Rose-Hulman Undergraduate Mathematics Journal

Volume 23
Issue 1

Article 9

# Numerical Analysis of a Model for the Growth of Microorganisms

Alexander Craig Montgomery
craigmontgomery12@gmail.com

Braden J. Carlson
*Southern Utah University*, bradenjcarlson@live.com

ℝose-Hulman Undergraduate Mathematics Journal

Volume 23, Issue 1, 2022

# Numerical Analysis of a Model for the Growth of Microorganisms

By *Craig Montgomery* and *Braden Carlson*

**Abstract.** A system that arises in a model for the growth of microorganisms in a chemostat is studied. A new semi-implicit numerical scheme is proposed. It is proven that the scheme is uniquely solvable and unconditionally stable. The convergence rate of the numerical solution to the true solution of the system is also given.

## 1 Introduction

A chemostat is a device that is used to measure the amount in the form of biomass or concentration of microorganisms by controlling its inherent biological reactions. Generally, a fresh medium infused with nutrients is continuously added to a vessel containing a particular amount of a microorganism, the medium is thoroughly mixed, then outflow of the mixture occurs at the same rate so that the volume of the liquid in the chemostat medium remains constant. The mixture that is removed continuously from the chemostat contains nutrients and microorganisms together with their metabolic end products. By controlling the rate the medium is added and measuring the biomass of the outflow produced, the growth rate of the microorganisms in the medium can be measured. This device was introduced in the field of microbiology some 70 years ago by Monod, Novick, and Szilard (see [7] and [11]).

Since the introduction of the chemostat, several mathematical models in the form of both ordinary and integro-differential equations have been introduced, such as those found in [2], [5], [13], [14], and references therein. As many as eight years before Monod had a hand in introducing the chemostat to the field of microbiology [9], he observed empirically rather than theoretically that the growth rate of microorganisms in an aqueous environment with known concentration of a limiting nutrient is well-approximated by what has come to be known as the *empirical Monod equation*. Growth that follows this model under its proposed conditions is said to follow *Monod kinetics*. The empirical Monod equation will be introduced below, where it is included in a system of differential equations. For this and many other contributions, the biochemist Jacques Monod (1910-1976) was awarded the Nobel Prize in Physiology or Medicine in 1965.

*Mathematics Subject Classification.* 92C40, 92E20, 65L06

*Keywords.* monod kinetics, differential equations, mathematical biology

In [4], a system of ordinary differential equations is used to model over time the growth of microorganisms as it relates to nutrient concentration in the chemostat under the assumption of Monod kinetics. This system is

$$\begin{cases} x' = [\mu(y) - d] \cdot x, \\ y' = d \cdot (c - y) - b \cdot \mu(y) x. \end{cases} \tag{1}$$

Here, the derivative is with respect to time $t$, $x$ denotes microorganism concentration in the chemostat, while $y$ is a measure of nutrient concentration. The function

$$\mu(y) = \frac{\mu_{max}}{\mathrm{K} + y} y$$

is the Monod equation to model the growth of the microorganisms referred to above. We note that $\mu_{max}$ is the maximum growth rate of the particular microorganism, and K is the value of $y$ when $\mu = 0.5\mu_{max}$.

In addition, $b$ is the (inverse of the) yield constant and $d$ is the dilution coefficient. That the dilution coefficient is $d$ implies that $[\mu(y) - d] \cdot x$ measures the amount of microorganisms removed from the chemostat per unit time, while if $c$ is the constant inflow rate of the nutrient, $d \cdot (c - y)$ corresponds to the rate of nutrient outflow. Here, $b, c, d, \mathrm{K}, \mu_{\max} \geq 0$.

Nondimensionalizing (1) as described in [10], the number of parameters in (1) can be reduced by setting

$$\tau = dt, \; x(t) = \frac{d \cdot \mathrm{K}}{b\mu_{max}} u(\tau), \text{ and } \; y(t) = \mathrm{K} v(\tau).$$

Applying these substitutions then renaming $\tau$ back to $t$, (1) becomes

$$\begin{cases} u' = u\left(\frac{a_1 v}{1+v} - 1\right) \\ v' = \frac{-uv}{1+v} - v + b_1 \end{cases} \tag{2}$$

where $a_1 = \mu_{max}/d$ and $b_1 = c/\mathrm{K}$, ensuring still that $a_1, b_1 \geq 0$. In addition, $u$ is a scaled measure of the density of microorganisms and $v$ is likewise a rescaling of the nutrient concentration $y$.

Throughout the rest of this paper, (2) will be studied. In Section 2, steady-state solutions of (2) and their stability are discussed using methods from [10] and [12]. In Section 3, a nonstandard finite difference method is proposed as a numerical approximation scheme to (2) to investigate the solution pair $(u(t), v(t))$ to (2). It is proven that this scheme is unconditionally uniquely solvable and stable. The properties of the numerical scheme is investigated. In Section 4, a proof that the stable, nonstandard numerical approximation of converges to the true solution pair $(u(t), v(t))$ of (2) as $\Delta t \to 0$. In Section 5, numerical experiments are presented using the proposed difference scheme to examine the nature of the true solution to (2).

# 2 Stability of Steady-state Solutions

Steady-state solutions are found by setting $u' = v' = 0$ in (2). Depending on the value of $u$, this gives rise to two steady states $(u_0^*, v_0^*)$ and $(u_1^*, v_1^*)$ given by

$$(u_0^*, v_0^*) = (0, b_1) \text{ and } (u_1^*, v_1^*) = \left(a_1 b_1 - \frac{a_1}{a_1 - 1}, \frac{a_1}{a_1 - 1}\right). \tag{3}$$

Setting

$$f(u,v) = u\left(\frac{a_1 v}{1+v} - 1\right) \text{ and } g(u,v) = \frac{-uv}{1+v} - v + b_1$$

from (2) and letting M be the Jacobian, or matrix of partials, of $f$ and $g$ about $(u, v)$ defined by

$$\mathrm{M}(u,v) = \begin{bmatrix} f_u(u,v) & f_v(u,v) \\ g_u(u,v) & g_v(u,v) \end{bmatrix},$$

stability of a steady state solution $(u^*, v^*)$ of (2) depends on the eigenvalues of $\mathrm{M}(u^*, v^*)$ following a standard theorem from [10], which ensures the asymptotic stability of a steady state solution $(u^*, v^*)$ of (2) if and only if the real parts of the eigenvalues of $\mathrm{M}(u^*, v^*)$ are both negative.

