\varphi\in X_+ : \eta_1 \leq \|\varphi\| \leq \frac{\overline{\beta}}{\gamma} + \epsilon\right\},$$

and let

$$B_\tau = \overline{\cup_{t\geq 0}W_\tau(t)(D_{\eta_1,\frac{\overline{\beta}}{\gamma}+\epsilon})}.$$

Then $\forall\tau\in[0,\tau^*]$, *i)* $W_\tau(t)B_\tau \subset B_\tau, \forall t\geq 0$; *ii)* $B_{X_+}(0,\frac{c_0}{c_1}\frac{\eta_1}{2}) \cap B_\tau = \emptyset$ *(where* $B_{X_+}(0,r) = \{\varphi\in X_+ : \|\varphi\| \leq r\}$*); iii)* $\forall\varphi\in X_+\setminus\{0\}, \exists t_0\geq 0$ *such that* $W_\tau(t_0)\varphi \in Int_{X_+}(B_\tau)$ *(where* $Int_{X_+}(B_\tau)$ *is the interior of* B_τ *relative to the metric space* X_+*); and iv)* $B_\tau \subset B_{X_+}(0,\frac{\overline{\beta}}{\gamma}+\epsilon)$.

Proof: We set $A_\tau = \cup_{t\geq 0}W_\tau(t)(D_{\eta_1,\frac{\overline{\beta}}{\gamma}+\epsilon})$. To prove *i)* it is sufficient to remark that by construction $W_\tau(t)A_\tau \subset A_\tau, \forall t\geq 0$, which implies by continuity of $\varphi\rightarrow W_\tau(t)\varphi$ that $W_\tau(t)B_\tau \subset B_\tau, \forall t\geq 0$. The proof of *ii)* is a direct consequence of lemma 4.4. Indeed, assume that $B_{X_+}(0,\frac{c_0}{c_1}\frac{\eta_1}{2}) \cap B_\tau \neq \emptyset$, which implies by the definition of B_τ that there exists $\varphi \in X_+$ such that$\|\varphi\| = \eta_1$, Thus, the solution $u(t)$ of equation (1.1) satisfies the property that there exists $t_0 > 0$ such that $\|u(t)\| \leq \eta_1, \forall t \in [0, t_0]$, and $\|u(t_0)\| = \frac{c_0}{c_1}\frac{\eta_1}{2}$. But this is impossible because from lemma 4.4, we know that

$$\|u(t)\| \geq e^{\frac{\lambda_0}{2}t}\frac{c_0}{c_1}V(u(0)) \geq \frac{c_0}{c_1}\eta_1 > \frac{c_0}{c_1}\frac{\eta_1}{2}, \forall t \in [0, t_0].$$

To prove *iii)* it is sufficient to remark that we know from lemma 4.4, and theorem 4.2 if $\varphi \in X_+ \setminus \{0\}$, and $\|\varphi\| \leq \eta_1$, or $\|\varphi\| > \frac{\overline{\beta}}{\gamma} + \epsilon$, then there exists $t_0 > 0$, such that $\eta_1 < \|u(t_0)\| < \frac{\overline{\beta}}{\gamma} + \epsilon$, which implies that $u(t_0) \in Int_{X_+}(B_\tau)$. Finally *iv)* is direct consequence of theorem 4.2.

We now use a result by Smith and Waltman [13] to analyze the asymptotic behavior of solutions of (1.1). One problem in applying this result is the fact that $X_+ \setminus \{0\}$ has empty interior. This case was also considered by Smith and Waltman (see [13], remark 2.1 p:449) and we will use their approach.

Let U be a subset of a Banach space X, and let Λ be a metric space with metric d. We use the notation $B_X(\phi, s)$ $(B_\Lambda(\lambda, s))$ for the open ball of radius s about the point $\phi \in X$ $(\lambda \in \Lambda)$. The following theorem is theorem 2.2 p:449 in Smith and Waltman [13] taking into account remark 2.1 p:449.

