

Stability in chemostat equations with delayed nutrient recycling*

E. Beretta¹, G. I. Bischi², and F. Solimano³

¹Istituto Matematico “U. Dini” dell’ Università, Viale Morgagni 67/A, I-50134 Firenze, Italy

²Via Reni 9, I-61033 Fermignano, Italy

³Istituto di Biomatemática dell’ Università, Via Saffi 1, I-61029 Urbino, Italy

Abstract. The growth of a species feeding on a limiting nutrient supplied at a constant rate is modelled by chemostat-type equations with a general nutrient uptake function and delayed nutrient recycling. Conditions for boundedness of the solutions and the existence of non-negative equilibria are given for the integrodifferential equations with distributed time lags. When the time lags are neglected conditions for the global stability of the positive equilibrium and for the extinction of the species are provided. The positive equilibrium continues to be locally stable when the time lag in recycling is considered and this is proved for a wide class of memory functions. Computer simulations suggest that even in this case the region of stability is very large, but the solutions tend to the equilibrium through oscillations.

Key words: Chemostat equations — Recycling — Time lags — Stability

1. Introduction

Models based on chemostat-type equations to simulate the growth of planktonic communities of unicellular algae in lakes and oceans have been studied by many authors, e.g., Hsu et al. (1977), Waltman et al. (1980). An important difference between a “chemostat” situation and a “lake” situation appears to be in the fact that lakes generally have residence time of nutrient and sediments measured in years (Powell and Richerson 1985). This implies that in models of natural systems a smaller wash-out rate constant and the regeneration of nutrient due to bacterial decomposition of the dead biomass must be considered (Svirezhev and Logofet 1983). The effect of material recycling on ecosystem stability has been

* Work performed within the activity of the research group “Equazioni di evoluzione e applicazioni Fisico-Matematiche”, MPI (Italy), and under the auspices of GNFM, CNR (Italy)

mainly studied for closed systems (Nisbet and Gurney 1976; Nisbet et al. 1983; Ulanowicz 1972).

Powell and Richerson (1985) and Nisbet and Gurney (1976) considered nutrient recycling as an instantaneous term thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition; such a delay is always present in a natural system and increases for decreasing temperature (Whittaker 1975).

In this paper we consider an open system with a single species feeding on a limiting nutrient which is partially recycled after the death of the organisms and we insert a distributed time lag in the recycling term in order to study its effect on the stability of the positive equilibrium.

The population may be any planktonic community of unicellular algae, and the nutrient in question may be phosphorous, nitrogen or even a vitamin such as B_{12} .

We assume the following general hypotheses on the nutrient-uptake function (Hale and Somolinos 1983):

- (i) the function is non-negative, increasing, and vanishes when there is no nutrient,
- (ii) there is a saturation effect when the nutrient is very abundant.

This class of functions includes the Michaelis–Menten function which is usually proposed to describe the nutrient uptake of phytoplankton in a chemostat, e.g. Caperon (1968).

In Sect. 2 the integrodifferential model is described and conditions for the boundedness of the solutions and the existence of non-negative equilibria are given. In Sect. 3 it is proved that when the time delay is neglected the positive equilibrium, if it exists, is asymptotically stable with respect to any positive initial condition, whereas when it does not exist the species becomes extinct. In Sect. 4 the stability of the positive equilibrium is studied for the model with distributed delay: we give a condition on the coefficients of the model to ensure local stability with general non-negative and normalized memory functions. Then the memory function is taken to be a gamma distribution of integer order and the stability of the positive equilibrium is proved for any value of the coefficients. Furthermore numerical solutions suggest that the region of stability is very large. Hence in this case the time delays do not destabilize the positive equilibrium. However computer simulations show that the trajectories approach the equilibrium through oscillations, whereas oscillations do not occur in the instantaneous case.

2. The model

We consider the following model:

$$\begin{aligned} \dot{S} &= D(S^0 - S) - mU(S)N + bD_1 \int_{-\infty}^t F(t - \tau)N(\tau) d\tau, \\ \dot{N} &= N[-(D + D_1) + m_1 U(S)] \end{aligned} \quad (2.1)$$

where S is the concentration of a limiting nutrient and N is a measure of the population of some organism. \dot{S} and \dot{N} are the time derivatives of S and N .

