A METHOD FOR NUMERICAL ANALYSIS OF A LOTKA-VOLTERRA FOOD WEB MODEL

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Abstract. We study the existence, uniqueness and continuous dependence on initial data of the solution for a Lotka-Volterra cascade model with one basal species and hierarchical predation. A uniquely solvable, stable, semi-implicit finite-difference scheme is proposed for this system that converges to the true solution uniformly in a finite interval.

Key words. Finite difference scheme, convergence.

1. Introduction

In a food web, a species is called basal if it is prey but is not predatory, intermediate if it is both prey and predator and top if it is only a predator; the composition of predator and prey relationships in a food web is referred to as its trophic structure and individuals levels as trophic levels. We use the word population to mean abundance or biomass of a species. If we let $x(t)$, $y(t)$ and $z(t)$ represent the populations of basal, intermediate and top species respectively in a food web at time $t$, a sensible model for the trophic structure of a closed food-web population at time $t$ is a generalized Lotka-Volterra system of the form

\begin{align}
\dot{x} &= ax - bx^2 - cxy - dxz, \\
\dot{y} &= -ey + fxy - gyz, \\
\dot{z} &= -hz + ixz + jyz, \\
x(0) &= x_0, \quad y(0) = y_0 \text{ and } z(0) = z_0,
\end{align}

where $a, b, \ldots, j > 0$. In this model, the basal species with population $x$ has intrinsic growth rate $a$ with environmental carrying capacity $a/b$ and the strength of the effect of predation from the other two species is measured by interaction-term coefficients $c$ and $d$. As the top species with population $z$ preys on both the basal and intermediate species, its interaction terms $xz$ and $yz$ have positive coefficients since $z$ increases under interaction with each of the other species. The intermediate species with population $y$ grows through interaction with the basal species but declines through interaction with the top species.

This system is a special case of the well-known Lotka-Volterra cascade model (cf. [3]) given by

\begin{equation}
\dot{x}_i(t) = x_i(t) \left[ e_i + \sum_{j=1}^{n} p_{ij} x_j(t) \right], \quad i = 1, 2, \ldots, n
\end{equation}
where $x_i(t)$ is the population of species $i$, $e_i$ is the intrinsic growth or decline rate of species $i$ and $p_{ij}$ is the interaction coefficient between species $i$ and $j$. The finite-difference scheme we introduce here for $n = 3$ applies to predict the population in the case of only one basal species, so that $p_{11} > 0$ and $p_{22} = p_{33} = 0$ in (1.5), and with hierarchal predation, meaning that each successive species preys on those below it. This means that in (1.5) species $j$ preys on species $i$ if and only if $i < j$, so that $p_{ij} < 0$ if $i < j$ and $p_{ij} > 0$ if $i > j$.

Although we present a numerical scheme only for the case of a trophic structure involving one basal and two non-basal species such as rabbits, foxes and wolves, our scheme can be applied to any geographically limited food web involving one basal species and any number of non-basal but hierarchal predators. We explain how this is done Section 3. Additionally, even though we analyze (1.1)-(1.4) specifically for three individual species, it may be thought of as representing an entire web of distinct basal species along with multiple species of intermediate and top predators, as long as no information about interaction between species at the same relative trophic level is sought.

The method used to discretize (1.1)-(1.4) in Section 3 is reminiscent of nonstandard finite difference schemes as proposed in [4] and [5], as well as in [6], [7] and [8] in the sense that it is not explicit in time. However, in these references, the methods proposed seek to find exact schemes that correctly exhibit the geometry of limit cycles when applied to various differential equations and systems. There it is demonstrated that a numerical scheme that is chosen semi-implicit in time and whose time step faithfully mimics the geometry of limit cycles by following certain rules has impressive numerical results. For an excellent summary of these methods, see [10].

The numerical method proposed in this paper uses a semi-implicit scheme as well, but in spirit more closely follows methods presented in [1], [2] and [11]. This is because we have little a priori global knowledge of the geometry of solutions, so although we use mixed time steps for the interaction terms of (1.1)-(1.4), this is done in a way that ensures nonnegativity and stability but still converges uniformly to the true solution. Therefore, instead of knowing properties of the solution and laying out a numerical method to match them as presented for a Lotka-Volterra system in [7], our numerical approach is to use a type of discretization that works for the system, prove that it converges to the solution of the system, then use these results to study the true solution.

It seems that there are very few results on the numerical solutions to the system (1.1)-(1.4) where a discretization is chosen that is shown to have all the desirable properties of a numerical method.

We organize this paper as follows. In Section 2, we prove the existence, uniqueness and global boundedness of the solution $(x, y, z)$ of (1.1)-(1.4). In Section 3, we develop a semi-implicit finite difference scheme for this system and prove that the difference scheme is stable and the numerical approximation converges to the solution of (1.1)-(1.4). In Section 4, some numerical experiments are carried out to study the solution of this system, then finish with some notes on a Hopf bifurcation that arises at a certain critical value.