Theorem 4.6. *([13]) Let U be a subset of a Banach space X and let Λ be a metric space with metric d. Let $W : U \times [0, +\infty) \times \Lambda \to U$ be continuous and define a family of semi-dynamical systems $\{W_\tau(t)\}_{t\geq 0}$ (where $W_\tau(t)(\phi) = W(\phi, t, \tau)$) parameterized by Λ. Let $(\phi_0, \tau_0) \in U \times \Lambda$. Assume also that for each $t > 0$ there exists $\delta = \delta(t) > 0$, $\eta = \eta(t) > 0$, such that $W_\tau(t)(\phi)$ can be extended to $B_X(\phi_0, \delta) \times B_\Lambda(\tau_0, \eta)$, and $D_\phi W_\tau(t)(\phi)$ exists and is continuous on that set and $B_X(\phi_0, \delta) \cap U$ is convex. Suppose that $W_{\tau_0}(t)(\phi_0) = \phi_0$ for all $t \geq 0$, $U(t) \equiv D_\phi W_{\tau_0}(t)(\phi_0)$ defines a strongly continuous linear semigroup with negative growth bound, and $W_{\tau_0}(t)(\phi) \to \phi_0$, as $t \to \infty$ for each $\phi \in U$. In addition, suppose that: (H1) For each $\tau \in \Lambda$, there is a subset B_τ of U such that for each $\phi \in U, W_\tau(t)(\phi) \in B_\tau$ for all large t, and (H2) $C \equiv \overline{\cup_{\tau\in\Lambda} W_\tau(s)(B_\tau)}$ is compact in U for some $s > 0$. Then there exists $\varepsilon_0 > 0$ and a continuous mapping $\widehat{\phi} : B_\Lambda(\tau_0, \varepsilon_0) \to U$ such that $\widehat{\phi}(\tau_0) = \phi_0$, $W_\tau(t)\widehat{\phi}(\tau) = \widehat{\phi}(\tau)$ for $t \geq 0$, and $W_\tau(t)\phi \to \widehat{\phi}(\tau)$ as $t \to \infty$, $\phi \in U$, $\tau \in B_\Lambda(\tau_0, \varepsilon_0)$.*

We apply theorem 4.6 with $W(\phi, t, \tau) = W_\tau(t)(\phi)$, $\Lambda = [0, \infty)$, and $\tau_0 = 0$. The nonlinear strongly continuous semigroup $\left\{\widetilde{S}_\tau(t)\right\}_{t\geq 0}$ associated with equation (4.7) satisfies

$$\widetilde{S}_\tau(t)\varphi = S(t)\varphi + \int_0^t S(t-s)(\tau[H(\widetilde{S}_\tau(s)\varphi) - \widetilde{S}_\tau(s)\varphi])ds. \qquad (4.10)$$

From theorem 3.1 and lemma 3.2 we have that $\{W_0(t)\}_{t\geq 0}$ satisfies the assumptions of theorem 4.6. We note that if we set $U = X_+ \setminus \{0\}$, and

$$B_\tau = \overline{\cup_{t\geq 0} W_\tau(t)(D_{\eta_1, \frac{\overline{\beta}}{\gamma}+\epsilon})},$$

then from theorem 4.5, the assumption $(H1)$ of theorem 4.6 is also satisfied. From assertion *iv)* of theorem 4.5 we know that $\forall \tau \in [0, \tau^*]$, $B_\tau \subset B_{X_+}(0, \frac{\overline{\beta}}{\gamma} + \epsilon)$, so to verify assumption $(H2)$ of theorem 4.6 it is sufficient to apply the following lemma:

Lemma 4.7. *For every bounded set $B \subset X_+$ and for every $t \geq 0$,*

$$\overline{\cup_{\tau\in[0,\tau^*]} W_\tau(t)(B)}$$

is compact.

Proof: Since $\widetilde{S}_\tau(t)$ maps X_+ into itself, we deduce from (4.8) that for every $\varphi \in X_+$, $\frac{1}{1+\int_0^t \mathcal{F}(S_\tau(s)\varphi)ds} \leq 1$. Thus

$$\overline{\cup_{\tau\in[0,\tau^*]} W_\tau(t)(B)} \subset \overline{co}((\cup_{\tau\in[0,\tau^*]}\widetilde{S}_\tau(t)(B)) \cup \{0\}).$$

So it is sufficient to prove that $\overline{\cup_{\tau\in[0,\tau^*]}\widetilde{S}_\tau(t)(B)}$ is compact. In order to prove this we use (4.10). Assuming that $\|S(t)\| \leq Me^{\omega t}$, which always holds, and denoting $k = \|H\|_{Lip}$, we have

$$\|\widetilde{S}_\tau(t)\varphi\| \leq Me^{\omega t}\|\varphi\| + \int_0^t \tau M e^{\omega(t-s)}(k+1)\|\widetilde{S}_\tau(s)\varphi\|ds.$$

