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EQUIVALENT DYNAMICS FOR A STRUCTURED POPULATION MODEL AND A RELATED FUNCTIONAL DIFFERENTIAL EQUATION

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In [**4**], the author established a relationship between the semiflows and global attractors for a simple structured population model of juvenile versus adult competition and a related functional differential equation (FDE) constructed from an analysis of the model. Building on this earlier work, we show in this paper that, under an additional assumption, the semiflows of the two systems, restricted to their respective global attractors, extend to flows which are topologically equivalent. In other words, the long-term dynamics generated by the hyperbolic system of equations representing the structured population model is faithfully represented by the long-term dynamics of the FDE. In particular, the wealth of theory available for the study of FDEs can be brought to bear on the problem of determining the long-term dynamics for the model. It should be emphasized that, at present, there does not exist a correspondingly well-developed theory for the analysis of structured population models.

Let us emphasize that the main point of this paper is to establish rigorously that in order to study the asymptotic behavior of the model system, it suffices to do the same for the simpler scalar FDE.

Future work will focus on describing the range of possible dynamical behavior for the FDE. In [**3, 5**] it was shown that periodic solutions can occur through Hopf bifurcation from the positive equilibrium.

The system of equations (1) below model the interaction of juveniles and adults of a single species. Adults are viewed as identical in every relevant aspect and their number is denoted by w. Juveniles vary in their level of maturity x between a newborn level $x = 0$ and a pre-adult level $x = 1$. Pre-adult juveniles mature to adults. Juveniles acquire maturity at a rate $dx/dt = P(w)$, that is, as a function of

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the (current) adult population size. Adults die at rate v and juveniles at the maturity-level dependent rate $\beta(x)$. The rate of birth of new juveniles is given by $b(w)$. The appropriate equations are given by (see [**3, 4**]):

$$
\begin{aligned}
\frac{\partial z}{\partial t} + P(w(t))\frac{\partial z}{\partial x} &= -\beta(x)z, \qquad 0 < x < 1,\ t > 0 \\
w'(t) &= -vw(t) + P(w(t))z(1,t), \qquad t > 0 \\
P(w(t))z(0,t) &= b(w(t)), \qquad t > 0 \\
z(x,0) &= z_0(x), \qquad 0 < x < 1 \\
w(0) &= w_0,
\end{aligned} \tag{1}
$$

where $w_0 \geq 0$ and $z_0 \in L^1_+$, the cone of nonnegative functions in the space of (equivalence classes) of Lebesgue integrable functions on $(0,1)$, $P : [0,\infty) \to (0,\infty)$, $b : [0,\infty) \to [0,\infty)$ are locally Lipschitz continuous, $b^{-1}(0) = \{0\}$ and $\beta : [0,1] \to (0,\infty)$ is continuous. Further, we assume:

(H1) $\lim_{u\to\infty} P(u) = \rho$ exists. If $\rho = 0$, then P is decreasing for large u. If $\rho > 0$ then $u/P(u)$ is increasing for large u.

(H2) The inequality

$$\gamma e^{-\beta_0 \rho^{-1}} < v \tag{2}$$

holds where

$$\gamma = \limsup_{u\to\infty} b(u)/u$$

and $\beta_0 = \int_0^1 \beta(x)\,dx$.

The reasons for assuming (H1) and (H2) will be clear later. For now, we point out that (2) holds if either γ or ρ are sufficiently small.

An interesting example of (1) with

$$
\begin{aligned}
P(w) &= T_0^{-1} e^{-cw} \\
b(w) &= \gamma w \\
\beta(x) &\equiv \beta_0
\end{aligned}
$$

is treated in [**3**]. In this example, the rate at which juveniles mature decreases as the adult population size increases. Therefore, juveniles spend a longer time in the juvenile class, subject to the juvenile mortality rate (possibly high relative to adult mortality). This is a potential control on the population size. Note that (H1) and (H2) hold for this example, the latter since $\rho = 0$.