2. Existence, Uniqueness and Global Boundedness

In order to get a better analysis for the system, we reduce the number of parameters using the nondimensionalization method as in [9] as follows.
Letting

$$u(T) = \frac{b}{a} x(t), \quad v(T) = \frac{c}{a} y(t), \quad \text{and} \quad w(T) = \frac{d}{a} z(t), \quad \text{with} \quad T = at,$$

we get

$$x'(t) = \frac{a^2}{x(t)}, \quad y'(t) = \frac{c^2}{y(t)} \quad \text{and} \quad z'(t) = \frac{d^2}{z(t)}.$$  \hspace{1cm} (2.1)

Substituting (2.1) into (1.1)-(1.4) and renaming $T$ to $t$, we have

$$u' = u(1 - u - v - w) \quad \text{and} \quad v' = v(-A + Bu - Cw).$$ \hspace{1cm} (2.2)

$$w' = w(-D + Eu + Fv).$$ \hspace{1cm} (2.3)

$$u(0) = u_0, \quad v(0) = v_0, \quad w(0) = w_0,$$

where

$$A = \frac{a}{a}, \quad B = \frac{b}{a}, \quad C = \frac{c}{a}, \quad D = \frac{d}{a}, \quad E = \frac{e}{a} \quad \text{and} \quad F = \frac{f}{a},$$

and with

$$u_0 = \frac{b}{a} x_0, \quad v_0 = \frac{c}{a} y_0 \quad \text{and} \quad w_0 = \frac{d}{a} z_0.$$  

By uniqueness of the solution $(u, v, w)$ to (2.2)-(2.5), it is clear that a solution with (say) $u_0 = 0$ will have $u(t) \equiv 0$ for all time $t$. This observation leads to the following lemma.

**Lemma 2.1.** The $uv, vw,$ and $uw$-coordinate planes are invariant under the flow of system (2.2)-(2.5).

**Theorem 2.2.** If $u_0 \geq 0, \ v_0 \geq 0$ and $w_0 \geq 0$, then there exists a unique solution $(u(t), v(t), w(t))$ of system (2.2)-(2.5) such that for all $t > 0, u(t) \geq 0, v(t) \geq 0$ and $w(t) \geq 0$. Furthermore, there exists $C(u_0, v_0, w_0) > 0$ independent of $t$ such that for all $t > 0,$

$$u(t) + \frac{E}{BE + FC} v(t) + \frac{C}{BE + FC} w(t) \leq C(u_0, v_0, w_0).$$ \hspace{1cm} (2.6)

**Proof.** Let $f_1, f_2$ and $f_3$ be those functions of $(u, v, w)$ on the right-hand sides of (2.2), (2.3) and (2.4), respectively. Then since each $f_i$ is locally Lipschitz continuous in $(u, v, w)$, the Picard theorem guarantees a unique solution $(u(t), v(t), w(t))$ which is defined on $(0, \tau)$ for some $\tau > 0$. We claim $\tau = \infty$.

Since $u_0 \geq 0, \ v_0 \geq 0$ and $w_0 \geq 0$, invoking Lemma 2.1 we get

$$u(t) \geq 0, \ v(t) \geq 0 \quad \text{and} \quad w(t) \geq 0$$

for $t \in (0, \tau)$.

Now considering (2.2) and (2.3), then (2.2) and (2.4), taken together, it follows that

$$Bu' + v' = Bu - Buw - bu^2 - Av - Cv \quad \text{and} \quad Fu' + w' = Fu - Fuv - Fu^2 - Dw + Ev,$$

from which we obtain

$$(BE + FC)u' + Ev' + Cw' = BEu - BEuw - BEu^2 - AEv + FCu - FCuv - FCu^2 - CDw.$$  

This implies that

$$u' = \frac{E}{BE + FC} v(t) + \frac{C}{BE + FC} w(t) \leq C(u_0, v_0, w_0).$$  \hspace{1cm} (2.7)
Since \( u \geq 0, v \geq 0, w \geq 0 \), the Young inequality applied to (2.7) gives

\[
(u' + \frac{E}{BE + FC} v' + \frac{C}{BE + FC} w' + u + \frac{AE}{BE + FC} v + \frac{CD}{BE + FC} w) \leq 1.
\]

Let \( m_1 = \min\{1, A, D\} \) and define the function \( k \) by

\[
k(t) = u(t) + \frac{E}{BE + FC} v(t) + \frac{C}{BE + FC} w(t).
\]

Then inequality (2.8) implies that

\[
k' + m_1 k \leq 1.
\]

Letting the constant \( C \) be given by

\[
C(u_0, v_0, w_0) = u(0) + \frac{E}{BE + FC} v(0) + \frac{C}{BE + FC} w(0) + \frac{1}{m_1},
\]

Gronwall’s lemma applied to (2.9) yields

\[
k(t) \leq k(0)e^{-m_1 t} + \frac{1}{m_1} \leq k(0) + \frac{1}{m_1} = C(u_0, v_0, w_0)
\]

for \( t \in (0, \tau) \).