Thus,

$$e^{\omega t}\|\widetilde{S}_\tau(t)\varphi\| \leq M\|\varphi\| + \tau M(k+1)\int_0^t e^{-\omega s}\|\widetilde{S}_\tau(s)\varphi\|ds.$$

By applying Gronwall's lemma, we obtain

$$\|\widetilde{S}_\tau(t)\varphi\| \leq M\|\varphi\|e^{([\tau M(k+1)+\omega]t)}. \tag{4.11}$$

From this inequality we deduce that for each bounded set $B \subset X$, and each $t > 0$, $\cup_{\tau\in[0,\tau^*]} \cup_{s\in[0,t]} \widetilde{S}_\tau(t)(B)$ is bounded. We are now in position to apply lemma 1.6 p:42 in Wu [16], and since $\{S(t)\}_{t\geq 0}$ is a compact strongly continuous linear semigroup, we deduce that $\overline{\cup_{\tau\in[0,\tau^*]}\widetilde{S}_\tau(t)(B)}$ is compact, whereby the result follows.

Lemma 4.8. $W : U \times [0,\infty) \times \Lambda \to U$ *is continuous.*

Proof: We prove that W is continuous with respect to each variable φ, τ, and t. For the variable t this is immediate, since by construction $t \to W_\tau(t)(\varphi)$ is continuous. For the continuous dependence with respect to the initial value φ, in the case where the nonlinear part is only Lipschitz continuous on bounded sets, we refer to proposition 4.3.7 p:58 in Cazenave and Haraux [5]. To prove the continuity of $\tau \to W_\tau(t)(\varphi)$, we observe from (4.8) that it is sufficient to show that $\tau \to \widetilde{S}_\tau(t)(\varphi)$ and $\tau \to \int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds$ are continuous. To prove this we need to obtain some estimates. We have

$$\begin{aligned}\widetilde{S}_\tau(t)\varphi - \widetilde{S}_{\tau'}(t)\varphi = &\int_0^t S(t-s)(\tau[H(\widetilde{S}_\tau(s)\varphi) - \widetilde{S}_\tau(s)\varphi])ds \\ &- \int_0^t S(t-s)(\tau'[H(\widetilde{S}_{\tau'}(s)\varphi) - \widetilde{S}_{\tau'}(s)\varphi])ds,\end{aligned}$$

so assuming $\|S(t)\| \leq Me^{\omega t}$, and k is Lipschitz constant for H, we have

$$\begin{aligned}\|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_{\tau'}(t)\varphi\| \leq &\int_0^t Me^{\omega(t-s)}|\tau' - \tau|(k+1)\|\widetilde{S}_{\tau'}(s)\varphi\|ds \\ &+ \int_0^t Me^{\omega(t-s)}\tau(k+1)\|\widetilde{S}_\tau(s)\varphi - \widetilde{S}_{\tau'}(s)\varphi\|ds.\end{aligned}$$

But from equation (4.11), we know that

$$\|\widetilde{S}_{\tau'}(t)\varphi\| \leq M\|\varphi\|e^{([\tau' M(k+1)+\omega]t)},$$

and thus

$$\begin{aligned}e^{-\omega t}\|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_{\tau'}(t)\varphi\| \leq &M\|\varphi\||\tau' - \tau|(k+1)\int_0^t e^{(\tau' M(k+1)s)}ds \\ &+ M\tau(k+1)\int_0^t e^{-\omega s}\|\widetilde{S}_\tau(s)\varphi - \widetilde{S}_{\tau'}(s)\varphi\|ds.\end{aligned}$$

So by applying Gronwall's lemma, we obtain

$$\begin{aligned} \|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_{\tau'}(t)\varphi\| \leq M\|\varphi\||\tau' \\ - \tau|(k+1)\int_0^t e^{(\tau' M(k+1)s)} ds e^{([M\tau(k+1)+\omega]t)}, \end{aligned} \tag{4.12}$$

and the result follows.