Since the determinant det(A) and the trace tr(A) of A are those invariants of a $2 \times 2$ matrix A that are the coefficients of its characteristic polynomial, real parts of eigenvalues of A will be negative, and steady-state solutions stable, if and only if $\det(\mathrm{A}) > 0$ and $\mathrm{tr}(\mathrm{A}) < 0$.

Following (2) for M as described above,

$$\mathrm{M}(u,v) = \begin{bmatrix} f_u(u,v) & f_v(u,v) \\ g_u(u,v) & g_v(u,v) \end{bmatrix} = \begin{bmatrix} \frac{a_1 v}{1+v} - 1 & \frac{a_1 u}{(1+v)^2} \\ -\frac{v}{1+v} & -\frac{u}{(1+v)^2} - 1 \end{bmatrix},$$

and the trace and determinant of $\mathrm{M}(u,v)$ are given by

$$\det(\mathrm{M}(u,v)) = \frac{u}{(1+v)^2} - \frac{a_1 v}{1+v} + 1 \text{ and } \mathrm{tr}(\mathrm{M}(u,v)) = \frac{a_1 v}{1+v} - \frac{u}{(1+v)^2} - 2.$$

The stability of steady state solutions in (3) will be investigated using two cases.

## 2.1 Case I

Computation of the invariants of $\mathrm{M}(0, b_1)$ yields

$$\det(\mathrm{M}(0,b_1)) = 1 - \frac{a_1 b_1}{1+b_1} \text{ and } \mathrm{tr}(\mathrm{M}(0,b_1)) = \frac{a_1 b_1}{1+b_1} - 2.$$

Following the stability requirements of the steady state solution $(u_0^*, v_0^*) = (0, b_1)$ leads to conditions

$$1 - \frac{a_1 b_1}{1+b_1} > 0 \text{ and } \frac{a_1 b_1}{1+b_1} - 2 < 0.$$

The conditions are satisfied simultaneously, and hence the steady-state solution

$$(0, b_1) \text{ is stable, if and only if } a_1 < \frac{1}{b_1} + 1.$$

### 2.2 Case II

Turning to the steady-state solution

$$(u_1^*, v_1^*) = \left(a_1 b_1 - \frac{a_1}{a_1 - 1}, \frac{1}{a_1 - 1}\right),$$

since the physical setting requires that both $u_1^*, v_1^* > 0$, it is assumed *a priori* that $a_1 > 1$ and $b_1 > \frac{1}{a_1-1}$. The invariants of $\mathrm{M}(u_1^*, v_1^*)$ are

$$\det((\mathrm{M}(u_1^*, v_1^*)) = \frac{(a_1 - 1)((a_1 - 1)b_1 - 1)}{a_1} \quad \text{and}$$
$$\operatorname{tr}((\mathrm{M}(u_1^*, v_1^*)) = \frac{(a_1 - 1)^2 \left(\frac{1}{a_1-1} - b_1\right)}{a_1} - 1.$$

As previously stated, for stability of the steady state $(u_1^*, v_1^*)$ is necessary and sufficient that $\det((\mathrm{M}(u_1^*, v_1^*)) > 0$ and $\operatorname{tr}((\mathrm{M}(u_1^*, v_1^*)) < 0$. The latter condition is automatically satisfied since $b_1 > \frac{1}{a_1-1}$, while some algebra applied to the determinant yields the same condition. Thus, the steady-state solution

$$(u_1^*, v_1^*) \text{ is stable if and only if } a_1 > \frac{1}{b_1} + 1.$$

## 3 Numerical Approximation By a Nonstandard Difference Scheme

Attempting to apply Euler's method to approximate a numerical solution with $\Delta t = 0.5$ results in the populations diverging when the condition in Case I, $a_1 < \frac{1}{b_1} + 1$, is satisfied despite the guarantee of stability. When the populations instead converge to a positive and negative solution as shown in Figure 1(a), violating required positivity of solutions. When Case II, $a_1 > \frac{1}{b_1} + 1$, is satisfied, stability fails as shown in Figure 1(b).

Although convergence to the correct steady states in Cases I and II seems to occur for choices of much smaller $\Delta t$, it is unclear at which choice for $\Delta t$ Euler's method convergence to the true solutions of (2) and, if so, what the order of convergence is to the true solution. However, through a nonstandard finite difference scheme proposed next convergence to the true solution of (2) can be guaranteed independent of the choice of $\Delta t$, and the order of convergence can be established.

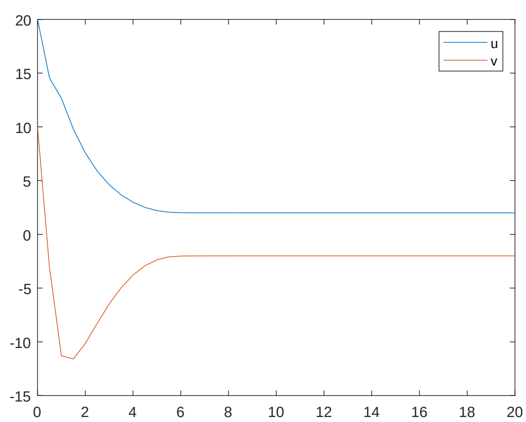


Figure 1(a): For $\Delta t = 0.5, a_1 = .5$, and $b_1 = 2$, $v \to -2$ using Euler's method.

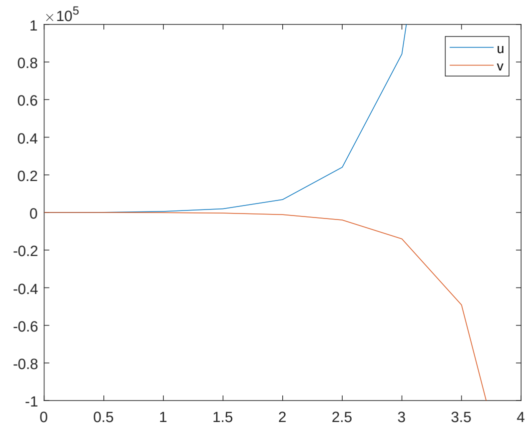


Figure 1(b): For $\Delta t = .5, a_1 = 6$, and $b_1 = 5$, $u, v$ diverge using Euler's method.