Since \( C(u_0, v_0, w_0) \) is independent of \( t \), the solution \( (u(t), v(t), w(t)) \) may be extended to all \( t > 0 \). Therefore, \( \tau = \infty \) and inequality (2.10) establishes (2.6). □

3. Analysis of the Proposed Scheme

In this section, we consider a semi-implicit finite difference scheme to approximate the solution of (2.2)-(2.5).

Consider the sequence \( \{t_i\} \) of time steps on \([0, \infty)\) given by

\[
\Omega_t = \{t_i \mid t_i = i \Delta t, \ i = 1, 2, \ldots \},
\]

where \( \Delta t \) is a fixed real number whose size will be given later.

Setting \( u^0 = u_0, v^0 = v_0 \) and \( w^0 = w_0 \), we propose the following difference scheme for (2.2)-(2.5).

\[
\frac{u^{k+1} - u^k}{\Delta t} = u^k - (u^{k+1})^2 + u^{k+1} v^k - u^{k+1} w^k
\]

\[
\frac{v^{k+1} - v^k}{\Delta t} = -A v^k + B u^{k+1} v^k - C v^{k+1} w^k
\]

\[
\frac{w^{k+1} - w^k}{\Delta t} = -D w^k + E u^{k+1} w^k + F v^{k+1} w^k
\]

for \( k = 0, 1, \ldots \).
From (3.2)-(3.4), we generate the numerical approximation. It is

\begin{align}
(3.5) \quad u^0 &= u_0, \quad v^0 = v_0, \quad w^0 = w_0 \\
(3.6) \quad u^{k+1} &= \frac{(1 + \Delta t - \Delta tu^k)u^k}{1 + (v^k + w^k)\Delta t} \\
(3.7) \quad v^{k+1} &= \frac{(1 - A\Delta t + Bu_{k+1}\Delta t)v^k}{1 + Cw^k\Delta t} \\
(3.8) \quad w^{k+1} &= [1 - D\Delta t + (Ev_{k+1} + Fw_{k+1})\Delta t]w^k
\end{align}

for \( k = 0, 1, 2, \ldots \). 

**Remark 3.1.** That we use \( u^{k+1}, v^{k+1} \) and \( w^{k+1} \) in (3.2)-(3.4) in combination with \( u^k, v^k \) and \( w^k \) means that the scheme is semi-implicit. Choosing this form for discretization of (2.2)-(2.5) will be shown to not only preserve the nonnegativity of the numerical solution for small \( \Delta t \), but also to ensure stability.

**Remark 3.2.** The same analysis that follows for (3.2)-(3.4) can be applied to a food web with hierarchal predation for any number of levels, meaning where there is one basal species, one top species and any number of intermediate species with each successive one preying on the previous ones. For example, in the case of two intermediate species with populations \( v \) and \( w \) with top predator population \( z \), the generalization of (3.2)-(3.4) for constants \( a_i > 0 \) takes the form

\begin{align}
(3.9) \quad \frac{u^{k+1} - u^k}{\Delta t} &= a_1 u^k - a_2 (u^k)^2 - a_3 u^{k+1} v^k - a_4 u^{k+1} w^k - a_5 u^{k+1} z^k \\
\frac{v^{k+1} - v^k}{\Delta t} &= -a_6 u^k + a_7 u^{k+1} v^k - a_8 v^{k+1} w^k - a_9 v^{k+1} z^k \\
\frac{w^{k+1} - w^k}{\Delta t} &= -a_{10} w^k + a_{11} u^{k+1} w^k + a_{12} v^{k+1} w^k - a_{13} w^{k+1} z^k \\
\frac{z^{k+1} - z^k}{\Delta t} &= -a_{14} z^k + a_{15} u^{k+1} z^k + a_{16} v^{k+1} z^k + a_{17} w^{k+1} z^k
\end{align}

for \( k = 0, 1, 2, \ldots \). Put simply, for the equations of species listed in ascending alphabetical order in the food web by hierarchy, in each interaction term between species the time step indexed to \( k + 1 \) in the first variable and has index \( k \) in the second when the terms are multiplied left to right in alphabetical order. The same properties we show to hold for (3.5)-(3.8) also apply to (3.9) under similar constraints; one must simply choose small enough \( \Delta t \) due to complications arising from so many unassigned coefficients.

**Theorem 3.3.** For the difference scheme (3.5)-(3.8),

(I) If \( u_0 \geq 1, v_0 \geq 0 \) and \( w_0 \geq 0 \), and if \( \Delta t \leq \min \left\{ \frac{1}{A}, \frac{1}{B}, \frac{1}{2000-1} \right\} \), then \( 0 \leq u^k \leq u_0, \quad v^k \geq 0 \) and \( w^k \geq 0 \) for \( k = 0, 1, 2, \ldots \).

