On a hypercycle equation with infinitely many members

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Abstract

A hypercycle equation with infinitely many types of macromolecules is formulated and studied both analytically and numerically. The resulting model is given by an integro-differential equation of the mixed type. Sufficient conditions for the existence, uniqueness, and non-negativity of solutions are formulated and proved. Analytical evidence is provided for the existence of non-uniform (with respect to the second variable) steady states. Finally, numerical simulations strongly indicate the existence of a stable nonlinear wave in the form of the wave train.

Keywords: Hypercycle, mixed functional differential equations, integro-differential equations.

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1 Introduction

An important class of replicator models involves systems of nonlinear ordinary differential equations with dynamics restrained by the standard simplex in the state space and describes macromolecular interactions in various problems of population genetics and evolutionary game theory \cite{21, 13, 14}, as well as in theories of the origin of life \cite{22, 11}.

Of special interest is the hypercycle model that was proposed by M. Eigen and P. Schuster \cite{11}. It was related to the prebiotic evolution hypothesis stating that self-replicating molecules are predecessors of RNA, DNA and eventually of cells. The hypercycle model has been thoroughly studied from the points of view of both population genetics \cite{13} and mathematical frameworks for systems of nonlinear ordinary differential equations \cite{21, 16}.

A classical hypercycle is a finite closed network of self-replicating macromolecules (species) which are connected so that each of them catalyzes the replication of the successor, with the last molecule...
reinforcing the first one; see Fig. 1. From the sociological perspective, the catalytic support for the replication of other molecules resembles altruistic behavior, in contrast to conventional autocatalysis [15, 13].

Let us briefly recall the mathematical formulation of the classical hypercycle model together with its key properties.

Consider a hypercycle with $n$ macromolecules (species) labeled by $i = 1, 2, \ldots, n$ (see Fig. 1), and denote the corresponding relative (normalized) time-varying frequencies by $u_i(t)$. One has

\[ u_i(t) \geq 0, \quad i = 1, 2, \ldots, n, \]

\[ \sum_{i=1}^{n} u_i(t) = 1, \quad t \geq 0, \quad u_i(0) = u_i^0, \quad i = 1, 2, \ldots, n. \]

Here $k_i u_{i-1}(t)$ is the fitness of the $i$-th species, and $f(t)$ is the mean fitness of the entire system (the representation for $f(t)$ can be obtained by adding up all of the $n$ dynamical equations and using the relation (2)). Note also that the standard simplex is invariant with respect to this dynamical system.

The following properties hold:

- the hypercyclic system is permanent [13 §13], i.e., there exists $\delta > 0$ (independent from the
initial coordinates \( u_1^0, u_2^0, \ldots, u_n^0 \) such that \( u_i^0 > 0, \ i = 1, 2, \ldots, n \), imply
\[
\liminf_{t \to \infty} u_i(t) > \delta, \ i = 1, 2, \ldots, n;
\]

- for \( n = 2, 3, 4 \), the hypercycle admits a globally stable steady state with positive components \[13\ \S12\], while there appears a stable limit cycle if \( n \geq 5 \) \[16\];
- when \( m \) disjoint hypercycles compete with each other in the same environment, a unique hypercycle is finally established with the other \( m - 1 \) going to extinction for almost all initial conditions \[12\];
- evolutionary adaptation can help hypercycles be resistant to parasites but also allows for a phase transition phenomenon similar to the error threshold in the quasispecies models (which divides the selective phase of evolution with a clear dominance from the random phase with a markedly more uniform distribution), as was numerically investigated in \[2\].

Moreover, the paper \[4\] studied an extension of the hypercycle model with each species distributed on a line segment and influenced by a homogeneous diffusion, which led to a system of \( n \) partial differential equations instead of the ordinary differential equations \[3\]. This modeling approach was further developed in \[5, 3, 6\].

However, the actual number of macromolecules in a hypercycle may be huge, and this may significantly complicate the numerical analysis of the associated dynamical system \[3\]. It may therefore be reasonable to represent the macromolecules as points in some line segment (of cardinality continuum) and to construct an appropriate distributed model of hypercyclic replication. Such a methodology was previously implemented for Crow–Kimura and Eigen quasispecies models, with a single integro-differential equation replacing a large number of ordinary differential equations \[10, 8, 7\]. A crucial step in the construction of a hypercycle model with a continuum of species is to incorporate the catalyzing effects (along a continuous loop in contrast to the finite closed chain in Fig. 1). Possible diffusive behavior is also worth taking into account. Besides, the cyclic structure has to be ensured by stating appropriate boundary conditions at the endpoints of the line segment describing the species. For these purposes, the current work formulates a new distributed hypercycle model based on a second-order partial integro-differential equation with spatial delay and mixed boundary conditions. It should be emphasized that the general theory of mixed functional differential equations including in particular partial or integro-differential equations with spatial delays is still at an early stage of development. An introduction to this promising area of mathematical research can be found in \[20\], and some related applications are presented in \[18, 1, 9\].

This paper is organized as follows. The problem is stated in Section 2. The existence, uniqueness, and nonnegativity of the solution are discussed in Section 3, with the proofs moved to Appendix. Section 4 provides steady-state analysis. Section 5 presents numerical simulation results for the dynamic model. Finally, concluding remarks are given in Section 6.

## 2 Problem statement

Let macromolecules (species) in a hypercycle be represented as points of the interval \( 0 \leq x < 2\pi \), and denote the relative frequency of macromolecule \( x \) at time \( t \) by \( u(x, t) \). The normalization condition \[2\]
from the classical model transforms to

$$\int_0^{2\pi} u(x, t) \, dx = 1 \quad \forall t \geq 0,$$

and it is also convenient to incorporate periodicity with respect to $x$:

$$u(x + 2\pi, t) = u(x, t) \quad \forall x \in \mathbb{R} \quad \forall t \geq 0.$$  

Hence, species $x$ and $x + 2n\pi$ are considered to be equivalent for any integer $n$. Furthermore, assume the existence of a constant parameter $h \in (0, 2\pi)$ such that replication of species $x$ is catalyzed by species $x - h$. Next, let $k(x)$ and $\varphi(x)$ be functions that describe the replication rates and initial distribution, respectively, and introduce a diffusion coefficient $\alpha > 0$.