Inspired by the methods in [1], [3], and [6], the nonstandard finite difference scheme for approximation of solutions $(u, v)$ to (2) given by

$$\frac{u_{n+1} - u_n}{\Delta t} = \frac{a_1 u_n}{1 + v_n} v_n - u_{n+1}, \tag{4}$$

$$\frac{v_{n+1} - v_n}{\Delta t} = \frac{-u_n v_{n+1}}{1 + v_n} - v_{n+1} + b_1 \tag{5}$$

shows promise in maintaining positivity of the numerical approximation and will show satisfaction of the desirable properties of stability and convergence to the true solution. Solving these for $u_{n+1}$ and $v_{n+1}$ respectively gives

$$u_{n+1} = \frac{(\frac{a_1 v_n \Delta t}{1+v_n} + 1) u_n}{1 + \Delta t}, \tag{6}$$

$$v_{n+1} = \frac{b_1 \Delta t + v_n}{1 + \frac{u_n \Delta t}{1+v_n} + \Delta t}. \tag{7}$$

**Remark:** If both $v_0, u_0 > 0$, induction readily applies to ensure that for all $u_n, v_n > 0$, $n = 1, 2, \ldots$.

### 3.1 Establishing an Upper Bound for $v_n$

**Lemma 3.1.** *For the sequence $\{v_n\}$ defined recursively by $v_0 > 0$ and $v_{n+1}$ defined in (7) for given $\Delta t > 0$, if $b_1 > 0$, then $v_n \le \max\{v_0, b_1\}$ for all $n$, $n = 1, 2, \ldots$.*

*Proof.* For all $n \geq 0$, $\frac{u_n \Delta t}{1+v_n} \geq 0$. Thus, $1 + \frac{u_n \Delta t}{1+v_n} + \Delta t \geq 1 + \Delta t$ implies that

$$\frac{b_1 \Delta t + v_n}{1 + \frac{u_n \Delta t}{1+v_n} + \Delta t} \leq \frac{b_1 \Delta t + v_n}{1 + \Delta t}.$$

Case 1: $v_0 > b_1$. Proceeding inductively, for $n = 0$, $v_0 \leq v_0$, thus $v_n \leq v_0$ is satisfied for $n = 0$. Assuming that $v_k \leq v_0$ for some $k > 0$,

$$v_{k+1} = \frac{b_1 \Delta t + v_k}{1 + \frac{u_k \Delta t}{1+v_k} + \Delta t} \leq \frac{b_1 \Delta t + v_k}{1 + \Delta t} \leq \frac{b_1 \Delta t + v_0}{1 + \Delta t} < \frac{v_0 \Delta t + v_0}{1 + \Delta t} = v_0.$$

This $v_0 > b_1$ implies that $v_n \leq v_0$ for all $n$, $n = 1, 2, \dots$.

Case 2: $v_0 \leq b_1$. Proceeding inductively again, for $n = 0$, $v_0 \leq b_1$ as desired. If for some $k > 0$ it is the case that $v_k \leq b_1$, then

$$v_{k+1} = \frac{b_1 \Delta t + v_k}{1 + \frac{u_k \Delta t}{1+v_k} + \Delta t} \leq \frac{b_1 \Delta t + v_k}{1 + \Delta t} \leq \frac{b_1 \Delta t + b_1}{1 + \Delta t} = b_1.$$

Therefore if $v_0 \leq b_1$, also $v_n \leq b_1$ for all $n$, $n = 1, 2, \dots$.

Thus for any initial $v_0 > 0$, if $\Delta t, b_1 > 0$, mathematical induction guarantees that $v_n \leq \max\{v_0, b_1\}$. □

### 3.2 Results for $\mathbf{a_1 < \frac{1}{b_1} + 1}$

In Section 2.1 it was established that the steady state $(0, b_1)$ was stable if and only if $a_1 < \frac{1}{b_1} + 1$. Several properties related to stability and convergence of the numerical approximation (6)-(7) to solutions $(u, v)$ of (2) may be established when this condition is satisfied.

**Lemma 3.2.** *Suppose in $a_1 < \frac{1}{b_1} + 1$. If the sequence $\{v_n\}$ defined in in (7) satisfies $v_n \leq b_1$ for all $n$, $n = 1, 2, \dots$, then the sequence $\{u_n\}$ defined in (6) satisfies $u_{n+1} < u_n$ for all $n$, $n = 1, 2, \dots$.*

*Proof.* Assume the hypotheses related to $a_1$ and $\{v_n\}$ as stated are satisfied. Then $a_1 - 1 < \frac{1}{b_1}$, and if in addition $v_n \leq b_1$, $(a_1 - 1) v_n < 1$. Thus

$$\frac{a_1 v_n}{1 + v_n} < 1,$$

$$\frac{a_1 v_n \Delta t}{1 + v_n} + 1 < \Delta t + 1, \text{ and}$$

$$\frac{(\frac{a_1 v_n \Delta t}{1+v_n}+1)u_n}{1+\Delta t} < u_n.$$

Therefore, $u_{n+1} < u_n$.

□

**Theorem 3.1.** Suppose that $a_1 < \frac{1}{b_1}+1$. If $v_0 < b_1$, then the sequence $\{u_n\}$ is monotone decreasing and converges to 0.

*Proof.* Lemma 3.1 and Theorem 3.1 ensure that $v_n \le b_1$ for all $n$, $n = 0,1,2,\ldots$. Additionally, Lemma 3.2 implies that $u_{n+1} < u_n$ for all $n$, $n = 0,1,2,\ldots$. Hence, $\{u_n\}$ is a monotone decreasing sequence. The sequence $\{u_n\}$ is also bounded below by zero, and therefore must be convergent to some $L \ge 0$. From equation (4), it follows that

$$\frac{u_{n+1}-u_n}{\Delta t}+u_{n+1} = \frac{a_1 u_n}{1+v_n} v_n. \tag{8}$$

Since $v_n < b_1$ is bounded, by the Bolzano-Weierstrass Theorem, $\{v_n\}$ has a convergent subsequence. If his subsequence is still denoted by $\{v_n\}$, then $v_n \to J$ as $n \to \infty$ for some $J \ge 0$.