(II) If \( 0 \leq u_0 \leq 1, v_0 \geq 0 \) and \( w_0 \geq 0 \), and if \( \Delta t \leq \min \left\{ \frac{1}{A}, \frac{1}{B}, 1 \right\} \), then \( 0 \leq u^k \leq 1, \quad v^k \geq 0 \) and \( w^k \geq 0 \) for \( k = 0, 1, 2, \ldots \).

(III) If \( \Delta t \) is chosen as in (I) or (II), then there exist constants \( C_0, \quad C_1 \) and \( C_2 \) which are independent of time \( t \) such that

\begin{align}
(3.10) \quad u^k + C_1 v^k + C_2 w^k \leq C_0
\end{align}

for \( k = 0, 1, 2, \ldots \).
Proof. First we prove (I) by induction.

If \( u_0 \geq 0, v_0 \geq 0 \) and \( w_0 \geq 0 \), then the statement is true for \( k = 0 \). Assume that the statement is true for \( u^k \); that is, \( 0 \leq u^k \leq u_0, \ v^k \geq 0 \) and \( w^k \geq 0 \).

Now consider \( u^{k+1} \). Since

\[
(3.11) \quad u^{k+1} = \frac{(1 + \triangle t - \triangle t u^k) u^k}{1 + (v^k + w^k) \triangle t} \geq \frac{(1 + \triangle t - \triangle t u_0) u^k}{1 + (v^k + w^k) \triangle t},
\]

then because \( \triangle t \leq \frac{1}{2u_0 - 1} \), \( u^k \geq 0 \), \( v^k \geq 0 \) and \( w^k \geq 0 \), \( (3.11) \) implies that

\[
(3.12) \quad u^{k+1} \geq 0.
\]

Now, the function \( g \) defined by \( g(u^k) = (1 + \triangle t - \triangle t u^k) u^k \) is quadratic in \( u^k \), so that \( g \) has a maximum at \( u^k = \frac{1}{2 \triangle t} \). Since \( \triangle t \leq \min\{\frac{1}{2}, \frac{1}{2u_0 - 1}\} \) and \( 0 \leq u^k \leq u_0 \leq \frac{1 + \triangle t}{2 \triangle t} \), we arrive at

\[
(3.13) \quad u^{k+1} = \frac{(1 + \triangle t - \triangle t u^k) u^k}{1 + (v^k + w^k) \triangle t} \leq \frac{(1 + \triangle t - \triangle t u_0) u_0}{1 + (v^k + w^k) \triangle t} \leq u_0.
\]

Hence, combining \( (3.12) \) and \( (3.13) \) we get that \( 0 \leq u^{k+1} \leq u_0 \), so that by induction, \( 0 \leq u^k \leq u_0 \) holds for all \( k \).

Since \( \triangle t \leq \min\{\frac{1}{2}, \frac{1}{2u_0 - 1}\} \) and \( u^{k+1} \geq 0 \), using the assumption \( v^k \geq 0 \) and \( w^k \geq 0 \) together with \( (3.7) \) we get

\[
(3.14) \quad v^{k+1} = \frac{(1 - A \triangle t + B u^{k+1} \triangle t) u^k}{1 + C w^k \triangle t} \geq 0,
\]

Similarly, we have

\[
(3.15) \quad w^{k+1} = [1 - D \triangle t + (E u^{k+1} + F v^{k+1} \triangle t)] w^k \geq 0.
\]

Taking \( (3.13), (3.14) \) and \( (3.15) \) together, we see that part (I) of the theorem has been established.

Since the proof for part (II) is similar to that for (I), we omit it here.

We now turn to part (III): Multiplying \( (3.2) \) by \( B \) and adding it to equation \( (3.3) \), we get

\[
(3.16) \quad B u^{k+1} + v^{k+1} + B(u^k)^2 \triangle t + A v^k \triangle t + C v^{k+1} w^k \triangle t + B u^{k+1} k \triangle t + B u^{k+1} v^k \triangle t = B u^k + v^k + B u^k \triangle t.
\]

Similarly, multiplying \( (3.2) \) by \( E \) and adding it to \( (3.4) \) gives

\[
(3.17) \quad E u^{k+1} + w^{k+1} + E(u^k)^2 \triangle t + D w^k \triangle t + E u^{k+1} v^k \triangle t + E w^k u^{k+1} \triangle t = E u^k + w^k + E u^k \triangle t + F v^{k+1} w^k \triangle t.
\]

If we now multiply \( (3.16) \) by \( F \) and \( (3.17) \) by \( C \) and add them together, we get

\[
(3.18) \quad (BF + CE) u^{k+1} + F v^{k+1} + C w^{k+1} + (BF + CE)(u^k)^2 \triangle t + A F v^k \triangle t + D C w^k \triangle t + (BF + CE) a^{k+1} v^k \triangle t + (BF + CE) w^k u^{k+1} \triangle t = (BF + CE) u^k + F v^k + C w^k + (BF + CE) u^k \triangle t.
\]
Since \( u^k, v^k, w^k \geq 0 \) for \( k = 0, 1, 2, \ldots \), then recalling (3.5), equation (3.18) implies that
\[
(BF + EC)u^{k+1} + Fv^{k+1} + Cw^{k+1} + (BF + EC)(u^k)^2 \Delta t
\]
\[
+ AFv^k \Delta t + DWC w^k \Delta t
\]
\[
\leq (BF + CE)u^k + Fv^k + Cw^k + (BF + CE)u^k \Delta t.
\]
(3.19)

