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Stability of a Steady State of Closed Microecosystem «algae – heterotrophic bacteria»

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Abstract. Two models of closed microecosystem "algae–heterotrophic bacteria" are considered in this paper. Mathematical models are the Cauchy problem for system of non-linear ordinary differential equations. To develop models the Liebig's law of the minimum is consistently used for both specific rate of biomass growth and specific mortality rate of algae and bacteria cells. To describe the specific rate of substrate utilization by algae and bacteria the Andrew model (substrate inhibition) is used. It is assumed that carbon and nitrogen are main biogenic elements. Both models predict stationary state of microecosystem «*Clorella vulgaris* *Pseudomonas* sp.» that is in reasonable agreement with experimental data. Stability of the obtained stationary state is examined by means of Lyapunov's indirect method and Lyapunov's direct method based on the proposed form of Lyapunov function.

Keywords: mathematical modelling of ecosystems, closed ecosystem, algae, heterotrophic bacteria, stationary state, stability, Lyapunov indirect method, Lyapunov direct method.

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1. Notations

x — biomass concentration of algae model cells, g/l
 y — biomass concentration of bacteria model cells, g/l
 μ_x, μ_y — specific growth rate of biomass (algae, bacteria), 1/h
 $\mu_{x,max}, \mu_{y,max}$ — maximal specific growth rate of biomass (algae, bacteria), 1/h
 d_x, d_y — specific mortality rate of cells (algae, bacteria), 1/h
 $d_{x,min}, d_{y,min}$ — specific mortality rate of cells at optimal conditions (algae, bacteria), 1/h
 $d_{x,max}, d_{y,max}$ — specific mortality rate of cells in the absence of nutrition (algae, bacteria), 1/h
 $q_x^{(c)}, q_y^{(c)}$ — specific consumption rates of carbon (algae, bacteria), 1/h
 $q_x^{(n)}, q_y^{(n)}$ — specific consumption rates of nitrogen (algae, bacteria), 1/h
 $q_{x,max}^{(c)}, q_{y,max}^{(c)}$ — maximal specific consumption rates of carbon (algae, bacteria), 1/h
 $q_{x,max}^{(n)}, q_{y,max}^{(n)}$ — maximal specific consumption rates of nitrogen (algae, bacteria), 1/h
 $C_{max}^{(x)}, C_{max}^{(y)}$ — carbon concentration whereby $\mu_{x,max}$ and $\mu_{y,max}$ are achieved (algae, bacteria), 1/h

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$N_{max}^{(x)}, N_{max}^{(y)}$ — nitrogen concentration whereby $\mu_{x,max}$ and $\mu_{y,max}$ are achieved (algae, bacteria), 1/h

γ_{xc}, γ_{xn} — stoichiometric coefficients for model cells of algae

γ_{yc}, γ_{yn} — stoichiometric coefficients for model cells of bacteria

C_m, N_m — concentration of mineral forms of carbon and nitrogen in water, g/l

C_b, N_b — concentration of biological forms of carbon and nitrogen (proteins, lipids, carbohydrates) in water, g/l

e — growth efficiency of heterotrophic bacteria

2. Introduction

Closed ecological systems (CES) constitute self-replenishing ecosystems which receive energy from outside but do not exchange matter with the outside environment. These systems have a number of applications. They are unique tools for studying fundamental processes and interactions in ecosystems. They also provide a basis for creating life support systems for space exploration. To gain insight into the functioning of CES mathematical models can be used. The elaboration of main principles of constructing mathematical models can be conveniently performed on the basis of closed microecosystems. Microecosystem (MES) is a small-scale, simplified, often laboratory based experimental ecosystem.

Mathematical models often represent the closed ecosystem as a set of first-order autonomous differential equations. Models based on so called flexible metabolism were suggested [1, 2]. It was found that these models of closed ecosystems tend to become more stable as the number of the described species increased. Various models of closed ecological systems with low species diversity were considered [3]. It was shown that models based on flexible metabolism have a stable stationary state in a wide range of parameters. Model of closed microecosystem «algae-heterotrophic bacteria» was proposed [4]. The Liebig's law of the minimum was consistently used for constructing this model. Concentration of the biomass in stationary state obtained with the use of the proposed model is in reasonable agreement with experimental data.

In a closed system external influences are not possible, and the system can only change due to internal processes. Therefore, once equilibrium is achieved, it will remain as long as the system stays closed. The concentrations of biomass and biogenic elements will remain constant, and the system will be in a state of dynamic equilibrium. Any plausible mathematical model of a CES must produce stable steady state solution. It means that model can describe an arbitrarily long existence of a CES.