**Assumption 2.1.** $h = \text{const} \in (0, 2\pi)$, $\alpha = \text{const} > 0$, $k : [0, 2\pi] \rightarrow (0, +\infty)$ is a twice continuously differentiable positive function satisfying $k(0) = k(2\pi)$, $k'(0) = k'(2\pi)$, and $\varphi : [-h, 2\pi] \rightarrow [0, +\infty)$ is a twice continuously differentiable nonnegative function satisfying

$$\int_0^{2\pi} \varphi(x) \, dx = 1, \quad \varphi(x) = \varphi(x + 2\pi) \quad \forall x \in [-h, 0].$$

A hypercycle model can then be stated in the form of the following initial-boundary value problem for a second-order partial integro-differential equation with a nonlinear source term involving a spatial delay:

$$\begin{cases}
\frac{\partial u(x,t)}{\partial t} = u(x,t) \left( k(x) u(x-h, t) - f[u(\cdot, t)] \right) + \alpha \frac{\partial^2 u(x,t)}{\partial x^2}, \\
u(x-h, t) = u(x-h + 2\pi, t) \quad \text{if} \quad -h \leq x - h < 0, \\
u(x,0) = \varphi(x) \quad \text{(initial condition)}, \\
u(0,t) = u(2\pi,t), \quad \frac{\partial u}{\partial x}(0,t) = \frac{\partial u}{\partial x}(2\pi,t) \quad \text{(boundary conditions)}, \\
0 \leq x \leq 2\pi, \quad t \geq 0.
\end{cases}$$

Here

$$f[u(\cdot, t)] = \int_0^{2\pi} k(x) u(x,t) u(x-h, t) \, dx \quad \forall t \geq 0$$

is the mean fitness of the system. This representation can be obtained by integrating the dynamic equation in (6) over $0 \leq x \leq 2\pi$ and using the normalization property (4) as well as the boundary condition for $\partial u/\partial x$. Similar arguments can also help us verify that, under Assumption 2.1, a solution of (6) should satisfy

$$\frac{d}{dt} \left( \int_0^{2\pi} u(x,t) \, dx \right) = 0 \quad \forall t \geq 0,$$

which ensures (4). Moreover, the mixed boundary conditions come from the aforementioned periodicity (cyclic structure) with respect to $x$. Thus, the relations (6) and (7) can serve as a distributed modification of the classical hypercycle model (3).

Note that the catalytic structure leading to a spatial delay is an important feature of our distributed hypercycle model in comparison with distributed quasispecies models [10, 8, 7].
3 Existence, uniqueness, and nonnegativity of the solution

This section addresses the existence, uniqueness, and nonnegativity of the classical solution to the initial-boundary value problem, with detailed proofs moved to Appendix.

Introduce an arbitrary time horizon \( T > 0 \) and the Banakh space \( C^{2,1}([0, 2\pi] \times [0, T]) \) consisting of continuous functions \( [0, 2\pi] \times [0, T] \ni (x, t) \mapsto w(x, t) \in \mathbb{R} \) such that \( \partial w/\partial x, \partial^2 w/\partial x^2, \partial w/\partial t \) are continuous on \([0, 2\pi] \times [0, T]\). The continuity on the boundary of the rectangle means that the corresponding bounded limits from the interior exist and are taken as the values on the boundary. The norm in \( C^{2,1}([0, 2\pi] \times [0, T]) \) is defined as

\[
\|w\|_{C^{2,1}([0, 2\pi] \times [0, T])} = \max_{0 \leq x \leq 2\pi, \ 0 \leq t \leq T} \left\{ \|w(x, t)\| + \left| \frac{\partial w(x, t)}{\partial x} \right| + \left| \frac{\partial^2 w(x, t)}{\partial x^2} \right| + \left| \frac{\partial w(x, t)}{\partial t} \right| \right\}.
\]

(8)

The classical solution is searched for in this space.

The space \( C^2([0, 2\pi]) \) is similarly defined (but with excluded dependence on \( t \)).

Consider the auxiliary linear problem

\[
\begin{align*}
Av(x, t) &= \frac{\partial v(x, t)}{\partial t} - \alpha \frac{\partial^2 v(x, t)}{\partial x^2} = \psi(x, t), \\
v(x, 0) &= \varphi(x) \quad \text{(initial condition)}, \\
v(0, t) &= v(2\pi, t), \quad \frac{\partial v}{\partial x}(0, t) = \frac{\partial v}{\partial x}(2\pi, t) \quad \text{(boundary conditions)}, \\
0 &\leq x \leq 2\pi, \quad 0 \leq t \leq T,
\end{align*}
\]

(9)

with a right-hand side \( \psi \) that lies in \( C^{2,1}([0, 2\pi] \times [0, T]) \) and satisfies the boundary conditions

\[
\psi(0, t) = \psi(2\pi, t), \quad \frac{\partial \psi}{\partial x}(0, t) = \frac{\partial \psi}{\partial x}(2\pi, t) \quad \forall t \in [0, T].
\]

(10)

The corresponding solution is obtained in Appendix A.1 and, with the help of Assumption 2.1, one can directly verify that it also belongs to \( C^{2,1}([0, 2\pi] \times [0, T]) \). The relations (A.1), (A.4), (A.5) give rise to the operators \( \mathcal{E}, \mathcal{E}_1, \mathcal{E}_2 \) such that

\[
v(x, t) = \mathcal{E}[\varphi, \psi](x, t) = \mathcal{E}_1\varphi(x, t) + \mathcal{E}_2\psi(x, t).
\]

(11)

Note that \( \mathcal{E}_1, \mathcal{E}_2 \) are linear operators. Straightforward calculations based on (A.1), (A.4), (A.5) lead to the estimates

\[
\begin{align*}
\|\mathcal{E}_1\varphi\|_{C^{2,1}([0, 2\pi] \times [0, T])} &\leq c_1 \|\varphi\|_{C^2([0, 2\pi])}, \\
\|\mathcal{E}_2\psi\|_{C^{2,1}([0, 2\pi] \times [0, T])} &\leq c_2 \|\psi\|_{C^{2,1}([0, 2\pi] \times [0, T])}, \\
\|\mathcal{E}[\varphi, \psi]\|_{C^{2,1}([0, 2\pi] \times [0, T])} &\leq c_1 \|\varphi\|_{C^2([0, 2\pi])} + c_2 \|\psi\|_{C^{2,1}([0, 2\pi] \times [0, T])}
\end{align*}
\]

(12)

with some positive constants \( c_1, c_2 \).