Setting \( M_1 = \frac{F}{BF + EC} \) and \( M_2 = \frac{C}{BF + EC} \), inequality (3.19) implies that
\[
u^{k+1} + M_1 v^{k+1} + M_2 w^{k+1} + (u^k)^2 \Delta t
\]
\[
+ AM_1 v^k \Delta t + DM_2 w^k \Delta t
\]
\[
\leq u^k + M_1 v^k + M_2 w^k + u^k \Delta t.
\]
(3.20)

Using \( 2u^k - 1 \leq (u^k)^2 \), (3.20) implies
\[
u^{k+1} + M_1 v^{k+1} + M_2 w^{k+1} + u^k \Delta t
\]
\[
+ AM_1 v^k \Delta t + DM_2 w^k \Delta t
\]
\[
\leq u^k + M_1 v^k + M_2 w^k + \Delta t.
\]
(3.21)

Now let \( M_3 = \min\{1, A, D\} \) and \( N^k = u^k + M_1 v^k + M_2 w^k \). From inequality (3.21), we have
\[
N^{k+1} + M_3 N^k \Delta t \leq N^k + \Delta t,
\]
which leads to
\[
N^{k+1} \leq (1 - M_3 \Delta t)N^k + \Delta t
\]
\[
\leq (1 - M_3 \Delta t)^2 N^{k-1} + (1 - M_3 \Delta t)\Delta t + \Delta t
\]
\[
\vdots
\]
\[
\leq (1 - M_3 \Delta t)^{k+1} N^0 + (1 - M_3 \Delta t)^k \Delta t + \ldots + \Delta t
\]
\[
= (1 - M_3 \Delta t)^{k+1} N^0 + \frac{1 - (1 - M_3 \Delta t)^{k+1}}{M_3}
\]
\[
\leq N^0 + \frac{1}{M_3}
\]
for \( k = 0, 1, 2, \ldots \).

Letting \( C_0 = N^0 + \frac{1}{M_3} \), \( C_1 = M_1 \) and \( C_2 = M_2 \) and invoking (3.23), we arrive at
\[
u^k + C_1 v^k + C_2 w^k \leq C_0
\]
(3.24)
for \( k = 0, 1, 2, \ldots \). This completes the proof.

Next we consider error estimates for the proposed scheme.

**Theorem 3.4.** If \( u_0 \geq 0, v_0 \geq 0 \) and \( w_0 \geq 0 \), then for any \( T > 0 \), the solution of the difference scheme (3.5)-(3.8) converges to the solution of the system (2.2)-(2.5) uniformly on \([0, T]\) as \( \Delta t \to 0 \) with convergence rate \( O(\Delta t) \).

**Proof.** Let \((u(t), v(t), w(t)) \) be the solution of the system (2.2)-(2.5). We use the notation
\[
\Omega_t = \{t_k | t_k = k\Delta t, 0 \leq k \leq N\},
\]
where $\Delta t = T/N$.

(3.25) $U^i = u(t_i), \ V^i = v(t_i), \ W^i = w(t_i)$ for $i = 0, 1, 2, \ldots N$.

From the Taylor expansion of $(u, v, w)$, we have the approximations

(3.26) $u'(t_k) = \frac{U^{k+1} - U^k}{\Delta t} + O(\Delta t)$

(3.27) $v'(t_k) = \frac{V^{k+1} - V^k}{\Delta t} + O(\Delta t)$

(3.28) $w'(t_k) = \frac{W^{k+1} - W^k}{\Delta t} + O(\Delta t)$

for $k \geq 0$. Furthermore, equations (2.2)-(2.4) imply the estimates

(3.29) $\frac{U^{k+1} - U^k}{\Delta t} = U^k - (U^k)^2 - U^kV^k + O(\Delta t)$

(3.30) $\frac{V^{k+1} - V^k}{\Delta t} = AV^k + BU^kV^k - CV^kW^k + O(\Delta t)$

(3.31) $\frac{W^{k+1} - W^k}{\Delta t} = -DW^k + EU^kW^k + FW^kV^k + O(\Delta t)$.

We define error terms

(3.32) $X^k = U^k - u^k, \ Y^k = V^k - v^k, \ Z^k = W^k - w^k$ for $k = 0, 1, \ldots N$.

Then from (3.5), note that

(3.33) $X^0 = 0, \ Y^0 = 0, \text{ and } Z^0 = 0$.