The change of variables

$$\begin{aligned} s &= \int_0^t P(w(r))\,dr \\ Z(x,s) &= z(x,t), \qquad W(s) = w(t) \end{aligned} \tag{3}$$

transforms (1) to an "aged-structured" form which is more easily integrated. This system is

$$\begin{aligned} \frac{\partial Z}{\partial s} + \frac{\partial Z}{\partial x} &= -\beta(x)P(W(s))^{-1}Z, \qquad 0 < x < 1,\ s > 0 \\ \frac{dW}{ds} &= -vW(s)P(W(s))^{-1} + Z(1,s), \qquad s > 0 \\ P(W(s))Z(0,s) &= b(W(s)), \qquad s > 0 \\ Z(x,0) &= z_0(x), \qquad 0 < x < 1 \\ W(0) &= w_0. \end{aligned} \tag{4}$$

The first equation can be easily integrated to give Z in terms of W as follows:

$$Z(x,s) = \begin{cases} z_0(x-s)\exp[-\int_0^s \beta(x-s+r)P(W(r))^{-1}\,dr], & s \le x \\ \frac{b(W(s-x))}{P(W(s-x))} \\ \qquad \cdot \exp[-\int_{-x}^0 \beta(x+r)P(W(s+r))^{-1}\,dr], & s > x. \end{cases} \tag{5}$$

Putting $x = 1$ into (5) gives $Z(1,s)$ in terms of W which can then be inserted in the second of equations (4) to give the two equations

$$\begin{aligned} \frac{dW}{ds} &= -v\frac{W(s)}{P(W(s))} \\ &\quad + z_0(1-s)\exp\left[-\int_0^s \beta(1-s+r)P(W(r))^{-1}\,dr\right] \end{aligned} \tag{6}$$

$0 < s < 1$, $W(0) = w_0$, and

$$\frac{dW}{ds} = -v\frac{W(s)}{P(W(s))} + \frac{b(W(s-1))}{P(W(s-1))}e^{-\tau(W_s)}, \qquad s > 1, \tag{7}$$

where $\tau : C_+ \to \mathbf{R}$ is given by

$$\tau(\phi) = \int_{-1}^{0} \beta(1+r)P(\phi(r))^{-1}\,dr,$$

and where the initial data, W_1, for the FDE (7) is provided by the solution of (6). C denotes the Banach space of continuous functions on $[-1, 0]$ with the uniform norm and C_+ is the cone of nonnegative functions. The standard notation W_s is used for the element of C_+ given by $W_s(\theta) = W(s+\theta)$, $-1 \le \theta \le 0$.

The following result, established in [**3**], basically says that, for each $(z_0, w_0) \in L^1_+ \times \mathbf{R}_+$, (6) can be uniquely solved for $W(s)$, $0 \le s \le 1$, and the corresponding $(z_0, w_0) \to W$ has nice properties.

Proposition 1. *There is a completely continuous map*

$$H : L^1_+ \times \mathbf{R}_+ \to C_+,$$

Lipschitz continuous on bounded subsets, such that if $W_1 = H(z_0, w_0)$, *then* $W(s) = W_1(1-s)$, $0 \le s \le 1$, *is the unique solution of* (6).

The FDE (7) generates a semiflow $\{T(s)\}_{s\ge 0}$ on C_+ where $W_s = T(s)W_0$ is the state of the system at time s which at time 0 is $W_0 \in C_+$. Note that, following the usual custom for autonomous FDEs, we have taken $s = 0$ to be the "start time" although in (7) the start time $s = 1$ is appropriate for the functions W coming from (4). This causes some awkwardness in formulas to follow, but hopefully will cause no confusion.

By virtue of (H1) and (H2) (see [**4**, Corollary 1.3]), the semiflow T has a global attractor A, that is, A is a compact, connected, invariant subset of C_+ which attracts bounded subsets of C_+.