Lemma 4.9. *For each $T > 0$ there exists $\delta = \delta(T) > 0$, $\eta = \eta(T) > 0$, such that for $t \in [0,T]$, $W_\tau^t \varphi$ can be extended to $B_X(u^*, \delta) \times [0, \eta]$, and $W_\tau^t \varphi$ is given for each $\varphi \in B_X(u^*, \delta)$ and $\tau \in [0, \eta]$ by formula (4.8).*

Proof: By using the same arguments as in the proof of lemma 4.7, we have

$$\|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_\tau(t)\varphi'\| \leq M\|\varphi - \varphi'\| e^{([\tau M(k+1)+\omega]t)}. \tag{4.13}$$

We know that

$$\widetilde{S}_\tau(t)u^* = e^{-\tau t} S(t)u^* + \int_0^t e^{-\tau(t-s)} S(t-s)(\tau H(\widetilde{S}_\tau(s)u^*))ds,$$

and since H maps X_+ into itself, we also have $\widetilde{S}_\tau(t)u^* \geq e^{-\tau t} S(t)u^* = e^{(\lambda_0 - \tau)t} u^*$. Thus,

$$\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds \geq \int_0^t e^{(\lambda_0-\tau)s} \mathcal{F}(u^*)ds - \int_0^t \|\widetilde{S}_\tau(t)u^* - \widetilde{S}_0(t)u^*\|ds.$$

But $\mathcal{F}(u^*) = \widetilde{\lambda}_0$, so by using equation (4.12), one has

$$\begin{aligned} \textstyle\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds \geq \widetilde{\lambda}_0 \int_0^t e^{(\lambda_0-\tau)s} ds \\ -M\|u^*\||\tau|(k+1)te^{([M\tau(k+1)+\omega]t)}. \end{aligned}$$

Thus,

$$\begin{aligned} \textstyle\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds \geq e^{-\tau^* t}(e^{\lambda_0 t} - 1) \\ -M\|u^*\||\tau|(k+1)\int_0^t s e^{([M\tau(k+1)+\omega]s)} ds. \end{aligned} \tag{4.14}$$

On the other hand, we have

$$\begin{aligned} |\textstyle\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds - \int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds| \leq \int_0^t \|\widetilde{S}_\tau(s)\varphi - \widetilde{S}_\tau(s)u^*\|ds \\ \leq \textstyle\int_0^t M\|\varphi - u^*\| e^{([\tau M(k+1)+\omega]s)} ds, \end{aligned} \tag{4.15}$$

and by using equation (4.14), we have

$$\begin{aligned} \textstyle\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds \geq -M\|u^*\||\tau|(k+1)\int_0^t s e^{([M\tau(k+1)+\omega]s)} ds \\ -M\|\varphi - u^*\| \textstyle\int_0^t e^{([\tau M(k+1)+\omega]s)} ds. \end{aligned}$$

We deduce that for each $\varepsilon_0 > 0$, there exists $\delta = \delta(\tau^*, T) > 0$ and $\eta = \eta(T) > 0$, such that for $\tau \in [0, \eta]$, and $\varphi \in B_X(u^*, \delta)$,

$$\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds \geq -1 + \varepsilon_0 > -1, \text{ for } t \in [0,T], \tag{4.16}$$

and the result follows.

Lemma 4.10. *For each $T > 0$, there exists $0 < \delta' < \delta = \delta(T)$, $0 < \eta' < \eta = \eta(T)$, (where $\delta(T)$ and $\eta(T)$ are defined in lemma 4.9) such that for each $t \in [0,T]$, $D_\varphi W_\tau(t)\varphi$ exists and is continuous on $B_X(u^*, \delta') \times [0, \eta']$.*

Proof: The main difficulty in proving this lemma is due to the fact that the mapping H is continuously differentiable only on $X \setminus \{0\}$. In order to avoid this difficulty we prove the following assertion:

Let $0 < \gamma < \|u^*\|$ and $T > 0$ be fixed. We will show that there exists $0 < \delta' < \delta = \delta(T)$, $0 < \eta' < \eta = \eta(T)$, such that for each $(\varphi, \tau) \in B_X(u^*, \delta') \times [0, \eta']$, $W_\tau(t)\varphi \in B_X(u^*, \gamma)$, for $t \in [0, T]$, and as $\gamma < \|u^*\|$, we will have $0 \notin B_X(u^*, \gamma)$.