The idea for the proof of an existence and uniqueness result for (1) is to apply the Banach fixed point theorem (see, e.g., [19, Theorem 4.16]) to the iterative process

\[
u^0(x, t) = \varphi(x), \quad u^{m+1} = \mathcal{E}[\varphi, \mathcal{F}u^m], \quad m = 0, 1, 2, \ldots,
\]

(13)
where

\[ F^m(x,t) = u^m(x,t) (k(x) u^m(x-h,t) - f[u^m(\cdot,t)]), \]
\[ f[u^m(\cdot,t)] = \int_0^{2\pi} k(x) u^m(x,t) u^m(x-h,t) \, dx \]

(14)

(see the right-hand side of the dynamic equation in (6), as well as the mean fitness definition (7)). Because of the nonlinearity in (14), this proof approach works only under the quite restrictive technical condition that the quantity

\[ \bar{k} = \max_{0 \leq x \leq 2\pi} \max \{|k(x)|, |k'(x)|, |k''(x)|\} \]

(15)

is sufficiently small. The proof of an extended existence and uniqueness result remains an open task. One may in general expect the unique solution to exist under weaker conditions.

Due to the boundary conditions for \( \varphi, \varphi', k, k' \) at \( x = 0 \) and \( x = 2\pi \) (recall Assumption 2.1), the relations (10) should hold with \( \psi = F^m \) for all \( m = 0, 1, 2, \ldots \) Using also the fact that \( \int_0^{2\pi} u^0(x,t) \, dx = \int_0^{2\pi} \varphi(x) \, dx = 1 \), one arrives at

\[ \int_0^{2\pi} u^m(x,t) \, dx = \int_0^{2\pi} F^m(x,t) \, dx = 1, \quad m = 0, 1, 2, \ldots \]

(16)

The following lemma is established in Appendix A.2.

**Lemma 3.1.** Under Assumption 2.1, the sequence of the norms \( \|u^m\|_{C^2([0,2\pi] \times [0,T])} \), \( m = 0, 1, 2, \ldots \), is uniformly bounded for sufficiently small values of (15).

The proof of the existence and uniqueness result (Theorem 3.2) is given in Appendix A.3.

**Theorem 3.2.** Let Assumption 2.1 hold. Then for for sufficiently small values of (15), there exists a unique classical solution \( u \in C^2([0,2\pi] \times [0,T]) \) to the distributed hypercycle problem (6).

The solution nonnegativity result (Theorem 3.3) is proved in Appendix A.4 under the condition that the catalytic shift (delay) parameter \( h \) is sufficiently small. This condition seems reasonable when comparing the distributed hypercycle model (6),(7) to the classical model (3) with a large number of species \( n \). Indeed, the relation between \( h \) and \( n \) can be set up to \( h = 2\pi/n \), so that \( h \to 0 \) as \( n \to \infty \).

**Theorem 3.3.** Let Assumption 2.1 hold, and let a solution \( u_h \in C^2([0,2\pi] \times [0,T]) \) to the problem (6) exist for all \( 0 < h \leq h_0 \), where \( h_0 = \text{const} \in (0,2\pi) \). Assume also

\[ \sup_{0 < h \leq h_0} \|u_h\|_{C^2([0,2\pi] \times [0,T])} < \infty. \]

(17)

Then \( u_h \) is a nonnegative function for sufficiently small \( h \).

**Remark 3.4.** Let Assumption 2.1 hold, and let \( \bar{k} \) be small enough to apply Lemma 3.1 and Theorem 3.2. First, note that \( c_1, c_2 \) in the estimates (12) do not depend on \( h \), since the auxiliary problem (9) does not contain \( h \). From the proofs of Lemma 3.1 and Theorem 3.2 in Appendix, one can see that the parameters in the corresponding estimates also do not depend on \( h \). Hence, the condition (17) is fulfilled in this case.
4 Steady-state analysis

System (6), (7) has the following equilibrium solution \( v(x) = (2\pi)^{-1} \) for \( k(x) = k = \text{const} > 0 \). First we show that this equilibrium is unstable.

Let \( \psi \in C^{2,1} \). Consider function

\[
v_{\varepsilon}(x,t) = \frac{1}{2\pi} + \varepsilon \psi(x,t)
\]

that satisfies condition (4). Then

\[
\int_0^{2\pi} \psi(x,t) dx = 0.
\]

Plugging \( v_{\varepsilon} \) into (6) and keeping only the linear with respect to \( \varepsilon \) terms we obtain

\[
\frac{\partial \psi}{\partial t}(x,t) = k\left(\psi(x,t) + \psi(x-h,t)\right) - k\psi(x,t) - \frac{k}{2\pi} \int_0^{2\pi} \left(\psi(x,t) - \psi(x-h,t)\right) dx + \alpha \frac{\partial^2 \psi}{\partial x^2}(x,t),
\]

\[
\psi(x,0) = \psi_0(x), \quad x \in [0,2\pi],
\]

which, after simplification and taking into account (19), leads to

\[
\frac{\partial \psi}{\partial t}(x,t) = k\psi(x-h,t) + \alpha \frac{\partial^2 \psi}{\partial x^2}(x,t), \quad t > 0,
\]

\[
\psi(x,0) = \psi_0(x), \quad x \in [0,2\pi].
\]

It is natural to look for a solution to this problem in the form of a Fourier series

\[
\psi(x,t) = \sum_{n=-\infty}^{+\infty} c_n(t)e^{-inx},
\]

which yields

\[
\frac{dc_n}{dt}(t) = c_n(t) \left(ke^{inh} - \alpha n^2\right), \quad n = 0, \pm 1, \pm 2, \ldots.
\]

For \( n = 0 \) \( c_0(t) \to \infty \) for \( t \to \infty \) and hence we proved that the equilibrium \( v(x) = (2\pi)^{-1} \) is unstable.

Now we look into possible spatially non-homogeneous equilibria, which must satisfy the following problem

\[
\alpha \frac{d^2 v}{dx^2}(x) + v(x)(kv(x-h) - \bar{f}) = 0, \quad x \in (0,2\pi),
\]

\[
v'(0) = v'(2\pi), \quad \bar{f} = k \int_0^{2\pi} v(x)v(x-h) dx,
\]

\[
v(x-h) = \begin{cases} v(x-h), & \text{if } x-h \geq 0, \\ v(2\pi + x-h), & \text{if } x-h < 0, \end{cases}
\]

\[
\int_0^{2\pi} v(x) dx = \int_0^{2\pi} v(x-h) dx = 1.
\]
As before, here we assume that \( k(x) = k = \text{const} > 0 \).