Taking limits on both sides of (8),

$$L = a_1 L\left(\frac{J}{1+J}\right).$$

Assuming by way of contradiction that $L \ne 0$, $\frac{1}{a_1} = \frac{J}{1+J}$, so that $J = \frac{1}{a_1-1}$. However, the assumption $a_1 < \frac{1}{b_1}+1$ implies that $\frac{1}{a_1-1} > b_1$, which leads to $J > b_1$. However, $\{v_n\}$ is bounded above by $b_1$, which implies that $J \le b_1$, a contradiction. Thus, it must be that $\{u_n\}$ converges to 0 under the given conditions. □

**Theorem 3.2.** Suppose $a_1 < \frac{1}{b_1}+1$. If $v_0 < b_1$, then the sequence $\{v_n\}$ converges to $b_1$.

*Proof.* By lemma 3.1 and Theorem 3.1, we have $v_n \le b_1$ for all $n$, and

$$\lim_{n\to\infty} u_n = 0.$$

Claim 1: There exists $N_0 > 0$ such that $v_{N_0+1} \ge v_{N_0}$. If the claim is not true, then $v_{n+1} \le v_n$ for all $n$. Thus $v_n$ is a monotone decreasing sequence. Since $0 < v_n \le b_1$, we have $\lim_{n\to\infty} v_n = J_1$, and $J_1 \le v_0$. From equation (7), we have

$$v_{n+1} = \frac{b_1 \Delta t + v_n}{1+\frac{u_n \Delta t}{1+v_n}+\Delta t} \tag{9}$$

Taking the limit of equation (9), we have

$$\mathrm{J}_1 = \frac{b_1 \Delta t + \mathrm{J}_1}{1+\Delta t} \tag{10}$$

Which implies that

$$\mathrm{J}_1 = b_1$$

Therefore $v_0 \geq \mathrm{J}_1 = b_1$. This contradicts that $v_0 < b_1$.

Claim 2: $v_n$ is monotone increasing if $n \geq \mathrm{N}_0$ (This means $v_n$ is monotone eventually increasing). For $n = \mathrm{N}_0$, the conclusion is true. Assume that the conclusion is true for $k \geq \mathrm{N}_0$, we have $v_{k+1} \geq v_k$. We prove that the conclusion is also true for $n = k+1$. In fact, since $u_k$ is monotone decreasing, we have $u_{k+1} \leq u_k$. This and $v_{k+1} \geq v_k$ imply that

$$\frac{1}{1+\frac{u_{k+1}\Delta t}{1+v_{k+1}}+\Delta t} \geq \frac{1}{1+\frac{u_k \Delta t}{1+v_k}+\Delta t} \tag{11}$$

Also, we have

$$b_1 \Delta t + v_{k+1} \geq b_1 \Delta t + v_k \tag{12}$$

Inequalities (11) and (12) imply that

$$\frac{b_1 \Delta t + v_{k+1}}{1+\frac{u_{k+1}\Delta t}{1+v_{k+1}}+\Delta t} \geq \frac{b_1 \Delta t + v_k}{1+\frac{u_k \Delta t}{1+v_k}+\Delta t} \tag{13}$$

thus $v_{k+2} \geq v_{k+1}$. Since $v_n$ is eventually increasing and bounded above, the limit of $v_n$ exists. Taking the limit in (9), we have

$$\lim_{n\to\infty} v_n = b_1$$

This completes the proof. □

**Theorem 3.3.** If $a_1 < 1$, for any $u_0 \geq 0, v_0 \geq 0$, then $(u_n, v_n)$ converges to $(0, b_1)$.

*Proof.* Assume that $a_1 < 1$. Then we have that $\frac{a_1 v_n}{1+v_n} < 1$. Thus $\frac{a_1 v_n \Delta t}{1+v_n} + 1 < 1 + \Delta t$. Recall from equation (6) that

$$u_{n+1} = \frac{(\frac{a_1 v_n \Delta t}{1+v_n}+1)u_n}{1+\Delta t}.$$

Thus if $a_1 < 1$, $u_n$ is monotone decreasing, and since $u_n$ is bounded below by zero, $u_n$ is convergent. Using similar arguments to Theorem 3.1 and Theorem 3.2, we get the results. □

### 3.3 Results when $a_1 > \frac{1}{b_1} + 1$

**Lemma 3.3.** *Suppose* $a_1 > \frac{1}{b_1} + 1$*. If* $v_N < \frac{1}{a_1 - 1}$ *for some* $N > 0$*, then* $u_{N+1} < u_N$*.*

*Proof.* Assume the hypotheses. Then

$$v_N < \frac{1}{a_1 - 1}.$$

This implies that

$$\begin{aligned}
(a_1 - 1)\,v_N &< 1 \\
a_1 v_N &< 1 + v_N \\
\frac{a_1 v_N}{1 + v_N} &< 1 \\
\frac{a_1 v_N}{1 + v_N}\Delta t + 1 &< \Delta t + 1 \\
\frac{\frac{a_1 v_N}{1+v_N}\Delta t + 1}{\Delta t + 1} &< 1 \\
\frac{\frac{a_1 v_N}{1+v_N}\Delta t + 1}{\Delta t + 1} u_N &< u_N \\
u_{N+1} &< u_N.
\end{aligned}$$

□

**Lemma 3.4.** *Suppose* $a_1 > \frac{1}{b_1} + 1$*. If* $v_N < \frac{1}{a_1 - 1}$ *and* $u_N > \frac{a_1}{1 - a_1} + a_1 b_1$ *for some* $N > 0$*, then* $v_{N+1} < \frac{1}{a_1 - 1}$*.*

*Proof.* Suppose $v_N < \frac{1}{a_1-1}$. Then $b_1 \Delta t + v_N < b_1 \Delta t + \frac{1}{a_1 - 1}$. From $0 < 1 + v_N < \frac{a_1}{a_1 - 1}$, we have

$$\begin{aligned}
\frac{1}{1 + v_N} &> \frac{a_1 - 1}{a_1} \\
1 + \frac{u_N \Delta t}{1 + v_N} + \Delta t &> 1 + \frac{u_N \Delta t (a_1 - 1)}{a_1} + \Delta t \\
0 < \frac{1}{1 + \frac{u_N \Delta t}{1 + v_N} + \Delta t} &< \frac{1}{1 + \frac{u_N \Delta t (a_1 - 1)}{a_1} + \Delta t}.
\end{aligned}$$