The constant $D > 0$ is the input and output flow, and is referred to as the wash-out rate. $S^0 > 0$ is the input concentration of the limiting nutrient, $m > 0$ is the maximum uptake rate of nutrient, $m_1 > 0$ is the maximum specific growth rate of the organism, $D_1 > 0$ is the death rate and $b \in (0, 1)$ is the fraction of nutrient recycled after the death of the species.

The constant $1/D$ has the physical dimension of a time and represents the average time that nutrient and waste products spend in the system (Smith 1981). The function $U(S)$ describes the nutrient uptake rate of the species.

From the hypotheses i) and ii) of Sect. 1 $U(S)$ is a continuous function defined on $[0, +\infty)$ and

$$U(0) = 0; \quad \frac{dU}{dS} > 0 \quad \text{and} \quad \lim_{S \rightarrow \infty} U(S) = 1. \quad (2.2)$$

In particular these hypotheses are satisfied by the Michaelis–Menten function:

$$U(S) = \frac{S}{A + S} \quad (2.3)$$

where $A > 0$ is the half-saturation constant.

The delay-kernel $F(u)$ is a non-negative bounded function defined on $[0, +\infty)$ and describes the contribution of the biomass dead in the past to the nutrient recycled at time t . The presence of the time lag must not affect the equilibrium values, so

$$\int_0^{\infty} F(u) \, du = 1. \quad (2.4)$$

The average time lag is defined as

$$T = \int_0^{\infty} uF(u) \, du. \quad (2.5)$$

The solutions of system (1), with initial conditions

$$\begin{aligned} S(t_0) &= S_0 > 0, \\ N(\tau) &= \phi(\tau), \end{aligned} \quad (2.6)$$

ϕ being a bounded continuous positive function defined on $(-\infty, t_0]$, exist for all $t \geq t_0$ and remain non-negative for $t \geq t_0$ (see, e.g., Cushing 1977; Gopalsamy 1983). Furthermore

Theorem 2.1. *If the inequality*

$$b < \frac{m(D + D_1)}{m_1 D_1} \quad (2.7)$$

holds, then all the solutions are bounded.

Proof. We prove that a Liapunov function exists whose derivative along the trajectories of (2.1) is negative outside a bounded region of the positive orthant of the plane (S, N) (see, e.g., Yoshizawa 1966). Let be

$$V(t, S, N) = S(t) + \frac{m}{m_1} N(t) + bD_1 \int_0^\infty F(s) \left(\int_{t-s}^t N(u) du \right) ds.$$

It is easy to see that $V \geq 0$ and $V \rightarrow +\infty$ when $|(S, N)| \rightarrow +\infty$. The derivative of V along the trajectories of (2.1) is

$$\begin{aligned} \dot{V} &= D(S^0 - S) - mU(S)N + bD_1 \int_0^\infty F(u)N(t-u) du \\ &\quad + \frac{m}{m_1} N[-(D + D_1) + m_1 U(S)] \\ &\quad + bD_1 \int_0^\infty F(s) \frac{\partial}{\partial t} \left(\int_{t-s}^t N(u) du \right) ds \\ &= D(S^0 - S) + bD_1 \int_0^\infty F(u)N(t-u) du - \frac{m}{m_1} (D + D_1)N \\ &\quad + bD_1 \int_0^\infty F(s)(N(t) - N(t-s)) ds \\ &= D(S^0 - S) - \left(\frac{m}{m_1} (D + D_1) - bD_1 \right) N. \end{aligned}$$

From the hypothesis the coefficient of N is negative. Thus outside the region of the positive orthant bounded by the axes and by the line

$$N = \frac{D(S^0 - S)}{(D + D_1)m/m_1 - bD_1}$$

\dot{V} is negative. This completes the proof.