Once W is known by solving (6) and (7), then Z is determined by (5). An elegant way of putting this simple observation was pointed out in [**4**]. Define

$$G : C_+ \to L^1_+ \times \mathbf{R}_+$$

by $G(\phi) = (\psi, \phi(0))$ where

$$\psi(x) = b(\phi(-x))P(\phi(-x))^{-1}\exp\left[-\int_{-x}^{0}\beta(x+r)P(\phi(r))^{-1}\,dr\right], \quad 0 \le x \le 1.$$

It is not difficult to see that G is Lipschitz continuous on bounded sets and that the following interesting relation holds on C^+ (see [**4**, Proposition 1.4]):

$$T(1) = H \circ G. \tag{8}$$

In other words, given initial data $\phi \in C_+$ for (7) and computing $W_1 = T(1)\phi$ gives the same result as solving (6) with the initial conditions $(z_0, w_0) = G(\phi)$.

Using the formula (5), it can be seen [**4**, Theorem 1.5] that (4) generates a dynamical system on $L^1_+ \times \mathbf{R}_+$. That is, there is a semiflow $\{U(s)\}_{s\geq 0}$, on $L^1_+ \times \mathbf{R}_+$ such that $U(s)(z_0, w_0) = (Z(\cdot, s), W(s))$ where Z and W satisfy (4) in an appropriate sense (see reference above). Moreover, (5) implies that

$$U(s) = G \circ T(s-1) \circ H, \qquad s \geq 1 \tag{9}$$

and this relation, in turn, implies that U has the global attractor $\mathcal{A}$ where (see [**4**, Theorem 1.6])

$$\mathcal{A} = G(A). \tag{10}$$

Note that (9) implies $U(1) = G \circ H$. The relation (9) can be represented by a commutative diagram

$$\begin{array}{ccc} L^1_+ \times \mathbf{R}^+ & \xrightarrow{U(s)} & L^1_+ \times \mathbf{R}^+ \\ {\scriptstyle H}\big\downarrow & & \big\uparrow{\scriptstyle G} \\ C_+ & \xrightarrow[T(s-1)]{} & C_+ \end{array}$$

which holds for $s > 1$.

It is well known [**1**] that there is a correspondence between elements of the global attractor A for (7) and initial data corresponding to bounded global solutions $W : \mathbf{R} \to \mathbf{R}^+$ for (7). It turns out (see [**4**, p. 23]) that the same correspondence holds for (4) and elements of $\mathcal{A}$ and, furthermore, $Z : [0,1] \times \mathbf{R} \to \mathbf{R}^+$ is C^1 and satisfies (4) in the classical sense.

In addition to the hypotheses (H1) and (H2) which were assumed in [**4**], we now assume the additional hypothesis:

(H3) $T(s)|_A : A \to A$ is one-to-one for each $s > 0$.

We note that if P and b are analytic, then (H3) holds by [**2**, Theorem 4.1.2]. In particular, (H3) holds for the example described above equation (2). See [**6**] for a discussion of the property (H3). When (H3) holds, the restriction of $T(s)$ to A extends to a group of mappings, where $T(-s) \equiv T(s)^{-1}$, $s > 0$. To emphasize that we restrict T (and other mappings as well) we write $T_A(t) = T(t)|_A$.

Restricting (8) to A, we see that (H3) and the fact that the attractor, $\mathcal{A}$, for (4), is given by (10) implies that both $H_{\mathcal{A}}$ and G_A are Lipschitz homeomorphisms. In fact, by (8), G_A must be one-to-one and $G_A : A \to \mathcal{A}$ is onto by (10). As $T(1)A = A$, it follows that $H_{\mathcal{A}} : \mathcal{A} \to A$ is one-to-one and onto.

Theorem 1. *If* (H3) *holds, then* $\mathcal{A}$ *and* A *are* (*Lipschitz*) *homeomorphic and the following commutative diagram is valid for all* $s \in \mathbf{R}$:

$$\begin{array}{ccc} \mathcal{A} & \xrightarrow{U_{\mathcal{A}}(s)} & \mathcal{A} \\ {\scriptstyle G_A^{-1}} \big\downarrow & & \big\uparrow {\scriptstyle G_A} \\ A & \xrightarrow[T_A(s)]{} & A \end{array}$$

In particular, the flow generated by (4) *on the attractor* $\mathcal{A}$ *is topologically conjugate to the flow generated by* (7) *on the attractor* A.