Recalling the fact from earlier, we see that

$$v_{N+1} = \frac{b_1 \Delta t + v_N}{1 + \frac{u_N \Delta t}{1 + v_N} + \Delta t} < \frac{b_1 \Delta t + \frac{1}{a_1 - 1}}{1 + \frac{u_N \Delta t (a_1 - 1)}{a_1} + \Delta t}$$

We now will show that

$$\frac{b_1\Delta t + \frac{1}{a_1-1}}{1+\frac{u_{\mathrm{N}}\Delta t(a_1-1)}{a_1}+\Delta t} < \frac{1}{a_1-1}.$$

From the assumption $u_{\mathrm{N}} > \frac{a_1}{1-a_1} + a_1 b_1$, we have

$$-u_{\mathrm{N}} < \frac{a_1}{a_1-1} - a_1 b_1.$$

This implies that

$$a_1 b_1 - u_{\mathrm{N}} < \frac{a_1}{a_1-1}$$

Noting that $a_1 > \frac{1}{b_1} + 1$ implies that $a_1 - 1 > 0$,

$$(a_1 b_1 - u_{\mathrm{N}})(a_1-1) < a_1.$$

This implies that

$$\begin{aligned}
a_1 b_1 \Delta t(a_1-1) &< u_n \Delta t(a_1-1) + a_1\Delta t\\
b_1\Delta t(a_1-1) &< \frac{u_n\Delta t(a_1-1)}{a_1} + \Delta t\\
b_1\Delta t(a_1-1)+1 &< \frac{u_n\Delta t(a_1-1)}{a_1} + \Delta t + 1\\
\frac{b_1\Delta t(a_1-1)+1}{1+\frac{u_n\Delta t(a_1-1)}{a_1}+\Delta t} &< 1\\
\frac{b_1\Delta t + \frac{1}{a_1-1}}{1+\frac{u_n\Delta t(a_1-1)}{a_1}+\Delta t} &< \frac{1}{a_1-1}.
\end{aligned}$$

Thus, we have

$$v_{\mathrm{N}+1} < \frac{b_1\Delta t + \frac{1}{a_1-1}}{1+\frac{u_{\mathrm{N}}\Delta t(a_1-1)}{a_1}+\Delta t} < \frac{1}{a_1-1}.$$

This completes the proof of the lemma.

□

## 4 The numerical experiments

In this section, we present some results of computational experiments to show that the proposed difference scheme is stable and gives reasonable solutions.

Case 1: $a_1 = 2$, $b_1 = 2$, $\Delta t = 0.5$, $u_0 = 20$, $v_0 = 10$.

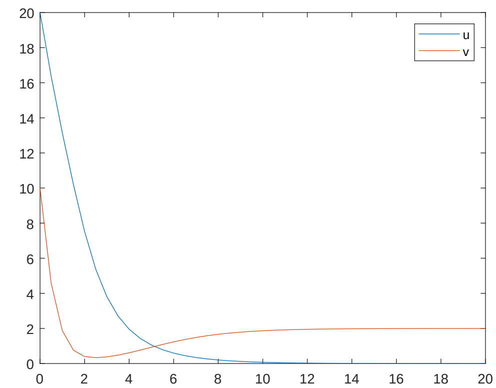


Figure 1: Solutions for $\Delta t = .5, a_1 = .5, b_1 = 2, u_0 = 20, v_0 = 10$.

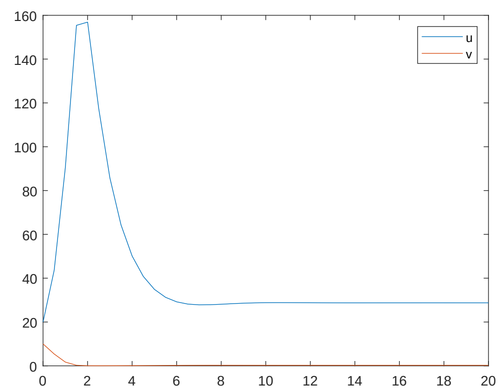


Figure 2: Solutions for $\Delta t = .5, a_1 = 6, b_1 = 5, u_0 = 20, v_0 = 10$.

The graph shows that the numerical solution $(u, v)$ converges to $(0, 2)$ which is a stable steady solution of the system as predicted.

Case 2: $a_1 = 6,\ b_1 = 5,\ \Delta t = 0.5,\ u_0 = 20,\ v_0 = 10$.
The graph shows that the numerical solution $(u, v)$ will converge to $(28.75, 0.25)$ which is also a stable steady solution of the system.

## 5 Error Analysis

We now discuss the error of the numerical scheme.

**Theorem 5.1.** The error for each of $u_n$ and $v_n$ is $O(\Delta t)$

The proof of this theorem comprises the remainder of this section.

Recall we have the following initial-value problem:

$$\begin{cases} u' = u(\frac{a_1}{1+v}v - 1) \\ v' = \frac{-uv}{1+v} - v + b_1 \\ u(0) = u_0 \\ v(0) = v_0 \end{cases} \tag{14}$$

The following theorem can be found in [10].

**Theorem 5.2.** If $u_0 > 0, v_0 > 0$, then system (14) has a unique solution $u(t) > 0, v(t) > 0$. Furthermore,

$$u(t), v(t) \leq \mathrm{M}$$

where M depends on $u_0, v_0, a_1, b_1$.