For $k \geq 0$, (3.2)-(3.4) and (3.29)-(3.31) imply that

(3.34) $X^{k+1} = X^k + \Delta t[X^k - (U^k)^2 + (u^k)^2 - U^kV^k + u^{k+1}v^k - U^kW^k + u^{k+1}w^k + O(\Delta t)]$

(3.35) $Y^{k+1} = Y^k + \Delta t[-AY^k + BU^kV^k - Bu^{k+1}v^k - CV^kW^k + Cv^{k+1}w^k + O(\Delta t)]$,

and

(3.36) $Z^{k+1} = Z^k + \Delta t[-DZ^k + EU^kW^k - Eu^{k+1}w^k + FV^kW^k - Fu^{k+1}w^k + O(\Delta t)]$.

From Theorems 2.2 and 3.3, there exists a constant $\alpha > 0$ such that

(3.37) $U^k, V^k, W^k, u^k, v^k, w^k \leq \alpha$

for all $k = 0, 1, 2, \ldots N$. Therefore,

(3.38) $- (U^k)^2 + (u^k)^2 = |U^k + u^k||X^k| \leq 2\alpha|X^k|$

(3.39) $- U^kV^k + u^{k+1}v^k \leq |U^kV^k - U^kV^k| + |U^kV^k - u^kV^k| + |u^kV^k - u^{k+1}v^k|$

$\leq \alpha|Y^k| + \alpha|X^k| + O(\Delta t)$, and
4. Numerical Results and a Hopf Bifurcation

In this section, we summarize properties of the linearized system in Section 4.1. Then in Section 4.2 we carry out some numerical experiments to demonstrate the stability of the proposed difference scheme (3.5)-(3.8) and show that it gives reasonable numerical solutions to (2.2)-(2.5). In Section 4.3, we give some final remarks about a Hopf bifurcation for the system.
4.1. The Linearization. For steady state solutions to (2.2)-(2.5) we are only interested in nonnegative solutions. Recalling that $A, \ldots, F$ are positive, we restrict our attention to the five steady states

\begin{align}
(0, 0, 0), (1, 0, 0), \left(\frac{D}{E}, 0, 1 - \frac{D}{E}\right), \left(\frac{A}{B}, 1 - \frac{A}{B}, 0\right) \text{ and } (h_1, h_2, h_3).
\end{align}

We call the coordinate triples in (4.1) $P_1, \ldots, P_5$, respectively. Here,

\begin{align}
(4.2) \quad h_1 &= \frac{AF - CD + CF}{BF - CE + CF}, \\
(4.3) \quad h_2 &= -\frac{AE + BD + CD - CE}{BF - CE + CF} \quad \text{and} \\
(4.4) \quad h_3 &= -\frac{AE + AF + BD - BF}{-BF + CE - CF}.
\end{align}

Coordinates of all five steady states are nonnegative if $A < B$, $D < E$ and $A \cdot B < AF - CD + CF + BF - CE + CF < D$. The linearization of (2.2)-(2.5) at a steady state solution $(u_0, v_0, w_0)$ is given by the equation

\begin{align}
\begin{pmatrix}
u' \\
w'
\end{pmatrix} = M(u_0, v_0, w_0) \begin{pmatrix} u - u_0 \\
v - v_0 \\
w - w_0
\end{pmatrix},
\end{align}

where $M$ is defined by

\begin{align}
M(u_0, v_0, w_0) = \begin{pmatrix}
1 - 2u_0 - v_0 - w_0 & -u_0 & -u_0 \\
Bv_0 & -A + Bu_0 - Cw_0 & -Cv_0 \\
Ew_0 & Fw_0 & -D + Eu_0 + Fv_0
\end{pmatrix}.
\end{align}

We determine stability of each steady state $P_i$ by considering, where possible, the eigenvalues $\lambda_{1}^{(i)}, \lambda_{2}^{(i)}$ and $\lambda_{3}^{(i)}$ for each matrix $M(P_i)$.

I. $P_1 = (0, 0, 0)$: $M(P_1)$ has eigenvalues

$\lambda_1^{(1)} = 1$, $\lambda_2^{(1)} = -A$ and $\lambda_3^{(1)} = -D$,

so $P_1$ is an unstable saddle point.

II. $P_2 = (1, 0, 0)$: $M(P_2)$ has eigenvalues

$\lambda_1^{(2)} = -1$, $\lambda_2^{(2)} = -A + B$ and $\lambda_3^{(2)} = -D + E$,

so $P_2$ is stable if $A > B$ and $E < D$ and unstable if $A < B$ or $E > D$.

III. $P_3 = \left(\frac{D}{B}, 0, 1 - \frac{D}{B}\right)$: $M(P_3)$ has eigenvalues

$\lambda_1^{(3)} = -\frac{AE + BD + CD - CE}{E},$

$\lambda_2^{(3)} = -\frac{D + \sqrt{D^2 - 4DE(E - D)}}{2E}$ \quad \text{and}

$\lambda_3^{(3)} = -\frac{D - \sqrt{D^2 - 4DE(E - D)}}{2E},$

so $P_3$ is stable if $AE + CE > BD + CD$ and $E > D$. It is unstable if $A + C < D(B + C)/E$. 