System (2.1) has the non-negative equilibrium $E_0 = (S^0, 0)$ which exists for all parameter values, and the equilibrium $E_1 = (S_e, N_e)$ with

$$S_e = U^{-1}((D + D_1)/m_1), \quad N_e = \frac{D(S^0 - S_e)}{mU(S_e) - bD_1}, \quad (2.8)$$

which is positive provided that (2.7) is true and

$$\frac{D + D_1}{m_1} < 1 \quad \text{and} \quad S_e < S^0. \quad (2.9)$$

3. The instantaneous model

When the time lag in the recycling term is neglected, i.e. the delay-kernel is a delta function $F(u) = \delta(u)$, the model becomes

$$\begin{aligned} \dot{S} &= D(S^0 - S) - mU(S)N + bD_1 N, \\ \dot{N} &= N[-(D + D_1) + m_1 U(S)]. \end{aligned} \quad (3.1)$$

This model has the same equilibria as (2.1). We shall prove that when the positive equilibrium E_1 exists it is globally asymptotically stable, whereas if it does not exist the equilibrium E_0 becomes globally stable, that is the species becomes extinct. We first give the following:

Lemma 3.1. *If $b < m/m_1$ then for each $\varepsilon > 0$ a \bar{t} exists such that*

$$S(t) \leq S^0 + \varepsilon \quad \text{for } t \geq \bar{t}.$$

Proof. Let $P(t) := S(t) + (m/m_1)N(t)$. Its time derivative is

$$\begin{aligned} \dot{P} &= D(S^0 - S) - mU(S)N + bD_1N + \frac{m}{m_1}N[-(D + D_1) + m_1U(S)] \\ &= -DP + DS^0 - D_1\left(\frac{m}{m_1} - b\right)N. \end{aligned}$$

From the hypothesis we obtain the differential inequality

$$\dot{P} < -DP + DS^0$$

which implies $P(t) < S^0 + A e^{-Dt}$, where A is a constant. Then

$$\lim_{t \rightarrow +\infty} S(t) + \frac{m}{m_1}N(t) \leq S^0$$

and since $N(t)$ is always positive if it starts positive, the thesis follows.

By the following theorem we give conditions for extinction of the species:

Theorem 3.1. *If $b < m/m_1$ and*

$$U(S^0) < \frac{D + D_1}{m_1}, \tag{3.2}$$

then the equilibrium $E_0 = (S^0, 0)$ is globally asymptotically stable in $\mathbb{R}_+^2 := \{(S, N) \in \mathbb{R}^2 \mid S > 0, N > 0\}$.

Proof. We prove the theorem by showing that

$$\lim_{t \rightarrow \infty} N(t) = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} S(t) = S^0.$$

From the second of (3.1) we have

$$N(t) = N(0) \exp \left[m_1 \int_0^t \left(U(S(t')) - \frac{D + D_1}{m_1} \right) dt' \right]. \tag{3.3}$$

Since $U(S)$ is a continuous function it follows from (3.2) that there is a constant $\varepsilon > 0$ such that $U(S^0 + \varepsilon) < (D + D_1)/m_1$. Then by Lemma 3.1 there exists \bar{t} such that if $t \geq \bar{t}$ then $S(t) \leq S^0 + \varepsilon$. This implies that $U(S(t)) \leq U(S^0 + \varepsilon)$ because $U(S)$ is an increasing function. Thus

$$\begin{aligned} N(t) &= N(0)C \exp \left[m_1 \int_{\bar{t}}^t \left(U(S(t')) - \frac{D + D_1}{m_1} \right) dt' \right] \\ &\leq N(0)C \exp \left[m_1 \int_{\bar{t}}^t \left(U(S^0 + \varepsilon) - \frac{D + D_1}{m_1} \right) dt' \right] \end{aligned} \tag{3.4}$$

with

$$C = \exp \left[m_1 \int_0^{\bar{t}} \left(U(S(t')) - \frac{D + D_1}{m_1} \right) dt' \right] > 0.$$

The exponent in (3.4) is negative, so $\lim_{t \rightarrow \infty} N(t) = 0$. Now $\lim_{t \rightarrow \infty} S(t) = S^0$ follows from the first of (3.1) with $N(t) = 0$.