If we assume that \( v \in C^2[0, 2\pi] \) then

\[
v(x - h) = v(x) - hv_x(x) + \frac{h^2}{2} v_{xx} + o(h^2).
\]

Using this representation and keeping only the terms up to \( o(h^2) \) the first equation in (22) becomes

\[
v_{xx}(x) \left( \alpha + \frac{k h^2}{2} v(x) \right) = \tilde{f} v(x) - k v(x) \left( v(x) - h v_x(x) \right).
\]

We rewrite this second order equation as the following system:

\[
\begin{aligned}
\frac{dv}{dx}(x) &= w(x), \\
\frac{dw}{dx}(x) &= \frac{\left( \tilde{f} - kv(x) + k hw(x) \right) v(x)}{\alpha + 2^{-1} k h^2 v(x)},
\end{aligned}
\]

with the boundary conditions \( w(0) = w(2\pi) \).

The standard analysis of (23) yields that there are two equilibria \( O(0,0) \) and \( A(\tilde{f} k^{-1}, 0) \). The former one is a saddle point for any parameter values, and the latter one is a stable focus for \( h < 0 \), unstable focus for \( h > 0 \); if \( h = 0 \) then the eigenvalues of the Jacobi matrix are pure imaginary complex conjugate.

We note that for \( h = 0 \) system (23) becomes Hamiltonian, with the Hamiltonian

\[
H(v, w) = \frac{w^2}{2} + U(v), \quad U(v) = \frac{v^2}{\alpha} \left( \frac{k v^2}{2} - \frac{\tilde{f}}{2} \right).
\]

The graph of potential \( U \) immediately implies that equilibrium \( A \) in the case \( h = 0 \) is Lyapunov stable, with a family of closed orbits surrounding it, which implies that there are infinitely many orbits that satisfy the condition \( w(x_1) = w(x_2) = 0 \) for two points \( x_2 > x_1 > 0 \) (see Fig. 2).

The conditions identified above are sufficient to invoke the Hopf bifurcation theorem (in the form given, e.g., in [17], Section 3C) to conclude that for sufficiently small \( |h| \) there must be nonconstant periodic solutions that collapse at a point when \( |h| \to 0 \). Among all such periodic solutions we are interested in one that satisfies \( w(0) = w(2\pi) = 0 \). We claim that such solution can always be found if one is allowed to consider sufficiently small values of \( \alpha \) (see Fig. 3).

Indeed, from equations (23) we see that decreasing \( \alpha = o(h) \) leads to increase of velocity of movements along the phase portrait, and therefore there will always be sufficiently small values of \( \alpha \) for which the required condition is satisfied; moreover, it is clear that for some choice of \( \alpha \) the orbit will travel around the equilibrium point only once, for some \( \alpha \) will travel twice, etc. As a result of these reasoning we put forward the following conjecture.

**Conjecture 4.1.** For sufficiently small values of \( h \) and diffusion coefficient \( \alpha = o(h) \) there exist periodic solutions to (22), with are \( o(h^2) \)-close to the periodic solutions to (23).

An additional support to this conjecture can be seen from the following argument.

If we assume that \( v \) is sufficiently smooth in (22), i.e.,

\[
v(x - h) = \sum_{j=0}^{N} \frac{(-1)^j}{j!} h^j v^{(j)}(x) + o(h^N),
\]

\[
\frac{dv}{dx}(x) = w(x), \quad \frac{dw}{dx}(x) = \frac{\left( \tilde{f} - kv(x) + k hw(x) \right) v(x)}{\alpha + 2^{-1} k h^2 v(x)},
\]

with the boundary conditions \( w(0) = w(2\pi) \).

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\]

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\]
Figure 2: Graph of the potential for system [23] with $h = 0$ (left) and the corresponding phase portrait (right).

Figure 3: Periodic solution of (23) for sufficiently small $\alpha$ and $h > 0$. 
then problem (22) can be rewritten as a system of $N$ (dropping the terms of the smaller order) equations of the first order

\[
\frac{dv_1}{dx}(x) = v_2(x), \quad \frac{dv_2}{dx}(x) = v_3(x), \quad \ldots, \quad \frac{dv_{N-1}}{dx}(x) = v_N(x), \quad \frac{dv_N}{dx}(x) = \frac{(-1)^{N+1}N!}{kh^N} \left( \sum_{j=0}^{N-1} \frac{(-1)^j}{j!} h^j v_{j+1} + \alpha v_3 v_1 - \bar{f} \right),
\]

(24)

which has the equilibrium $A(\bar{f}k^{-1}, 0, \ldots, 0)$. Linearizing around this equilibrium yield the Jacobi matrix with the characteristic polynomial

\[
(-1)^{N+1} \frac{kh^N}{N!} \lambda^N + (-1)^{N-1} \frac{h^{N-1}}{(N-1)!} \lambda^{N-1} + \ldots - \frac{h^3}{3!} \lambda^3 + \left( \frac{h^2}{2!} + \alpha \bar{f} \right) \lambda^2 - h \lambda + 1.
\]

When $h \to 0$ we again have two purely imaginary complex root, and the same Hopf theorem implies the existence of periodic solutions that collapse into the point when $h \to 0$.

Therefore, it is highly probably that problem (22) admits solutions different from a constant, which may be non-unique; and therefore the original system (6), (7) admits spatially non-uniform equilibria.

5 Numerical solutions

In the previous section we found a family of spatially-nonhomogeneous stationary solution. We did not study their stability analytically because it represents an independent and complex problem on its own. Here we present some numerical evidence that these solutions are most probably unstable because in numerical experiments spatial and temporal oscillations are usually observed.

To conduct the numerical experiments we use an explicit finite difference scheme and numerical approximation of the integral on the given interval. Choosing the parameters as follows: $x \in [0, 2\pi]$, $\alpha = 0.05$, $t \in [0, 300]$, $h = 0.4$, $k(x) = 1$, $\varphi(x) = (2\pi)^{-1}(\sin(5x + \pi/4) + 1)$ we can see that the numerically obtained solution $u$ represents a non-linear wave which oscillates with respect to both spatial and temporal variables (see Fig. 4).