Proof. First consider $s > 1$ and observe that, by (9),

$$\begin{aligned} U_{\mathcal{A}}(s) &= G_A \circ T_A(s-1) \circ H_{\mathcal{A}} \\ &= G_A \circ T_A(s) \circ T_A(-1) \circ H_{\mathcal{A}} \\ &= G_A \circ T_A(s) \circ (T_A(1)^{-1} \circ H_{\mathcal{A}}) \\ &= G_A \circ T_A(s) \circ G_A^{-1}, \end{aligned}$$

where the last step follows from restricting (8) to A. Therefore, the assertion holds for $s > 1$.

In order to see that it holds for all $s \in \mathbf{R}$, fix $s > 0$, $x \in \mathcal{A}$, let $s_0 > 1$

and let $y \in \mathcal{A}$ be such that $U_{\mathcal{A}}(s_0)y = x$. Then

$$\begin{aligned} U_{\mathcal{A}}(s)x = U_{\mathcal{A}}(s+s_0)y &= G_A \circ T(s+s_0) \circ G_A^{-1} y \\ &= G_A \circ T(s) \circ G_A^{-1} \circ G_A \circ T(s_0) \circ G_A^{-1} y \\ &= G_A \circ T(s) \circ G_A^{-1} \circ U_{\mathcal{A}}(s_0) y \\ &= G_A \circ T(s) \circ G_A^{-1} x. \end{aligned}$$

As $x \in \mathcal{A}$ was arbitrary, we see that $U_{\mathcal{A}}(s) = G_A \circ T(s) \circ G_A^{-1}$ holds for all $s \geq 0$. It follows that $U_{\mathcal{A}}(s)$ is one-to-one for $s > 0$ and that the formula holds for all s by inverting both sides of the relation. □

We can say that the asymptotic behavior of (4) and (7) are identical if (H3) holds. But what of the behavior of (1)? In [**4**, Theorem 1.8] it is shown that (1) generates a semiflow $\{S(t)\}_{t\geq 0}$ on $L^1_+ \times \mathbf{R}_+$ which has the same global attractor $\mathcal{A}$ as $\{U(s)\}_{s\geq 0}$. Moreover, if $\pi_2 : L^1_+ \times \mathbf{R}_+ \to \mathbf{R}_+$ is the projection onto the second factor, then

$$S(t)(z_0, w_0) = U(s)(z_0, w_0)$$

where s and t are related by

$$t = \int_0^s P(\pi_2(U(r)(z_0, w_0)))^{-1}\, dr. \tag{11}$$

We denote this relationship by $s = \tau(t, z_0, w_0)$. It simply reflects the change of variable which is inverse to (3). In our final result, we restrict S to the attractor $\mathcal{A}$, showing that the dynamics of (1) and (4) are topologically equivalent on the global attractor. For simplicity of notation we write 'a' for a generic point of $\mathcal{A}$.

Theorem 2. *Let* (H3) *hold. Then there exists a continuous function* $\tau : \mathbf{R} \times \mathcal{A} \to \mathbf{R}$ *satisfying*:

(i) $\tau(0, a) = 0$, $a \in \mathcal{A}$.

(ii) *There exists* $k_1, k_2 > 0$ *such that*

$$k_1 \leq \frac{\partial \tau}{\partial t}(t, a) \leq k_2, \qquad (t, a) \in \mathbf{R} \times \mathcal{A}.$$

(iii) $S_{\mathcal{A}}(t)a = U_{\mathcal{A}}(\tau(t,a))a$, $(t,a) \in \mathbf{R} \times \mathcal{A}$.

In particular, the flows $\{S_{\mathcal{A}}(t)\}_{t\in\mathbf{R}}$ *and* $\{U_{\mathcal{A}}(t)\}_{t\in\mathbf{R}}$ *are topologically equivalent.*

Proof. The continuity of τ follows immediately from (11). Assertion (ii) follows since $\{\pi_2(U_{\mathcal{A}}(r)a) : r \geq 0\}$ is bounded independent of $a \in \mathcal{A}$ and by the properties of P. Assertion (iii), for $t > 0$, is just (11).