Let us note that if $m_1 < (D + D_1)$, i.e. the mortality plus the wash-out rate is greater than the maximum growth, the inequality (3.2) is true for each value of the input concentration S^0 . When $m_1 > (D + D_1)$ and (3.2) holds true then the extinction of the species is due to lack of nutrient. The following theorem states the evolution of the system when the species does not become extinct:

Theorem 3.2. *If the positive equilibrium $E_1 = (S_e, N_e)$ exists then it is globally asymptotically stable in \mathbb{R}_+^2 .*

Proof. We define the Liapunov function

$$V(S, N) = w_1 \int_{S_e}^S \frac{g(x)}{U(x)} dx + w_2 \int_{N_e}^N \frac{x - N_e}{x} dx \tag{3.5}$$

where $g(x) = m_1 U(x) - (D + D_1)$ is an increasing function such that $g(S_e) = 0$, and $w_1, w_2 \in \mathbb{R}_+$. Then $V \geq 0$ and $V(S, N) = 0$ if and only if $S = S_e, N = N_e$. The time derivative of V along the trajectories of (3.1) is

$$\begin{aligned} \dot{V} &= w_1 \frac{g(S)}{U(S)} [D(S^0 - S) - mU(S)N + bD_1N] + w_2(N - N_e)g(S) \\ &= w_1 g(S) \left[\frac{D(S^0 - S)}{U(S)} - mN + \frac{bD_1N}{U(S)} - \frac{D(S^0 - S_e)}{U(S_e)} + mN_e - \frac{bD_1N_e}{U(S_e)} \right] \\ &\quad + w_2(N - N_e)g(S) \end{aligned}$$

where we have used the equilibrium condition for the first of (3.1).

We fix the positive constants w_1 and w_2

$$w_1 = 1; \quad w_2 = m - \frac{bD_1}{U(S_e)}$$

where $w_2 > 0$ if (2.7) holds true. Since

$$NU(S_e) - N_e U(S) = U(S)(N - N_e) - N(U(S) - U(S_e)),$$

we obtain

$$\dot{V} = -g(S) \frac{DS^0 + bD_1N}{U(S)U(S_e)} (U(S) - U(S_e)) - g(S) \frac{D}{U(S)U(S_e)} (SU(S_e) - S_e U(S)).$$

But, from (2.8), $g(S) = m_1(U(S) - U(S_e))$. Then, since $SU(S_e) - S_e U(S) = -S_e(U(S) - U(S_e)) + U(S_e)(S - S_e)$, we obtain

$$\begin{aligned} \dot{V} &= -\frac{m_1}{U(S)U(S_e)} (DS^0 + bD_1N - DS_e)(U(S) - U(S_e))^2 \\ &\quad - \frac{m_1 D}{U(S)} (S - S_e)(U(S) - U(S_e)). \end{aligned} \tag{3.6}$$

The first term is negative because $DS^0 > DS_e$. The second term is negative because $U(S)$ is an increasing function. Then $\dot{V} \leq 0$, and $\dot{V} = 0$ if and only if $S = S_e$. But the largest invariant subset of the set of the points where $\dot{V} = 0$ is (S_e, N_e) . Then the global stability of (S_e, N_e) follows from the La Salle extension of Liapunov's Theorem (La Salle and Lefschetz 1961).

Concerning the assumptions on the function $U(S)$, remark that in the above theorem we only use that it is an increasing function. The results stated in Theorems 3.1 and 3.2 can also be applied when $b = 0$, thus extending the results given in literature for chemostat equations with a Michaelis–Menten uptake function, as in Waltman et al. (1980).

However from (3.6) we can see that the recycling (i.e. $b \neq 0$) has a stabilizing role for the positive equilibrium.

4. The model with delayed recycling: stability and numerical solutions

We study here the local stability of the positive fixed point of model (2.1) in order to see if the presence of the time lag in the recycling term can change its stability.

Once linearized around the positive equilibrium E_1 the model (2.1) reads

$$\begin{aligned} \dot{x} &= -(D + mU'(S_e)N_e)x - mU(S_e)y + bD_1 \int_{-\infty}^t F(t - \tau)y(\tau) dt \\ \dot{y} &= m_1U'(S_e)N_e x \end{aligned} \tag{4.1}$$

where $x = S(t) - S_e$ and $y = N(t) - N_e$. If we define the positive constant

$$k = U'(S_e)N_e \tag{4.2}$$

and recall that $U(S_e) = (D + D_1)/m_1$ then the characteristic equation of (4.1) is

$$\lambda^2 + (D + mk)\lambda + m(D + D_1)k - bD_1m_1k\mathcal{L}(\lambda) = 0 \tag{4.3}$$

where $\mathcal{L}(\lambda)$ is the Laplace transform of the delay kernel (MacDonald 1978)

$$\mathcal{L}(\lambda) = \int_0^\infty F(u) e^{-\lambda u} du.$$

The positive fixed point is locally asymptotically stable if and only if all the roots of (4.3) have negative real parts.