Set $\mathrm{U}^i = u(t_i), \mathrm{V}^i = v(t_i)$. Then

$$\begin{cases} \frac{\mathrm{U}^{n+1} - \mathrm{U}^n}{\Delta t} & = \mathrm{U}^n(\frac{a_1 \mathrm{V}^n}{1+\mathrm{V}^n} - 1) + \mathrm{O}(\Delta t) \\ \frac{\mathrm{V}^{n+1} - \mathrm{V}^n}{\Delta t} & = -\mathrm{U}^n(\frac{\mathrm{V}^n}{1+\mathrm{V}^n}) - \mathrm{V}^n + b_1 + \mathrm{O}(\Delta t) \end{cases} \tag{15}$$

and recall our numerical scheme given by

$$\begin{cases} \frac{u_{n+1} - u_n}{\Delta t} & = \frac{a_1 u_n}{1+v_n} v_n - u_{n+1} \\ \frac{v_{n+1} - v_n}{\Delta t} & = \frac{-u_n v_{n+1}}{1+v_n} - v_{n+1} + b_1 \end{cases}. \tag{16}$$

Now define $\mathrm{X}^n = \mathrm{U}^n - u_n$ and $\mathrm{Y}^n = \mathrm{V}^n - v_n$ for all $n$, so $|\mathrm{X}^n|$ and $|\mathrm{Y}^n|$ represent the errors of the numerical approximations for $u_n$ and $v_n$. Then consider the equations above for $\mathrm{U}^n$ and $u_n$. Multiplying through by $\Delta t$ and subtracting one equation from the other gives us the following:

$$
\begin{aligned}
&\left|X^{n+1}-X^n\right| = \left|\frac{a_1 U^n V^n}{1+V^n}\Delta t - U^n\Delta t + O(\Delta t^2) - \frac{a_1 u_n v_n}{1+v_n}\Delta t + u_{n+1}\Delta t\right| \\
&= \left|a_1\Delta t\left(\frac{U^n V^n}{1+V^n} - \frac{u_n v_n}{1+v_n}\right) + (u_{n+1}-U^n)\Delta t + O(\Delta t^2)\right| \\
&= \left|a_1\Delta t\left(\frac{U^n V^n + U^n V^n v_n - u_n v_n - u_n v_n V^n}{(1+V^n)(1+v_n)}\right) + (u_{n+1}-u_n+u_n-U^n)\Delta t + O(\Delta t^2)\right| \\
&\le a_1\Delta t\left|U^n V^n + U^n V^n v_n - u_n v_n - u_n v_n V^n\right| + \left|u_{n+1}-u_n+u_n-U^n\right|\Delta t + O(\Delta t^2) \\
&= a_1\Delta t\left|U^n V^n - u_n v_n + V^n v_n(U^n-u_n)\right| + \left|u_{n+1}-u_n+u_n-U^n\right|\Delta t + O(\Delta t^2) \\
&= a_1\Delta t\left|(U^n V^n - U^n v_n + U^n v_n - u_n v_n) + V^n v_n(U^n-u_n)\right| + \left|O(\Delta t) - X^n\right|\Delta t + O(\Delta t^2) \\
&\le a_1\Delta t\left|(U^n(V^n-v_n) + (U^n-u_n)v_n) + V^n v_n(U^n-u_n)\right| + O(\Delta t^2) + \left|X^n\right|\Delta t + O(\Delta t^2) \\
&= a_1\Delta t\left|U^n Y^n + X^n v_n + V^n v_n X^n\right| + \left|X^n\right|\Delta t + O(\Delta t^2) \\
&\le \left|Y^n(U^n a_1)\right|\Delta t + \left|X^n(v_n a_1 + V^n v_n a_1)\right|\Delta t + \left|X^n\right|\Delta t + O(\Delta t^2)
\end{aligned}
$$

Note that $U^n, V^n, u_n, v_n$ are all bounded above by constants, so this becomes

$$
\begin{aligned}
\left|X^{n+1}-X^n\right| &\le C_2\Delta t\left|Y^n\right| + C_1\Delta t\left|X^n\right| + O(\Delta t^2) \\
\left|X^{n+1}\right| - \left|X^n\right| &\le C_2\Delta t\left|Y^n\right| + C_1\Delta t\left|X^n\right| + O(\Delta t^2) \\
\left|X^{n+1}\right| &\le (1+C_1\Delta t)\left|X^n\right| + C_2\Delta t\left|Y^n\right| + O(\Delta t^2)
\end{aligned}
$$

We now derive a similar inequality for Y.

$$
\begin{aligned}
&\mathrm{Y}^{n+1}-\mathrm{Y}^{n}=-\frac{\mathrm{U}^{n}\mathrm{V}^{n}}{1+\mathrm{V}^{n}}\Delta t-\mathrm{V}^{n}\Delta t+b_1\Delta t+\mathrm{O}(\Delta t^2)+\frac{u_n v_{n+1}}{1+v_n}\Delta t+v_{n+1}\Delta t-b_1\Delta t\\
&=\frac{u_n v_{n+1}(1+\mathrm{V}^n)-\mathrm{U}^n\mathrm{V}^n(1+v_n)}{(1+\mathrm{V}^n)(1+v_n)}\Delta t+(v_{n+1}-\mathrm{V}^n)\Delta t+\mathrm{O}(\Delta t^2)\\
&=\frac{u_n v_{n+1}+u_n v_{n+1}\mathrm{V}^n-\mathrm{U}^n\mathrm{V}^n-\mathrm{U}^n\mathrm{V}^n v_n}{(1+\mathrm{V}^n)(1+v_n)}\Delta t+(v_{n+1}-\mathrm{V}^n)\Delta t+\mathrm{O}(\Delta t^2)\\
&=\frac{(u_n v_{n+1}-u_n\mathrm{V}^n+u_n\mathrm{V}^n-\mathrm{U}^n\mathrm{V}^n)+\mathrm{V}^n(u_n v_{n+1}-u_n v_n+u_n v_n-\mathrm{U}^n v_n)}{(1+\mathrm{V}^n)(1+v_n)}\Delta t\\
&+(v_{n+1}-v_n+v_n-\mathrm{V}^n)\Delta t+\mathrm{O}(\Delta t^2)\\
&=\frac{u_n(v_{n+1}-v_n+v_n-\mathrm{V}^n)-\mathrm{V}^n\mathrm{X}^n+\mathrm{V}^n(u_n(v_{n+1}-v_n)-v_n\mathrm{X}^n)}{(1+\mathrm{V}^n)(1+v_n)}\Delta t\\
&+(\mathrm{O}(\Delta t)-\mathrm{Y}^n)\Delta t+\mathrm{O}(\Delta t^2)\\
&=\frac{u_n(\mathrm{O}(\Delta t)-\mathrm{Y}^n)-\mathrm{V}^n\mathrm{X}^n+\mathrm{V}^n(u_n\mathrm{O}(\Delta t)-v_n\mathrm{X}^n)}{(1+\mathrm{V}^n)(1+v_n)}\Delta t-\mathrm{Y}^n\Delta t+\mathrm{O}(\Delta t^2)\\
&=\frac{u_n(1+\mathrm{V}^n)}{(1+\mathrm{V}^n)(1+v_n)}\mathrm{O}(\Delta t^2)-\frac{u_n\mathrm{Y}^n}{(1+\mathrm{V}^n)(1+v_n)}\Delta t-\frac{(1+v_n)\mathrm{V}^n\mathrm{X}^n}{(1+\mathrm{V}^n)(1+v_n)}\Delta t\\
&-\mathrm{Y}^n\Delta t+\mathrm{O}(\Delta t^2)\\
&=\left(\frac{u_n}{(1+v_n)}\right)\mathrm{O}(\Delta t^2)-\left(\frac{u_n}{(1+\mathrm{V}^n)(1+v_n)}+1\right)\mathrm{Y}^n\Delta t-\left(\frac{\mathrm{V}^n}{(1+\mathrm{V}^n)}\right)\mathrm{X}^n\Delta t+\mathrm{O}(\Delta t^2)
\end{aligned}
$$