Indeed, since $0 < \delta' < \delta = \delta(T)$, $0 < \eta' < \eta = \eta(T)$, we have for each $(\varphi, \tau) \in B_X(u^*, \delta') \times [0, \eta']$, and from (4.8)

$$\begin{aligned}\|W_\tau(t)\varphi - u^*\| &= \|W_\tau(t)\varphi - W_\tau(t)u^*\| \\ &= \|\frac{\widetilde{S}_\tau(t)\varphi}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds} - \frac{\widetilde{S}_\tau(t)u^*}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds}\| \\ &\le \|\widetilde{S}_\tau(t)\varphi\| |\frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds} - \frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds}| \\ &\quad + |\frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds}| \|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_\tau(t)u^*\|.\end{aligned}$$

Denote

$$(I) = \|\widetilde{S}_\tau(t)\varphi\| |\frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds} - \frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds}|$$

and we have by using equations (4.11) and (4.16)

$$(I) \le M\|\varphi\| e^{([\tau M(k+1)+\omega]t)} \frac{1}{4} |(1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds) - (1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)\varphi)ds)|.$$

Thus, by using (4.15) we have

$$\begin{aligned}(I) &\le M\|\varphi\| e^{([\tau M(k+1)+\omega]t)} \tfrac{1}{4} \int_0^t \|\varphi - u^*\| M e^{([\tau M(k+1)+\omega]s)} ds \\ &\le \|\varphi - u^*\| M^2(\|u^*\|+\gamma) e^{([\eta' M(k+1)+\omega]2T)} \tfrac{1}{4} T.\end{aligned}$$

On the other hand, denoting

$$(II) = |\frac{1}{1+\int_0^t \mathcal{F}(\widetilde{S}_\tau(s)u^*)ds}| \|\widetilde{S}_\tau(t)\varphi - \widetilde{S}_\tau(t)u^*\|$$

we have by using (4.13) and (4.16) $(II) \le \frac{1}{2}M\|\varphi - u^*\| e^{([\tau M(k+1)+\omega]t)}$, so $(II) \le \frac{1}{2}M\|\varphi - u^*\| e^{([\eta' M(k+1)+\omega]T)}$. Finally, we obtain

$$\begin{aligned}\|W_\tau(t)\varphi - u^*\| \le \|\varphi - u^*\| (&M^2(\|u^*\|+\gamma) e^{([\eta' M(k+1)+\omega]2T)} \tfrac{1}{4} T \\ &+ \tfrac{1}{2} M e^{([\eta' M(k+1)+\omega]T)})\end{aligned} \tag{4.17}$$

and the proof is complete. Using the same arguments, one can also prove that for each $\varphi, \varphi' \in B_X(u^*, \delta')$, $\tau \in [0, \eta']$, $t \in [0, T]$

$$\begin{aligned}\|W_\tau(t)\varphi - W_\tau(t)\varphi'\| \le \|\varphi - \varphi'\| (&M^2(\|u^*\|+\gamma) e^{([\eta' M(k+1)+\omega]2T)} \tfrac{1}{4} T \\ &+ \tfrac{1}{2} M e^{([\eta' M(k+1)+\omega]T)}).\end{aligned} \tag{4.18}$$

Let us now study the differentiability of $\varphi \to W_\tau(t)\varphi$ in $B_X(u^*, \delta')$, for each $t \in [0, T]$, and $\tau \in [0, \eta']$. Recall that the weak solution of equation (1.1) is also given by the following variation constant formula: for each $\varphi \in B_X(u^*, \delta')$, $\tau \in [0, \eta']$, $t \in [0, T]$,

$$\begin{aligned}W_\tau(t)\varphi &= S(t)\varphi \\ &+ \int_0^t S(t-s)[\tau[H(W_\tau(s)\varphi) - W_\tau(s)\varphi] - \mathcal{F}(W_\tau(s)\varphi)W_\tau(s)\varphi]ds.\end{aligned} \tag{4.19}$$