Without specifying any particular memory function $F(u)$ we give the following stability result:

Theorem 4.1. *If*

$$D_1 \leq \frac{D^2 + m^2k^2}{2mk}, \tag{4.4}$$

then the positive equilibrium of (2.1) is always locally asymptotically stable.

Proof. We follow the argument given in MacDonald (1978), p. 27. Since each root of (4.3) is a continuous function of the parameters and when $T = 0$ all the roots of the characteristic equation lie in the left hand half plane (we have stability for zero delay) a necessary condition for a stability change is that the characteristic equation has a pure imaginary solution $\lambda = i\omega$, i.e. a pair of conjugate complex roots cross the imaginary axis. It suffices to seek roots with $\omega \in \mathbb{R}_+$ since $\lambda = 0$ is not a root, because $m(D + D_1)k - bD_1m_1k > 0$ from (2.7).

Thus we substitute $\lambda = i\omega$, $\omega \in \mathbb{R}_+$ in (4.3), and obtain

$$H(i\omega) = \mathcal{L}(i\omega) \tag{4.5}$$

where

$$H(i\omega) := \frac{mk(D + D_1) - \omega^2 + i\omega(D + mk)}{bD_1m_1k}$$

Since $|\mathcal{L}(i\omega)| \leq \int_0^\infty F(u)|e^{-i\omega u}| du = 1$ we have that a necessary condition for the existence of a solution of (4.5) is

$$|H(i\omega)| \leq 1. \tag{4.6}$$

We study the function

$$R(\omega) := |H(i\omega)|^2 = \frac{[mk(D + D_1) - \omega^2]^2 + \omega^2(D + mk)^2}{b^2m_1^2k^2D_1^2} \tag{4.7}$$

$$R(0) = \frac{m^2(D + D_1)^2}{b^2m_1^2D_1^2} + \frac{mk^2D(D + 2D_1)}{b^2m_1^2k^2D_1^2} > 1 \tag{4.8}$$

because of (2.7). We also have $\lim_{\omega \rightarrow +\infty} R(\omega) = +\infty$ and the derivative

$$R'(\omega) = \frac{4\omega^3 + 2\omega(D^2 + m^2k^2 - 2mkD_1)}{b^2m_1^2k^2D_1^2}. \tag{4.9}$$

If $D_1 \leq (D^2 + m^2k^2)/2mk$ then $R(\omega)$ is an increasing function of ω and from (4.8) it follows that $R(\omega) > 1$ for each $\omega \geq 0$. Thus $|H(i\omega)| > 1$ for $\omega \geq 0$ and this excludes the possibility of changes of stability. This completes the proof.

Let us note that Theorem 4.1 still holds for a discrete delay, i.e. when $F_T(u) = \delta(u - T)$. In fact the Laplace transform of the delta distribution is $e^{-\lambda T}$ and $|\mathcal{L}(i\omega)| = 1$.

In order to see what happens when $D_1 > (D^2 + m^2k^2)/2mk$ we restrict our analysis to the class of memory functions:

$$g(u) = \frac{a^{p+1}}{p!} u^p e^{-au} \tag{4.10}$$

where p is a non-negative integer and $a \in \mathbb{R}_+$ is linked to the mean time lag by

$$T = \frac{p + 1}{a}. \tag{4.11}$$

These kernels are often used in literature, e.g., MacDonald (1978), Cushing (1977). The Laplace transform is

$$\mathcal{L}(\lambda) = \left(\frac{a}{a + \lambda} \right)^{p+1} \quad (4.12)$$

and the characteristic equation has the polynomial form:

$$\begin{aligned} \lambda^2(a + \lambda)^{p+1} + (D + mk)\lambda(a + \lambda)^{p+1} + m(D + D_1)k(a + \lambda)^{p+1} \\ - a^{p+1}bD_1m_1k = 0. \end{aligned} \quad (4.13)$$

For $p = 0$ the memory function (4.10) is a decreasing function, and Eq. (4.13) becomes a third degree algebraic equation. By the Routh–Hurwitz criterion (see Appendix) it is easy to prove that in this case the positive equilibrium is locally asymptotically stable for each value of the parameters.