Since $u_n, \mathrm{V}^n$ bounded above by constants, we have

$$\left|\mathrm{Y}^{n+1}\right| \le (1+\mathrm{C}_3\Delta t)\left|\mathrm{Y}^n\right|+\mathrm{C}_4\Delta t\left|\mathrm{X}^n\right|+\mathrm{O}(\Delta t^2).$$

We have derived these inequalities

$$
\begin{aligned}
\left|\mathrm{X}^{n+1}\right| &\le (1+\mathrm{C}_1\Delta t)\left|\mathrm{X}^n\right|+\mathrm{C}_2\Delta t\left|\mathrm{Y}^n\right|+\mathrm{O}(\Delta t^2)\\
\left|\mathrm{Y}^{n+1}\right| &\le (1+\mathrm{C}_3\Delta t)\left|\mathrm{Y}^n\right|+\mathrm{C}_4\Delta t\left|\mathrm{X}^n\right|+\mathrm{O}(\Delta t^2).
\end{aligned}
\tag{17}
$$

Now define the following

$$\mathrm{W}^n=\left|\mathrm{X}^n\right|+\left|\mathrm{Y}^n\right| \text{ for all } n, \text{ and } \mathrm{C}=\max\{\mathrm{C}_1+\mathrm{C}_3, \mathrm{C}_2+\mathrm{C}_4\}.$$

Then we have

$$
\begin{aligned}
\mathrm{W}^{n+1}&=\left|\mathrm{X}^{n+1}\right|+\left|\mathrm{Y}^{n+1}\right|\\
&\le (1+\mathrm{C}_1\Delta t)\left|\mathrm{X}^n\right|+\mathrm{C}_2\Delta t\left|\mathrm{Y}^n\right|+(1+\mathrm{C}_3\Delta t)\left|\mathrm{Y}^n\right|+\mathrm{C}_4\Delta t\left|\mathrm{X}^n\right|+\mathrm{O}(\Delta t^2)\\
&=(1+(\mathrm{C}_1+\mathrm{C}_4)\Delta t)\left|\mathrm{X}^n\right|+(1+(\mathrm{C}_2+\mathrm{C}_3)\Delta t)\left|\mathrm{Y}^n\right|+\mathrm{O}(\Delta t^2)\\
&\le (1+\mathrm{C}\Delta t)(\left|\mathrm{X}^n\right|+\left|\mathrm{Y}^n\right|)+\mathrm{O}(\Delta t^2)\\
&=(1+\mathrm{C}\Delta t)\mathrm{W}^n+\mathrm{O}(\Delta t^2).
\end{aligned}
\tag{18}
$$

Using this newly found inequality

$$W^{n+1} \le (1 + C\Delta t)W^n + O(\Delta t^2). \tag{19}$$

We will show by induction that for any $n \ge 0$, we have

$$W^n \le \sum_{i=0}^{n} O(\Delta t^2)(1 + C\Delta t)^i. \tag{20}$$

Note the base case when $n = 0$ is handled by (19) since $W^0 = \left|X^0\right| + \left|Y^0\right| = 0$. Now, assume the inductive hypothesis for $n = k$.

$$W^k \le \sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^i. \tag{21}$$

From (19), we have

$$W^{k+1} \le (1 + C\Delta t)W^k + O(\Delta t^2). \tag{22}$$

Thus

$$\begin{aligned} W^{k+1} &\le (1 + C\Delta t)\left(\sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^i\right) + O(\Delta t^2) \\ &= \sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^{i+1} + O(\Delta t^2) \\ &= \sum_{i=1}^{k+1} O(\Delta t^2)(1 + C\Delta t)^i + O(\Delta t^2) \\ &= \sum_{i=0}^{k+1} O(\Delta t^2)(1 + C\Delta t)^i. \end{aligned} \tag{23}$$

This proves the claim for all $n$. Furthermore, we may pull out the $O(\Delta t^2)$ of this sum and interpret it as a geometric series:

$$\begin{aligned} W^n &\le \sum_{i=0}^{n} O(\Delta t^2)(1 + C\Delta t)^i \\ &= O(\Delta t^2)\frac{1 - (1 + C\Delta t)^{n+1}}{1 - (1 + C\Delta t)} \\ &= O(\Delta t^2)\frac{(1 + C\Delta t)^{n+1} - 1}{C\Delta t} \\ &= O(\Delta t)[(1 + C\Delta t)^{n+1} - 1] \\ &\le O(\Delta t)(1 + C\Delta t)^{n+1} \\ &= O(\Delta t)(1 + C\Delta t)^n. \end{aligned} \tag{24}$$

In summary,

$$W^n \leq O(\Delta t)(1 + C\Delta t)^n. \tag{25}$$

Suppose we are considering this numerical scheme over some finite length T. We will show the expression $(1 + C\Delta t)^n$ is bounded above by some constant that is independent of $\Delta t$, but dependent on T. We begin this process with a theorem.