By formally differentiating equation (4.19), one obtains the following variation of constants formula for each $\varphi \in B_X(u^*, \delta')$, $\tau \in [0, \eta']$:

$$\begin{cases} U_{\tau,\varphi}(t) = S(t) + \\ \int_0^t S(t-s)[\tau(D_\varphi H(W_\tau(s)\varphi) - I) - D_\varphi G(W_\tau(s)\varphi)]U_{\tau,\varphi}(s)ds, \end{cases} \tag{4.20}$$

where $U_{\tau,\phi} \in C([0,T], \mathcal{L}(X))$ and $G(\varphi) = \mathcal{F}(\varphi)\varphi$, for each $\varphi \in X$. From the first part of the proof we also know that $D_\varphi H(W_\tau(s)\varphi)$ exists, since $W_\tau(s)\varphi \neq 0, \forall s \in [0,T]$. Finally to apply theorem 4.6, it remains to remark that $B_X(u^*, \delta) \cap U$ is convex for any $\delta > 0$. We can summarized the results obtained so far in the following theorem:

Theorem 4.11. *For each $\varphi \in X_+$ and each $\tau \geq 0$, problem (1.1) has a unique global weak solution. Denote by $\{W_\tau(t)\}_{t\geq 0}$ the nonlinear semigroup in X_+ associated with this problem. Let $\tilde{\lambda}_0 > 0$. Then, there exists $\eta_0 > 0$ and a continuous mapping $\widehat{\phi} : [0, \eta_0] \to X_+ \setminus \{0\}$ such that $\widehat{\phi}(0) = u^*$, $W_\tau(t)\widehat{\phi}(\tau) = \widehat{\phi}(\tau)$ for $\tau \in [0, \eta_0], t \geq 0$, and for each $\varphi \in X_+ \setminus \{0\}$, $\tau \in [0, \eta_0]$, $W_\tau(t)\varphi \to \widehat{\phi}(\tau)$, as $t \to \infty$.*

REFERENCES

[1] H. Brezis, "Analyse Fonctionnelle", Masson, 1983.

[2] K.J. Brown and C.C. Lin, *On the existence of positive eigenfunctions for an eigenvalue with an indefinite weight function*, J. Math. Anal. Appl. 75 (1980), 112-120.

[3] R.S. Cantrell and C. Cosner, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol. 29 (1991), 315-338 .

[4] R.S. Cantrell, C. Cosner, and R. Hutson, *Ecological models, permanance, and spatial heterogeneity*, Rocky Mtn. J. Math. (1) 26 (1996), 1-36.

[5] T. Cazenave and A. Haraux, *Introduction aux problèmes d'évolution semi-linéaires*, SMAI (1990).

[6] Ph. Clement, H.J.A.M. Heijmans, S. Angement, C.J. van Duijn, and B. de Pagter, "One Parameter Semigroups", North-Holland, 1987.

[7] K. Deimling, "Nonlinear Functional Analysis", Springer-Verlag, New York, 1985.

[8] B. Fristedt and L. Gray, "A Modern Approach to Probability Theory", Birkhäuser, Boston, 1996.

[9] J.K. Hale, "Theory of Functional Differential Equations", Springer-Verlag, New York, 1977.

[10] J.K. Hale, "Asymptotic Behavior of Dissipative Systems", Amer. Math. Soc., Providence, Rhode Island, 1988.

[11] A. Pazy, "Semigroups of Linear Operators and Applications to Partial Differential Equations", Springer-Verlag, New York, 1983.

[12] M.C. Ponce, K.Y. Tham, and M.J. Blaser, *Helicobacter pylori Lewis antigen expression in experimentally infected gerbils and mice*, to appear.

[13] H.L. Smith and P. Waltman, *Perturbation of globally stable steady state*, Proc. Amer. Math. Soc. (2) 127 (1999), 447-453.

[14] G.F. Webb, *Logistic models of structured population growth*, Comp. Math. Appl. (4/5) 12A (1986), 527-539.

[15] H.P. Wirth, M. Yang, R. M. Peek, J. Höök-Nikanne, M. Fried, and M.J. Blaser, *Phenotypic diversity in Lewis expression of Helicobacter pylori isolates from the same host*, J. Lab. Clin. Med. (133) 5 (1999), 488-500.

[16] J. Wu, "Theory and Applications of Partial Functional Differential Equations", Springer-Verlag, New York, 1996.

[17] M. Zerner, *What can the theory of the positivity do for you*, in "Mathematical Population Dynamics" (ed. O. Arino *et al.*), Marcel Dekker, New York (1991).

Received for publication Oct. 1999.

E-mail address: magal.pierre@@wanadoo.fr, webbgf00@@ctrvax.vanderbilt.edu