When $p > 0$ the kernels (4.10) have a single maximum occurring at $u = p/a$, and the width of the peak decreases with increasing p . Usually the destabilizing effect of distributed delays with kernels (4.10) increases with increasing p . For our model we can give the following result.

Theorem 4.2. *The positive equilibrium of the Eq. (2.1) with delay-kernels (4.10) is locally asymptotically stable for each non-negative order p of the kernels.*

Proof. We consider the characteristic equation (4.13) with $\lambda = i\omega$

$$\begin{aligned} -\omega^2(a + i\omega)^{p+1} + (D + mk)i\omega(a + i\omega)^{p+1} + m(D + D_1)k(a + i\omega)^{p+1} \\ - a^{p+1}bD_1m_1k = 0. \end{aligned} \quad (4.14)$$

We introduce an auxiliary angle variable θ with

$$\tan \theta = \frac{\omega}{a}, \quad 0 < \theta < \frac{\pi}{2} \quad (4.15)$$

and (4.14) reads:

$$\begin{aligned} -\omega^2(\cos \theta + i \sin \theta)^{p+1} + i\omega(D + mk)(\cos \theta + i \sin \theta)^{p+1} \\ + m(D + D_1)k(\cos \theta + i \sin \theta)^{p+1} = bD_1m_1k(\cos \theta)^{p+1}, \end{aligned}$$

i.e.

$$e^{i(p+1)\theta}[-\omega^2 + m(D + D_1)k + i\omega(D + mk)] = bD_1m_1k(\cos \theta)^{p+1}.$$

By taking the square modulus of both the sides we obtain

$$R(\omega) = (\cos \theta)^{2(p+1)} \quad (4.16)$$

where $R(\omega)$ is the function defined in (4.7). The Routh–Hurwitz critical values must correspond to solutions of Eq. (4.16). We have already proved (see Appendix) that for $p = 0$ there are no such critical values and $R(\omega) > 1$ for $\omega > 0$. As p increases the right hand side of (4.16) becomes smaller because $0 < \cos \theta < 1$ and this implies that (4.16) has no solutions.