4.2. Some Numerical Experiments. For the numerical scheme (2.2)-(2.5), we divide the experiments into two parts: In Figures 1-4, we allow at least one zero initial condition, while in Figures 5-9, we consider the case where all initial data are positive. Throughout, we choose $\Delta t = 0.01$, which readily agrees with requirements in Theorem 3.3.

Figures 1-3. We choose $A = 1, B = 4, C = 1, D = 1, E = 2$ and $F = 1$. By the preceding discussion of steady states, this gives possible equilibrium solutions for (2.2)-(2.4) of

\[(4.6) \quad (0, 0, 0), (1, 0, 0), (1/4, 3/4, 0), (1/2, 0, 1/2) \text{ and } (1/3, 1/3, 1/3).
\]

Although the only stable steady state of these is the last one, all nonzero initial conditions would be necessary for an orbit to approach it since, as noted in Lemma 2.1, the coordinate planes are invariant under the flow of (2.2)-(2.5). We describe each figure in some more detail as follows.

**Figure 1:** We choose initial data $u(0) = 1/2, v(0) = 0$ and $w(0) = 0$. The figure shows that $v^k = 0$ and $w^k = 0$ for all $k = 0, 1, 2, \ldots$, while $u^N \to 1$ as $N \to \infty$. The second equilibrium in (4.6) is approached, which means that the population of the basal species approaches carrying capacity in absence of the intermediate and top species as expected.

**Figure 2:** Initial conditions are $u(0) = 0, v(0) = 2$ and $w(0) = 2$. The figure shows that as $v^N \to 0$, so does $w^N \to 0$ as $N \to \infty$. The top species will remain as long as there is an intermediate species to prey on, while the intermediate species dies off exponentially in absence of a basal species. The steady state $(0, 0, 0)$ in (4.6) is approached with the given initial data.

**Figure 3:** Initial conditions in this figure are $u(0) = 2, v(0) = 0$ and $w(0) = 2$. We see that $u^N \to D/E = 1/2$ while $w^N \to 1 - D/E = 1/2$ as $N \to \infty$. Populations of species oscillate as food web populations progress toward equilibrium. The fourth steady state in (4.6) is approached.

**Figure 4:** Here we choose $A = 1, B = 4, C = 1, D = 2, E = 1$ and $F = 1$. This gives rise to $(0, 0, 0), (1, 0, 0)$ and $(1/4, 3/4, 0)$ as equilibria of (2.2)-(2.4). We choose initial conditions $u(0) = 2, v(0) = 0$ and $w(0) = 2$. By invariance of the coordinate planes, as $N \to \infty$ the steady state $(1, 0, 0)$ is approached by
Figure 1. Solutions for $u(0) = 0.5$, $v(0) = 0$ and $w(0) = 0$.

Figure 2. Solutions for $u(0) = 0$, $v(0) = 2$ and $w(0) = 2$.

$(u^N, v^N, w^N)$. In contrast to Figure 3, Figure 4 shows that if the death rate of the top species is too large, this species will go to extinction, at least compared to the system with relatively large interaction rate with the basal species compared to death rate for the top species.

Remark 4.1. The numerical results from Cases 1—4 coincide with the theoretical results for a system involving two species.
Remark 4.2. If \( u(0) > 0, v(0) > 0, w(0) = 0 \), we have similar results to those in Cases 3 and 4, so we omit them here.

Figure 5: We choose \( A = 1, B = 4, C = 1, D = 2, E = 1 \) and \( F = 1 \), giving rise to equilibria for (2.2)-(2.4) of \((0, 0, 0)\), \((1, 0, 0)\) and \((1/4, 3/4, 0)\) as those with all coordinates nonnegative. We choose initial data \( u(0) = 2, v(0) = 2 \) and \( w(0) = 2 \). The figure suggests that since the death rate \( D \) of the top species is relatively
larger than the interaction rate $E$ between the basal and top species, and if the death rate $A$ of the intermediate species is relatively smaller than the interaction rate $B$ between the basal and intermediate species, then the population of the basal species will approach $A/B = 1/4$ while the intermediate species approaches $1 - A/B$. The top species becomes extinct.

Figure 6: This figure has $A = 2$, $B = 1$, $C = 1$, $D = 1$, $E = 2$ and $F = 1$, so equilibria of (2.2)-(2.4) are $(0, 0, 0)$, $(1, 0, 0)$, and $(1/2, 0, 1/2)$. With initial conditions chosen as $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$, $(u^N, v^N, w^N) → (1/2, 0, 1/2)$. In general, if the death rate $D$ of the top species is smaller than the interaction rate $E$ between the basal and top species and the death rate $A$ of the intermediate species is larger than the interaction rate $B$ between the basal and intermediate species, then the population of the basal species will approach $D/E$, the population of the top species will approach $1 - D/E$ and the intermediate species declines to extinction.