Choosing a different initial condition does not change the result qualitatively (see Fig. 5). Among other things we can see that the numerical simulations strongly indicate that the spatially continuous hypercyclic system (6) is permanent similar to its discrete counterpart. It is an interesting open mathematical problem to analyze the observed oscillations analytically.

6 Conclusion

In this paper we introduced a continuous analogue of the classical discrete hypercycle (3). The dynamics of (3) is well understood; it is, however, an open challenge to fully investigate the properties of the solutions of the introduced partial integro-differential equation with spatial delay (6). Here we started such investigation by proving the existence and uniqueness theorem for this problem and showing, according to biological interpretation of the model, non-negativity of its solutions. We also presented some analytical evidence that there are spatially nonuniform stationary solutions and numerical evidence that the actual asymptotic behavior of the system tends to both spatial and
Figure 4: Numerical solution of problem (6) with $x \in [0, 2\pi]$, $\alpha = 0.05$, $t \in [0, 300]$, $h = 0.4$, $k(x) = 1$, $\varphi(x) = (2\pi)^{-1}(\sin(5x + \pi/4) + 1)$.

Figure 5: Numerical solution of problem (6) with $x \in [0, 2\pi]$, $\alpha = 0.05$, $t \in [0, 500]$, $h = 0.4$, $k(x) = 1$, $\varphi(x) = (2\pi)^{-1}(\sin(x + \pi/4) + 1)$. 
temporal oscillations. It is a challenging open problem to provide an analytical support for our observations.

We would like to conclude this paper with a short historic anecdote. Famous Soviet mathematician Anatolii Myshkis (1920–2009) is mostly known as one of the founders of the field of delay differential equations. Less known is the fact that the last significant mathematical object of his study was a class of differential equations with delay with respect to other than time variable. Two of the authors of the present paper were fortunate to attend a talk by prof. Myshkis in early 2000’s devoted to this topic. As it was usual in mathematical presentations in Soviet Union and later in Russia, the talk concluded with a somewhat long discussion of the results. In particular prof. Myshkis mentioned that the class of problem he had been studying did not get much attention in the mathematical community in part because of the lack of applications and mathematical models of natural phenomena described by such equations. Several ideas were suggested in which direction one may look for applications, but none of them was very convincing. For us it is important to state that the mathematical model we consider in this text is very similar to the mixed functional differential equations considered in and it is our hope that our model will attract more attention to this interesting class of mathematical problems.

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Appendix

A.1 Solution of the auxiliary linear problem \((9)\)

The boundary conditions are obviously satisfied if one represents the solution as the Fourier series

\[
v(x, t) = \frac{a_0(t)}{2} + \sum_{n=1}^{\infty} (a_n(t) \cos(nx) + b_n(t) \sin(nx)).
\] (A.1)

Similarly, the initial profile and the right-hand side of the equation are written as

\[
\varphi(x) = \frac{\varphi_{10}}{2} + \sum_{n=1}^{\infty} (\varphi_{1n} \cos(nx) + \varphi_{2n} \sin(nx)),
\] (A.2)

\[
\psi(x, t) = \frac{\psi_{10}(t)}{2} + \sum_{n=1}^{\infty} (\psi_{1n}(t) \cos(nx) + \psi_{2n}(t) \sin(nx)).
\] (A.3)

Here we use the fact that the functional system \(1/\sqrt{2\pi}, (1/\sqrt{\pi}) \cos(nx), (1/\sqrt{\pi}) \sin(nx), n = 1, 2, 3, \ldots\), is orthonormal in the Hilbert space \(L^2([0, 2\pi]; \mathbb{R})\) of square Lebesgue-integrable real-valued functions on \([0, 2\pi]\). The Fourier coefficients in (A.2) and (A.3) are determined by

\[
\varphi_{10} = \frac{1}{\pi} \int_{0}^{2\pi} \varphi(x) \, dx, \quad \psi_{10}(t) = \frac{1}{\pi} \int_{0}^{2\pi} \psi(x, t) \, dx,
\]

\[
\varphi_{1n} = \frac{1}{\pi} \int_{0}^{2\pi} \varphi(x) \cos(nx) \, dx,
\]

\[
\varphi_{2n} = \frac{1}{\pi} \int_{0}^{2\pi} \varphi(x) \sin(nx) \, dx,
\]

\[
\psi_{1n}(t) = \frac{1}{\pi} \int_{0}^{2\pi} \psi(x, t) \cos(nx) \, dx,
\]

\[
\psi_{2n}(t) = \frac{1}{\pi} \int_{0}^{2\pi} \psi(x, t) \sin(nx) \, dx,
\]

\(n = 1, 2, 3, \ldots\)
Using integration by parts together with the conditions \( \varphi(0) = \varphi(2\pi) \), \( \varphi'(0) = \varphi'(2\pi) \) (recall Assumption 2.1), and (10), one arrives at the following representations:

\[
\begin{align*}
\varphi_{1n} &= \frac{1}{n\pi} \int_0^{2\pi} \varphi(x) \sin(nx) \, dx = -\frac{1}{n\pi} \int_0^{2\pi} \varphi'(x) \sin(nx) \, dx, \\
\varphi_{2n} &= -\frac{1}{n\pi} \int_0^{2\pi} \varphi(x) \cos(nx) \, dx = \frac{1}{n\pi} \int_0^{2\pi} \varphi'(x) \cos(nx) \, dx,
\end{align*}
\]

\( n = 1, 2, 3, \ldots \) (A.4)

\[
\begin{align*}
\psi_{1n}(t) &= -\frac{1}{n^2\pi} \int_0^{2\pi} \frac{\partial^2 \psi(x, t)}{\partial x^2} \cos(nx) \, dx, \\
\psi_{2n}(t) &= -\frac{1}{n^2\pi} \int_0^{2\pi} \frac{\partial^2 \psi(x, t)}{\partial x^2} \sin(nx) \, dx,
\end{align*}
\]