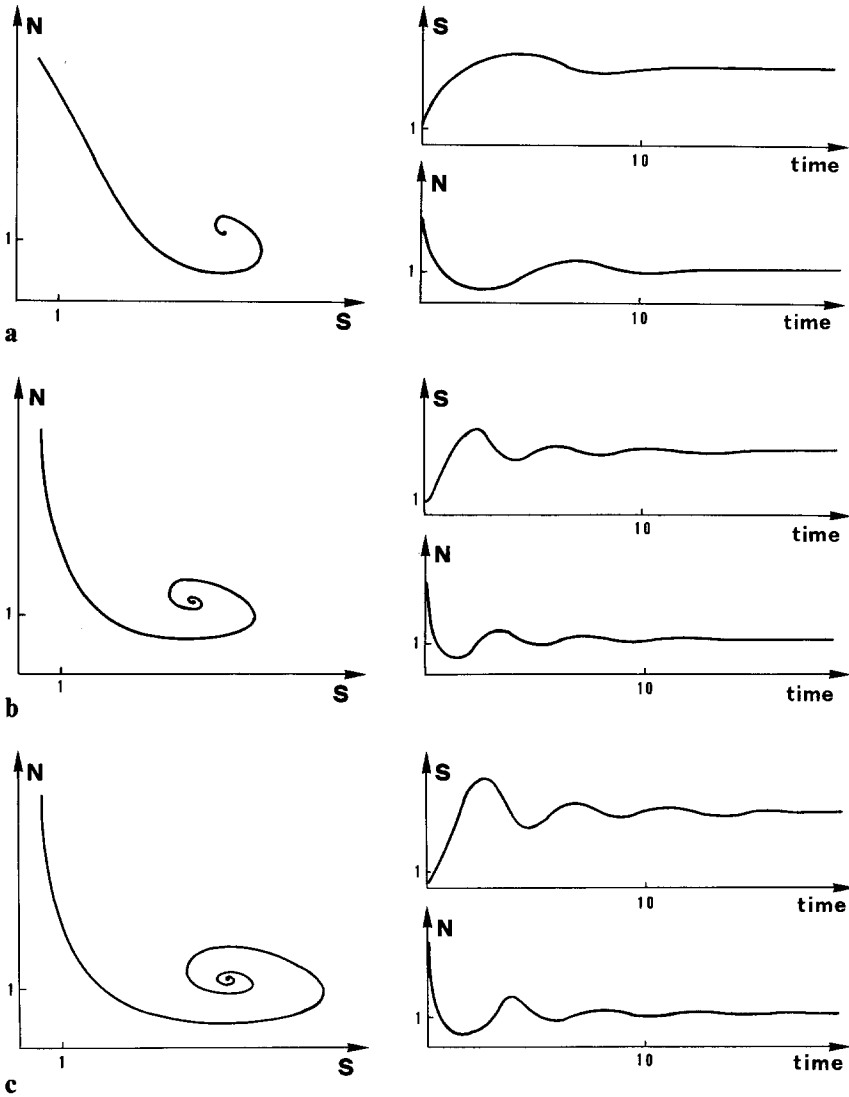


Fig. 1a-c. Numerical solutions of the instantaneous model (3.1) and the model (2.1) with time lag and delay-kernel (4.10) and with Michaelis–Menten uptake function (2.3) are represented on the plane (S, N) and versus time. They are obtained with the same fixed set of parameters $D = 0.1$, $S^0 = 20$, $D_1 = 4$, $m = 10$, $m_1 = 9$, $A = 6$, $b = 0.8$. **a** Instantaneous model (3.1); **b** model (2.1) with exponentially decreasing delay-kernel (4.10) with $p = 0$. The average time lag is $T = 5$. The trajectory is obtained by a numerical solution of the expanded system (4.17). The region of stability of the positive equilibrium appears to be very large; **c** model (2.1) with delay-kernel (4.10) with a maximum in the past, i.e. $p = 1$, and the same average time lag $T = 5$

We only proved the local stability of the positive equilibrium of the model with time lags whereas we proved its global stability for the instantaneous case. However numerical solutions of the system (2.1) with an uptake function of Michaelis–Menten type (2.3) and kernels (4.10) with $p = 0$ and $p = 1$ suggest that the positive equilibrium is practically globally stable.

In Fig. 1 numerical solutions of the instantaneous model (3.1) and of system (2.1) with delay-kernels (4.10) with $p = 0$ and $p = 1$ respectively are plotted on the plane (S, N) . These trajectories are the projections on the plane (S, N) of the solutions of the expanded system of ordinary differential equations obtained by the “linear chain trick technique” (MacDonald 1978). For example when $p = 0$ we define the new variable

$$y = \int_{-\infty}^t a e^{-a(t-\tau)} N(\tau) d\tau$$

and the integrodifferential system (2.1) is transformed into an equivalent system of three ordinary differential equations:

$$\begin{aligned} \dot{S} &= D(S^0 - S) - mU(S)N + bD_1y, \\ \dot{N} &= N[-(D + D_1) + m_1U(S)], \\ \dot{y} &= aN - ay \end{aligned} \quad (4.17)$$

where the variable $y(t)$ can be interpreted as an intermediate component which causes the delay, such as the dead biomass in the sediments.

From a comparison of these numerical simulations we can see that the oscillations are more evident in the model with a delay-kernel with a maximum in the past (Fig. 1c) whereas they are absent in the instantaneous model (Fig. 1a).

5. Conclusions

We have studied the growth of a population depending on a limiting nutrient which is partially recycled after the death of organisms. The population in question may be a planktonic community of unicellular algae and the nutrient may be phosphorous, nitrogen or even a vitamin such as B_{12} .

We have considered generalized chemostat equations with a fairly general nutrient uptake function and a nutrient recycling term with distributed delay, and we have given conditions for boundedness of the solutions.