**Theorem 5.3.** Suppose f is a real-valued function, and $\lim_{x\to\infty} f(x) = c$.

a) If f is strictly decreasing on $(0, \infty)$, then $f(x) > c$ for $x \in (0, \infty)$.

b) If f is strictly increasing on $(0, \infty)$, then $f(x) < c$ for $x \in (0, \infty)$

*Proof.* We prove only part *a*, as part *b* follows similarly. Assume the hypotheses. Suppose for a contradiction that $f(x_0) = d \leq c$ for some $x_0 \in (0, \infty)$.
First, consider the case in which $d < c$. Since $f$ tends to $c$, there is some $x_1 > x_0$ such that for all $x > x_1$, $\left|c - f(x)\right| < \frac{c-d}{2}$. But then

$$f(x) > c - \frac{c-d}{2} > d = f(x_0),$$

which contradicts $f$ being strictly decreasing.

Now consider the case where $d = c$. Let $x_2 > x_0$. Since $f$ is strictly decreasing, we have $f(x_2) = k < f(x_0) = c$. Then the first case may be applied using $x_2$ and $k$ in place of $x_0$ and $d$, giving the same contradiction. □

Now, consider the function

$$f(x) = (1 + D/x)^x, \tag{26}$$

which we will show is an increasing function for $x > 0$ given that D is a positive constant. Consider this function's derivative:

$$f'(x) = f(x)\left(\ln(1 + \frac{D}{x}) - \frac{1}{x + D}\right). \tag{27}$$

Obviously, $f(x)$ is positive. We will show the other term must also be positive, implying $f$ is increasing. Let

$$g(x) = \ln\left(1 + \frac{D}{x}\right) - \frac{1}{x + D}.$$

First, notice

$$\lim_{x\to\infty} g(x) = \ln(1) - 0 = 0.$$

Also, consider the derivative of $g(x)$:

$$g'(x) = \frac{-D^2}{x(x + D)^2}. \tag{28}$$

We see $g'(x)$ is negative, so $g$ is strictly decreasing; also, $g(x)$ asymptotically approaches zero. This allows us to conclude that $g(x)$ must be positive by theorem 5.3, meaning $f(x)$ is increasing.

We may now show $(1+C\Delta t)^n$ is bounded above by $(1+TC)e^{TC}$. Suppose we divide the interval $[0,T]$ into N intervals, so $\Delta t = T/N$. Then for $n \leq N$,

$$(1+C\Delta t)^n = \left(1+\frac{TC}{N}\right)^n \leq \left(1+\frac{TC}{N}\right)^N. \tag{29}$$

Recall we have shown the function (26) is increasing; we may interpret TC to be D and N as being a particular input of the function

$$f(x) = \left(1+\frac{TC}{x}\right)^x.$$

Note this function approaches $e^{TC}$ as $x$ tends to infinity. Again applying theorem 5.3, we see that $f(x) < e^{TC}$ for all real $x$, including N. Therefore,

$$(1+C\Delta t)^n < \left(1+\frac{TC}{N}\right)^N < e^{TC}. \tag{30}$$

We have $(1+C\Delta t)^n$ bounded above by a constant. Then since

$$W^n \leq O(\Delta t)(1+C\Delta t)^n \leq O(\Delta t)e^{TC} = O(\Delta t), \tag{31}$$

we have that $W^n$ converges to zero at a rate of $O(\Delta t)$.
Since $W^n = |X^n| + |Y^n|$, this implies $X^n$ and $Y^n$, which represent the errors of $u$ and $v$ in the numerical scheme, must also converge to zero with a rate of $O(\Delta t)$. This proves Theorem 5.1.

## 6 Acknowledgements

We would like to thank our advisors, Drs. Jianlong Han, Seth Armstrong, and Sarah Duffin, professors in the Department of Mathematics at Southern Utah University for all their help and encouragement. This paper was paritally supported by the Walter Maxwell Gibson Research Fellowship. We thank them for their generosity and support.

## References

[1] S. Armstrong and J. Han, A method for numerical analysis of a Lotka-Volterra food web model Int. J. Numer. Anal. Mod., Series B, Vol 1(2012), 1-19.

[2] G. J. Butler and G. S. K. Wolkowicz, A mathematical model of the cheemostat with a general class of functions describing nutrient uptake, SIAM J. Appl. Math., 45(1985), 137-151.

[3] D. Dimitrov and H.V. Kojouharov, Nonstandard finite-difference schemes for general two-dimensional autonomous dynamical systems, Appl. Math. Lett., 18 (2005), 769-775.

[4] C. Fritsch, J. Harmand, and F Campillo, *A modeling approach of the chemostat*, [Research Report] (2014).

[5] S-B Hsu, S.P. Hubbell, and P. Waltman A mathematical theory for single-nutrient competition in continuous culture of micro-organisms, SIAM J. Appl. Math. 32(1977), 366-383.

[6] R.E. Mickens, Applications of Nonstandard Finite Difference Schemes, World Scientific (2000), 155-180.

[7] J. Monod, La technique de culture continue, theorie et applications, Ann. Inst. Pasteur. 79(1950), 390-410.

[8] J. Monod *The growth of bacterial cultures*, Annual Review of Microbiology 3 (1949), 371–394.

[9] J. Monod, *Recherches sur la croissance des cultures bactériennes*, Paris: Hermann (1942)

[10] J.D. Murray, Mathematical Biology I, II (3rd ed), Springer (2003)

[11] A. Novick and L. Szilard, Description of the chemostat, Science.112, (1950), 715-716.

[12] S. Pavlou and I.G. Kevrekidis, Microbial predation in a periodically operated chemostat: a global study of the interaction between natural and externally imposed frequencies, Math Biosci., 108(1992), 1-55.

[13] Per Erik Strandberg. Mathematical models of bacteria population growth in bioreactors: formulation, phase space pictures, optimisation and control, Master thesis, Linkoping University,(2004), 1-61.

[14] H. L. Smith and P. Waltman, The theory of the chemostat, Cambridge Univ. Press, Cambridge, 1994.

**Craig Montgomery**
Southern Utah University
craigmontgomery12@gmail.com

**Braden Carlson**
Southern Utah University
bradenjcarlson@live.com