Plugging the relations (A.1), (A.3) into the equation of (9) yields

\[
\begin{align*}
\dot{a}_0(t) &= \psi_{10}(t), & \dot{a}_n(t) + \alpha n^2 a_n(t) &= \psi_{1n}(t), & \dot{b}_n(t) + \alpha n^2 b_n(t) &= \psi_{2n}(t),
\end{align*}
\]

while the initial condition with (A.1), (A.2) implies

\[
\begin{align*}
a_0(0) &= \varphi_{10}, & a_n(0) &= \varphi_{1n}, & b_n(0) &= \varphi_{2n},
\end{align*}
\]

and one consequently obtains the sought-after Fourier coefficients:

\[
\begin{align*}
a_0(t) &= \varphi_{10} + \int_0^t \psi_{10}(s) \, ds, \\
a_n(t) &= e^{-\alpha n^2 t} \varphi_{1n} + \int_0^t e^{-\alpha n^2 (t-s)} \psi_{1n}(s) \, ds, \\
b_n(t) &= e^{-\alpha n^2 t} \varphi_{2n} + \int_0^t e^{-\alpha n^2 (t-s)} \psi_{2n}(s) \, ds,
\end{align*}
\]

(A.5)

\( n = 1, 2, 3, \ldots \)

A.2 Proof of Lemma 3.1

From (14)–(16), one derives

\[
\mathcal{F}u^m(x, t) = u^m(x, t) \int_0^{2\pi} (k(x) u^m(x-h, t) - k(\xi) u^m(\xi-h, t)) \, d\xi
\]

and, therefore,

\[
\|\mathcal{F}u^m\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_3 \|u^m\|_{C^{2,1}([0,2\pi] \times [0,T])}^3, \quad m = 0, 1, 2, \ldots
\]

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where \(c_3 = \text{const} > 0\). Together with (12) and (13), this yields
\[
\|u^{m+1}\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_4 + c_2c_3\bar{k} \|\varphi\|_{C^2([0,2\pi])}^3, \quad m = 0, 1, 2, \ldots, \quad c_4 = c_1 \|\varphi\|_{C^2([0,2\pi])}, \quad u^0(x,t) = \varphi(x).
\]

We need the following auxiliary algebraic properties for nonnegative parameters:
\[
(p_1 + p_2)^3 = p_1^3 + 3p_1^2p_2 + 3p_1p_2^2 + p_2^3
\leq p_1^3 + 6 (\max \{p_1, p_2\})^3 + p_2^3
\leq p_1^3 + 6 (p_1^3 + p_2^3) + p_2^3
\leq 7 (p_1^3 + p_2^3),
\]
\[
(p_1 + p_2 + p_3)^3 \leq 7p_1^3 + 7(p_2 + p_3)^3 \leq 7p_1^3 + 7^2 p_2^3 + 7^2 p_3^3,
\]
\[
(p_1 + p_2 + \ldots + p_l)^3 \leq 7p_1^3 + 7^2 p_2^3 + \ldots + 7^{l-2} p_{l-2}^3 + 7^{l-1} p_{l-1}^3 + 7^l p_l^3,
\]
\[
p_1 \geq 0, \quad p_2 \geq 0, \quad \ldots, \quad p_l \geq 0, \quad l = 2, 3, 4, \ldots
\]

Let \(\bar{k}\) be small enough to satisfy
\[
c_2c_3\bar{k} \leq \beta, \quad c_2c_3\bar{k} \|\varphi\|_{C^2([0,2\pi])}^3 \leq \beta, \quad 0 < \beta < 1,
\]
\[
7^3\beta^2c_4^4 \leq 1, \quad 7^3\beta^5 \leq 1.
\]

Then
\[
\|u^1\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_4 + c_2c_3\bar{k} \|\varphi\|_{C^2([0,2\pi])}^3
= c_4 + c_2c_3\bar{k} \|\varphi\|_{C^2([0,2\pi])}^3 \leq c_4 + \beta,
\]
\[
\|u^2\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_4 + c_2c_3\bar{k} \|u^1\|_{C^{2,1}([0,2\pi] \times [0,T])}^3
\leq c_4 + \beta(c_4 + \beta)^3 \leq c_4 + 7\beta (c_4^3 + \beta^3)
\leq c_4 + 7\beta c_4^3 + 7\beta^4.
\]

Let us now verify the general relation
\[
\|u^m\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_4 \sum_{i=0}^{m-1} (7\beta c_4^2)^i + (7\beta^4)^{m-1},
\]
\[
m = 2, 3, 4, \ldots
\]
by induction. Since (A.9) serves as the basis of induction (\(m = 2\)), it remains to show that (A.10) implies
\[
\|u^{m+1}\|_{C^{2,1}([0,2\pi] \times [0,T])} \leq c_4 \sum_{i=0}^{m} (7\beta c_4^2)^i + (7\beta^4)^m.
\]

(A.11)
Using (A.6)–(A.8) and (A.10), one obtains
\[
\|u^{m+1}\|_{C^{1,1}(0,2\pi \times [0,T])} \leq c_4 + c_2 c_3 k \|u^m\|_{C^{1,1}(0,2\pi \times [0,T])}^3 \\
\leq c_4 + \beta \left( \sum_{i=0}^{m-1} (7\beta)^i c_4^{2i+1} + (7\beta^4)^{m-1} \right) \\
\leq c_4 + \beta \left( \sum_{i=0}^{m-1} 7^{i+1} (7\beta)^{3i} c_4^{3(2i+1)} + 7^m (7\beta^4)^{3(m-1)} \right) \\
= c_4 + c_4 \sum_{i=1}^{m} \beta 7^i (7\beta)^{3i-3} c_4^{6i-4} + \beta 7^m (7\beta^4)^{3m-3} \\
\leq c_4 + c_4 \sum_{i=1}^{m} (7\beta c_4^2)^i (7^{3i-3} \beta^2 c_4^{4i-4}) + (7\beta^4)^{2m} (7^{3m-3} \beta^8 m^{-11}) \\
\leq c_4 + c_4 \sum_{i=1}^{m} (7\beta c_4^2)^i (7^3 \beta^2 c_4^4)^{i-1} + (7\beta^4)^{2m} (7^3 \beta^5)^{m-1} \beta^{3m-6}.
\]

This leads to (A.11), because $7^3 \beta^2 c_4^4 \leq 1$, $7^3 \beta^5 \leq 1$, and $\beta^{3m-6} \leq \beta^0 = 1$ ($m \geq 2$) in line with (A.8). Thus, (A.10) holds, and, consequently,
\[
\|u^m\|_{C^{1,1}(0,2\pi \times [0,T])} \leq c_4 \sum_{i=0}^{\infty} (7\beta c_4^2)^i + 1 < \infty,
\]
\[
m = 2, 3, 4, \ldots
\]
(one has $7\beta c_4^2 = 7^{-\frac{1}{2}} (7^3 \beta^2 c_4^4)^{\frac{1}{2}} < 1$ and $7\beta^4 = (7^3 \beta^5)^{\frac{1}{2}} \beta^2 \beta^{-2} < 1$ according to (A.8)), which completes the proof.