In order to see that $S_{\mathcal{A}}(t)$ is one-to-one, suppose that $a, b \in \mathcal{A}$, $a \neq b$, and $S_{\mathcal{A}}(t_0)a = S_{\mathcal{A}}(t_0)b$ for some $t_0 > 0$. We may assume that $S_{\mathcal{A}}(t)a \neq S_{\mathcal{A}}(t)b$ for $0 \leq t < t_0$. It follows that $U_{\mathcal{A}}(s_a)a = U_{\mathcal{A}}(s_b)b$ where $s_a = \tau(t_0, a)$, $s_b = \tau(t_0, b)$ and, since $U_{\mathcal{A}}(s)$ is one-to-one, we can assume that $s_a > s_b$ and $U_{\mathcal{A}}(s_a - s_b)a = b$. Therefore, b belongs to the $U_{\mathcal{A}}$-orbit through a. Since the $U_{\mathcal{A}}$-orbit through a and the $S_{\mathcal{A}}$-orbit through a are identical, there exists a $t_1 > 0$ such that $S_{\mathcal{A}}(t_1)a = b$. Furthermore, t_1 can be taken as $t_1 = \tau(\cdot, a)^{-1}(s_a - s_b)$.

Now $S_{\mathcal{A}}(t_0)a = S_{\mathcal{A}}(t_0)b = S_{\mathcal{A}}(t_0 + t_1)a$ implies that $S_{\mathcal{A}}(t + t_1)a = S_{\mathcal{A}}(t)a$ for all $t \geq t_0$. Consequently, $U_{\mathcal{A}}(\tau(t + t_1, a))a = U_{\mathcal{A}}(\tau(t,a))a$ holds for $t \geq t_0$, which implies that, since $U_{\mathcal{A}}$ is one-to-one, $U_{\mathcal{A}}(t + \omega)a = U_{\mathcal{A}}(t)a$ for all $t \in \mathbf{R}$ where, e.g., $\omega = \tau(t_0 + t_1, a) - \tau(t_0, a) > 0$.

Given $0 < h < t_0$, let $a_h = S(t_0 - h)a$, $b_h = S(t_0 - h)b$ and observe that $a_h \neq b_h$ and $S(h)a_h = S(h)b_h$. The arguments above imply that $U_{\mathcal{A}}(t + \omega_h)a_h = U_a(t)a_h$ hold for all $t \in \mathbf{R}$ where $\omega_h = \tau(h + t_h, a_h) - \tau(h, a_h)$ and $t_h = \tau(\cdot, a_h)^{-1}(|\tau(h, a_h) - \tau(h, b_h)|)$. As $h \to 0+$, $a_h \to S(t_0)a$, $b_h \to S(t_0)a$ so by continuity, $t_h \to 0$ and $\omega_h \to 0$. But a_h belongs to the $U_{\mathcal{A}}$-orbit through a and so $U_{\mathcal{A}}(t + \omega_h)a = U_{\mathcal{A}}(t)a$ holds for all $t \in \mathbf{R}$ and all small h. Therefore, $U_{\mathcal{A}}(t)a$ is periodic in t with arbitrarily small periods. This implies that a is an equilibrium. Since $b = U_{\mathcal{A}}(s_a - s_b)a$, it follows that $a = b$. This contradiction proves that $S_{\mathcal{A}}(t)$ is one-to-one for each $t > 0$. □

Finally, note that $S_{\mathcal{A}}(-t)a = b$, $t > 0$, implies that $a = U_{\mathcal{A}}(\tau(t,b))b$ and $b = U_{\mathcal{A}}(-\tau(t,b))a$ so $\tau(-t,a) = -\tau(t, S_{\mathcal{A}}(-t)a)$.

The topological equivalence is the identity map on $\mathcal{A}$.

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