Figure 7: Here, $A = 2$, $B = 1$, $C = 1$, $D = 2$, $E = 1$ and $F = 1$, so that the only possible equilibria of (2.2)-(2.4) are $(0, 0, 0)$ and $(1, 0, 0)$. With initial conditions of $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$ and given that only $(1, 0, 0)$ is stable, this is the one approached over time. The figure confirms that if the death rate $A$ of the intermediate species is larger than the interaction rate $B$ between the basal and top species, and the death rate $D$ of the top species is larger than the interaction rate $E$ between the basal and top species, then the population of the basal species will approach the carrying capacity while the intermediate and top species become extinct.

Figure 8: Choosing $A = 1$, $B = 8$, $C = 1$, $D = 1$, $E = 4$ and $F = 1$ gives rise to $(0, 0, 0)$, $(1, 0, 0)$, $(1/8, 7/8, 0)$, $(1/4, 0, 3/4)$ and $(1/5, 1/5, 3/5)$ as steady states of (2.2)-(2.4). With initial conditions $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$
and given that the only stable steady state is \((1/5, 1/5, 3/5)\), the figure confirms that \((u^N, v^N, w^N)\) approaches the steady state solution \(P_5 = (h_1, h_2, h_3) = (1/5, 1/5, 3/5)\) as \(N \to \infty\).

In general, if (a) the death rate \(A\) of the intermediate species is exceeded by the interaction rate \(B\) between basal and intermediate species, (b) the death rate \(D\) of the top species is exceeded by the interaction rate \(E\) between basal and top species, and finally (c) if the ratio \(A/B\) of the death rate and the interaction
rate between the basal and intermediate species is less than the ratio $D/E$ of the death rate and the interaction rate between the basal and top species, then there exists a stable equilibrium where all three species can coexist without extinction.

Figure 9: With $A = 1$, $B = 10$, $C = 1$, $D = 1$, $E = 4$ and $F = 1$, all equilibria are unstable. Choosing $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$, the figure confirms that $(u_N, v_N, w_N)$ will not approach (for example) the steady state solution $(h_1, h_2, h_3) = (1/7, 3/7, 3/7)$ as $N \to \infty$ — although $A/B < D/E$ — but rather a periodic solution. This suggests a limit cycle. We will investigate this next.

4.3. A Hopf Bifurcation. We claim that for an appropriate choice of constants $A$ and $C-F$, a value of $B$ exists across which a periodic orbit arises through a change in the stability properties; specifically, there is a Hopf bifurcation arising at this $B$-value.

To demonstrate this, we fix $A = 1$, $C = 1$, $D = 1$, $E = 4$, $F = 1$ and consider solutions of (2.2)-(2.5) as the value of $B$ is varied. The steady state of interest in this case is $P_B = (\frac{B}{B-3}, \frac{B-7}{B-3}, \frac{3}{B-3})$, from which we extract the initial requirement that $B > 7$ so that this is a first-octant steady-state equilibrium.

The matrix $M(P_B)$ from (4.5) of the linearization about $P_B$ has eigenvalues $\lambda$ that are roots of the characteristic polynomial

\begin{equation}
    p_B(\lambda) = \lambda^3 + \frac{1}{b-3} \lambda^2 + \frac{b^2 - 4b - 9}{(b-3)^2} \lambda + \frac{3b - 21}{(b-3)^2}.
\end{equation}

The Routh-Hurwitz stability criterion ensures that the roots of $p_B$ lie in the negative complex half-plane as long as each coefficient is positive and the product of the coefficients of $\lambda$ and $\lambda^2$ exceeds the product of the coefficient of $\lambda^3$ and the constant term. Solving these simple inequalities shows that $2 + \sqrt{13} < B < 9$ which, together with the initial requirement that $B > 7$ means that $p_B$ has three roots — two complex conjugates and one real — with negative real part as long as $7 < B < 9$. 

Figure 8. Solutions for $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$. 

Figure 9. Solutions for $u(0) = 2$, $v(0) = 2$ and $w(0) = 2$.

For $B = 9$, we get eigenvalues of $M(P_9)$ in (4.5) to be $-1/6$ and $\pm i$. For $B > 9$, roots of $p_B$ have the form $\{\lambda_1, \lambda_2, \lambda_3\}$, where $\lambda_1 < 0$ while $\lambda_2$ and $\lambda_3$ are conjugates with positive real part.

Remark 4.3. The foregoing computations show that the system (2.2)-(2.5) undergoes a Hopf bifurcation for $A = 1$, $C = 1$, $D = 1$, $E = 4$, $F = 1$ across $B = 9$. For $7 < B < 9$, the system has a stable equilibrium point $P_B$ as described above whereas $P_9$ is a stable center. For $B > 9$ solutions of the system approach a limit cycle as demonstrated in Figure 9.

References

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