A.3 Proof of Theorem 3.2

By virtue of (11)–(13), one has
\[
\|u^{m+1} - u^m\|_{C^{1,1}(0,2\pi \times [0,T])} = \|\mathcal{E}_2 (\mathcal{F}u^m - \mathcal{F}u^{m-1})\|_{C^{1,1}(0,2\pi \times [0,T])} \\
\leq c_2 \|\mathcal{F}u^m - \mathcal{F}u^{m-1}\|_{C^{1,1}(0,2\pi \times [0,T])}, \quad m = 1, 2, 3, \ldots
\]

If one obtains the estimate
\[
\|\mathcal{F}u^m - \mathcal{F}u^{m-1}\|_{C^{1,1}(0,2\pi \times [0,T])} \\
\leq c_5 k \|u^m - u^{m-1}\|_{C^{1,1}(0,2\pi \times [0,T])}, \quad m = 1, 2, 3, \ldots, \quad c_5 = \text{const} > 0,
\]
then
\[
\|u^{m+1} - u^m\|_{C^{1,1}(0,2\pi \times [0,T])} \leq c_2 c_5 k \|u^m - u^{m-1}\|_{C^{1,1}(0,2\pi \times [0,T])}, \quad m = 1, 2, 3, \ldots,
\]

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and the Banach fixed point theorem (see, e.g., [19, Theorem 4.16]) implies the sought-after result (note that $\varepsilon_2 c_5 \tilde{k} < 1$ for sufficiently small $\tilde{k}$). But (A.12) follows from the representations

$$
F u^m(x, t) - F u^{m-1}(x, t) = u^m(x, t) (k(x) u^m(x - h, t) - f[u^m(\cdot, t)])
- u^{m-1}(x, t) (k(x) u^{m-1}(x - h, t) - f[u^{m-1}(\cdot, t)])
= k(x) u^m(x - h, t) (u^m(x, t) - u^{m-1}(x, t))
+ k(x) u^{m-1}(x, t) (u^m(x - h, t) - u^{m-1}(x - h, t))
- u^m(x, t) (f[u^m(\cdot, t)] - f[u^{m-1}(\cdot, t)])
- f[u^{m-1}(\cdot, t)] (u^m(x, t) - u^{m-1}(x, t)),
$$

where

$$
f[u^{m-1}(\cdot, t)] = \int_0^{2\pi} k(x) u^{m-1}(x, t) u^{m-1}(x - h, t) \, dx,
$$

$$
f[u^m(\cdot, t)] = \int_0^{2\pi} k(x) u^m(x, t) u^m(x - h, t) \, dx,
$$

and the uniform boundedness of $\{\|u^m\|_{C^2,1([0,2\pi] \times [0,T])}\}_{m=0}^\infty$ (the latter takes place for sufficiently small $\tilde{k}$ due to Lemma 3.1). This completes the proof.

### A.4 Proof of Theorem 3.3

For $h \in (0, h_0)$, let $x^*_h \in [0, 2\pi]$ and $t^*_h \in [0, T]$ satisfy

$$
u_h(x^*_h, t^*_h) = \min_{0 \leq x \leq 2\pi, \ 0 \leq t \leq T} u_h(x, t). \tag{A.13}
$$

The first-order necessary minimum conditions imply

$$
\frac{\partial u_h}{\partial t}(x^*_h, t^*_h) \geq 0 \text{ for } t^*_h = 0,
\frac{\partial u_h}{\partial t}(x^*_h, t^*_h) = 0 \text{ for } 0 < t^*_h < T, \tag{A.14}
\frac{\partial u_h}{\partial t}(x^*_h, t^*_h) \leq 0 \text{ for } t^*_h = T.
$$

If $0 < x^*_h < 2\pi$, the first- and second-order necessary minimum conditions yield $\frac{\partial u_h}{\partial x}(x^*_h, t^*_h) = 0$ and

$$
\frac{\partial^2 u_h}{\partial x^2}(x^*_h, t^*_h) \geq 0. \tag{A.15}
$$
If \( x_h^* = 0 \) or \( x_h^* = 2\pi \), then
\[
\begin{align*}
    u_h(x_h^*, t_h^*) &= u_h(0, t_h^*) = u_h(2\pi, t_h^*), \\
    \frac{\partial u_h}{\partial x}(x_h^*, t_h^*) &= \frac{\partial u_h}{\partial x}(0, t_h^*) = \frac{\partial u_h}{\partial x}(2\pi, t_h^*)
\end{align*}
\]
(by virtue of the boundary conditions in (6)), and the minimum can be reached at both points \((0, t_h^*)\), \((2\pi, t_h^*)\) only for \( \frac{\partial u_h}{\partial x}(x_h^*, t_h^*) = 0 \), so Taylor’s theorem with the Lagrange remainder again leads to (A.15).

Since \( u_h, \frac{\partial u_h}{\partial x}, \frac{\partial^2 u_h}{\partial x^2} \) are continuous on \([0, 2\pi] \times [0, T]\) and \( u_h(x - h, t) = u_h(x - h + 2\pi, t) \) for \(-h \leq x - h \leq 0\), Taylor’s theorem with Lagrange remainder and the condition (17) imply
\[
\max_{0 \leq x \leq 2\pi, 0 \leq t \leq T} \left| u_h(x - h, t) - \left( u_h(x, t) - h \frac{\partial u_h(x, t)}{\partial x} \right) \right| \leq c_6 h^2
\]

where
\[
c_6 = \sup_{0 < h < h_0} \max_{0 \leq x \leq 2\pi, 0 \leq t \leq T} \left| \frac{\partial^2 u_h(x, t)}{\partial x^2} \right| < \infty. \tag{A.17}
\]

Hence,
\[
f[u_h(\cdot, t)] = \int_0^{2\pi} k(x) u_h(x, t) u_h(x - h, t) \, dx
\]
\[
= \int_0^{2\pi} k(x) (u_h(x, t))^2 \, dx - h \int_0^{2\pi} k(x) u_h(x, t) \frac{\partial u_h(x, t)}{\partial x} \, dx + o(h, t)
\]
\[
\forall h \in (0, h_0],
\]
where
\[
\lim_{h \to +0} \frac{\max_{0 \leq t \leq T} |o(h, t)|}{h} = 0. \tag{A.18}
\]