We have also considered the model with instantaneous recycling and we have stated conditions for the global stability of the positive equilibrium and conditions for the extinction of the species. Then we have studied the effect of time delays in nutrient recycling and, with a fairly general class of memory-functions we have proved that the positive equilibrium continues to be locally stable, independently of the value of the time lag. Numerical solutions have

shown that the region of stability of the positive equilibrium is large, but the trajectories approach the equilibrium through oscillations when time lags are considered.

Appendix

By the Routh–Hurwitz criterion we prove that all the roots of the characteristic equation (4.13) have negative real parts when $p = 0$. If $p = 0$ Eq. (4.13) becomes $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ with

$$a_1 = a + D + mN_e U'(S_e) > 0,$$

$$a_2 = aD + amN_e U'(S_e) + mm_1 N_e U(S_e) U'(S_e) > 0,$$

$$a_3 = am_1 N_e U'(S_e) [mU(S_e) - bD_1] > 0$$

where the last inequality follows from (2.7):

$$U(S_e) = \frac{D + D_1}{m_1} > \frac{bD_1}{m}.$$

The Routh–Hurwitz criterion says that $\operatorname{Re}(\lambda_i) < 0$, $i = 1, \dots, 3$ if and only if

$$a_1 a_2 - a_3 > 0.$$

In our case

$$\begin{aligned} & (a + D + mN_e U'(S_e))(aD + amN_e U'(S_e) + mm_1 N_e U(S_e) U'(S_e)) \\ & > am_1 N_e U'(S_e) [mU(S_e) - bD_1] \end{aligned}$$

because

$$\begin{aligned} & amn_1 N_e U(S_e) U'(S_e) + (\text{positive terms}) > amn_1 N_e U(S_e) U'(S_e) \\ & - bD_1 am_1 N_e U'(S_e). \end{aligned}$$

References

1. Caperon, J.: Population growth response of *Isochrysis galbana* to nitrate variation at limiting concentration. *Ecology* **49**, 866–872 (1968)
2. Cushing, J. M.: Integrodifferential equations and delay models in population dynamics. (Lect. Notes Biomath., vol. 20) Berlin Heidelberg New York: Springer 1977
3. Gopalsamy, K.: Transit delays and dispersive populations in patchy habitats. *Int. J. System Sci.* **14**, 239–268 (1983)
4. Hale, J. K., Somolinos, A. S.: Competition for fluctuating nutrient. *J. Math. Biol.* **18**, 255–280 (1983)
5. Hsu, S. B., Hubbel, S., Waltman, P.: A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. Appl. Math.* **32**, 366–383 (1977)
6. La Salle, J., Lefschetz, S.: Stability by Liapunov's direct method. New York: Academic Press 1961

7. MacDonald, N.: Time lags in biological models. (Lect. Notes Biomath., vol. 27) Berlin Heidelberg New York: Springer 1978
8. Nisbet, R. M., Gurney, W. S. C.: Model of material cycling in a closed ecosystem. *Nature* **264**, 633–635 (1976).
9. Nisbet, R. M., McKinstry, J., Gurney, W. S. C.: A strategic model of material cycling in a closed ecosystem. *Math. Biosci.* **64**, 99–113 (1983)
10. Powell, T., Richerson, P. J.: Temporal variation, spatial heterogeneity and competition for resources in plankton system: a theoretical model. *Am. Nat.* **125**, 431–464 (1985)
11. Smith, H. L.: Competitive coexistence in an oscillating chemostat. *SIAM J. Appl. Math.* **40**, 498–522 (1981)
12. Svirezhev, Y. M., Logofet, D. O.: Stability of biological communities. Moscow: Mir 1983
13. Ulanowicz, R. E.: Mass and energy flow in closed ecosystems. *J. Theor. Biol.* **34**, 239–253 (1972)
14. Waltman, P., Hubbel, S. P., Hsu, S. B.: Theoretical and experimental investigations of microbial competition in continuous culture. In: Burton, T. (ed.) *Modeling and differential equations in biology*. New York: Dekker 1980
15. Whittaker, R. H.: *Communities and ecosystems*. New York: Macmillan 1975
16. Yoshizawa, T.: *Stability theory by Liapunov's second method*. The Mathematical Society of Japan 1966

Received January 16, 1989; received in revised form May 16, 1989