Using integration by parts and the boundary conditions for \( k \) and \( u_h \) (see Assumption 2.1 and (6)), one arrives at
\[
\int_0^{2\pi} k(x) u_h(x, t) \frac{\partial u_h(x, t)}{\partial x} \, dx
\]
\[
= \frac{1}{2} \left( k(x) (u_h(x, t))^2 \right)_{x=0}^{x=2\pi} - \frac{1}{2} \int_0^{2\pi} k'(x) (u_h(x, t))^2 \, dx
\]
\[
= -\frac{1}{2} \int_0^{2\pi} k'(x) (u_h(x, t))^2 \, dx
\]
\[
\forall h \in (0, h_0],
\]
and, therefore,
\[
f[u_h(\cdot, t)] = \int_0^{2\pi} \left( k(x) + \frac{h}{2} k'(x) \right) (u_h(x, t))^2 \, dx + o(h, t) \quad \forall h \in (0, h_0].
\]
According to Assumption 2.1, \( k \) is continuously differentiable and positive on \([0, 2\pi]\), so there exist constants \( c_7 > 0 \) and \( h'_0 \in (0, h_0] \) such that
\[
\min_{0 \leq x \leq 2\pi} \left\{ k(x) + \frac{h}{2} k'(x) \right\} \geq c_7 \quad \forall h \in (0, h'_0],
\]
leading to
\[
f[u_h(\cdot,t)] \geq c_7 \int_0^{2\pi} (u_h(x,t))^2 \, dx + o(h,t) \quad \forall h \in (0, h'_0].
\]
Furthermore, the normalization condition (1) and the Cauchy–Schwarz inequality for the Hilbert space \( L^2([0, 2\pi]; \mathbb{R}) \) yield
\[
1 = \left( \int_0^{2\pi} u_h(x,t) \, dx \right)^2 \leq 2\pi \int_0^{2\pi} (u_h(x,t))^2 \, dx
\]
and, consequently,
\[
f[u_h(\cdot,t)] \geq \frac{c_7}{2\pi} + o(h,t) \quad \forall h \in (0, h'_0].
\]
Together with (A.18), this implies the existence of a constant \( h''_0 \in (0, h'_0] \) such that
\[
c_8 = \inf_{0 < h \leq h''_0} \min_{0 \leq t \leq T} f[u_h(\cdot,t)] > 0. \tag{A.19}
\]
Let also
\[
w_h(x,t) = u_h(x,t) e^{\Phi_h(t)}, \quad \Phi_h(t) = \int_0^t f[u_h(\cdot,s)] \, ds \quad \forall h \in (0, h_0], \tag{A.20}
\]
Then
\[
\frac{\partial w_h}{\partial t}(x_h^*, t_h^*) = \frac{\partial u_h}{\partial t}(x_h^*, t_h^*) e^{\Phi_h(t_h^*)}
+ u_h(x_h^*, t_h^*) e^{\Phi_h(t_h^*)} f[u_h(\cdot,t_h^*)] \quad \forall h \in (0, h_0]. \tag{A.21}
\]
Moreover, (9) and (A.20) lead to
\[
\frac{\partial w_h}{\partial t}(x_h^*, t_h^*) = k(x_h^*) u_h(x_h^*, t_h^*) u_h(x_h^* - h, t_h^*) e^{\Phi_h(t_h^*)}
+ \alpha \frac{\partial^2 u_h}{\partial x^2}(x_h^*, t_h^*) e^{\Phi_h(t_h^*)} \quad \forall h \in (0, h_0],
\]
and, therefore,
\[
\frac{\partial w_h}{\partial t}(x_h^*, t_h^*) \geq k(x_h^*) u_h(x_h^*, t_h^*) u_h(x_h^* - h, t_h^*) e^{\Phi_h(t_h^*)}
\]
\[
\forall h \in (0, h_0],
\]
due to (A.15) and \( \alpha > 0 \). Together with the relations (17), (A.16) and the continuity of \( k \) on \([0, 2\pi]\), this yields the existence of a constant \( c_9 > 0 \) such that
\[
\frac{\partial w_h}{\partial t}(x_h^*, t_h^*) \geq k(x_h^*) (u_h(x_h^*, t_h^*))^2 e^{\Phi_h(t_h^*)}
- c_9 h |u_h(x_h^*, t_h^*)| e^{\Phi_h(t_h^*)} \quad \forall h \in (0, h_0]. \tag{A.22}
\]
Let us now establish the sought-after property by contradiction. Assume the existence of a sequence 
\( \{h_i\}_{i=1}^{\infty} \subset (0, h'_0] \) such that \( \lim_{i \to \infty} h_i = 0 \) and \( u_{h_i}(x^*_h, t^*_h) < 0 \) for all \( i \in \mathbb{N} \). Then \( t^*_h \neq 0 \) (since \( u_{h_i}(x, 0) = \varphi(x) \geq 0 \)), (A.14) reduces to 
\[
\frac{\partial u_{h_i}}{\partial t}(x^*_h, t^*_h) \leq 0,
\]
and (A.21) leads to 
\[
\frac{\partial w_{h_i}}{\partial t}(x^*_h, t^*_h) \leq u_{h_i}(x^*_h, t^*_h) e^{\Phi_{h_i}(t^*_h)} f[u_{h_i}(\cdot, t^*_h)].
\] (A.23)

From (A.22) and (A.23), one obtains 
\[
u_{h_i}(x^*_h, t^*_h) f[u_{h_i}(\cdot, t^*_h)] \geq k(x^*_h) (u_{h_i}(x^*_h, t^*_h))^2 - c_9 h_i |u_{h_i}(x^*_h, t^*_h)|,
\]
and, consequently, 
\[
f[u_{h_i}(\cdot, t^*_h)] \leq k(x^*_h) u_{h_i}(x^*_h, t^*_h) + c_9 h_i
\]
(due to \( u_{h_i}(x^*_h, t^*_h) < 0 \)). Together with (A.19) and the positivity of \( k \) on \([0, 2\pi]\), this implies that \( 0 < c_8 < c_9 h_i \) for all \( i \in \mathbb{N} \), which contradicts with \( \lim_{i \to \infty} h_i = 0 \). Thus, \( u_h \) should indeed be a nonnegative function for sufficiently small \( h \).