In this paper two models of closed microecosystem «algae-heterotrophic bacteria» are considered. Both models predict stationary state of microecosystem that is in reasonable agreement with experimental data. Stability of the obtained stationary state is examined by means of Lyapunov's indirect method and Lyapunov's direct method based on the proposed form of Lyapunov function.

3. Stoichiometric ratios and physical factors influencing population growth

Let us introduce model cells that consist of only from carbon and nitrogen (basic biogenic elements). Values of the stoichiometric coefficients for model cells of algae and bacteria are calculated using given C/N ratio for real cells:

$$\gamma_{sc}/\gamma_{sn} = \text{given}, \quad \gamma_{sc} + \gamma_{sn} = 1, \quad s = (x, y).$$

Mass of model cell is related to the dry mass of real cell as $m_a = r \cdot m_c$, where coefficient $r < 1$ is determined from the ratio of the mass of carbon and nitrogen to the dry mass of real cell.

Light intensity is one of the important factors for algal photosynthesis. To describe its effect on algal growth function $f_1(I)$ is introduced. The effect of temperature on production of biomass of algae and bacteria is described by function $f_{2,s}(T)$. Algae and bacteria are able to grow in some pH range of medium. In what follows, it is assumed that ecosystem is kept at optimal light intensity and pH of medium ($f_1(I) = 1$, $f_{3,x}(pH) = 1$, $f_{3,y}(pH) = 1$).

4. Models of closed microecosystem «algae – heterotrophic bacteria»

The first model was presented in detail in [4]. It was assumed that specific substrate consumption rate of biogenic elements (C and N) by algae and bacteria is defined using modified Andrew's equation [5]. It was also assumed that specific mortality rate of algae and bacteria depends on the concentration of biogenic elements [6, 7]. The model can be expressed in the form of a system of differential equations

$$\begin{aligned} d\mathbf{s}_1/dt &= \mathbf{f}_1(\mathbf{s}_1), \\ \mathbf{s}_1 &= (x, y, C_b, C_m, N_b, N_m)^T, \quad \mathbf{f}_1(\mathbf{s}_1) = (f_{1,1}(\mathbf{s}_1), \dots, f_{1,6}(\mathbf{s}_1))^T. \end{aligned} \quad (1)$$

Let us consider now second model. Specific growth rate of population can be defined in the form that is equivalent to modified Andrew's equation

$$\begin{aligned} v_s(b) &= f_{2,s}(T) \frac{b_{1/2}^{(s)}/b_{\max}^{(s)} + b_{\max}^{(s)}/b_{1/2}^{(s)} - 2}{b/b_{\max}^{(s)} + b_{\max}^{(s)}/b + b_{1/2}^{(s)}/b_{\max}^{(s)} + b_{\max}^{(s)}/b_{1/2}^{(s)} - 4}, \\ s &= (x, y), \quad b = (C, N), \end{aligned}$$

where $b_{s,1/2}$ — substrate saturation constant (substrate concentration when $\nu(b_{s,1/2}) = 1/2$). Let C_{yb} and N_{yb} be concentrations of organic carbon and nitrogen that can be consumed by bacteria (organic matter in water and in algae). It is assumed that carbon and nitrogen are consumed independently by bacteria. Then consumption rates of organic carbon and nitrogen by bacteria are

$$\begin{aligned} dC_{yb}/dt &= dC_b/dt + \gamma_{xc} dx_{eaten}/dt, \\ dN_{yb}/dt &= dN_b/dt + \gamma_{xn} dx_{eaten}/dt, \end{aligned}$$

where dC_b/dt and dN_b/dt are consumption rates of organic carbon and nitrogen in water, dx_{eaten}/dt is consumption rates of algae by bacteria. Consumption rates dC_b/dt , dN_b/dt and dx_{eaten}/dt are proportional to C_b , N_b and x_{eaten} , respectively. Then

$$dC_b/dx_{eaten} = C_b/x, \quad dN_b/dx_{eaten} = N_b/x.$$

Let us express C_b and N_b from the condition of closeness

$$\begin{aligned} \gamma_{xc}x + \gamma_{yc}y + C_b + C_m &= C_0 = \text{const}, \\ \gamma_{xn}x + \gamma_{yn}y + N_b + N_m &= N_0 = \text{const}, \end{aligned}$$

and obtain

$$\begin{aligned} dC_{yb}/dt &= ((C_0 - \gamma_{xc}x - \gamma_{yc}y - C_m)/x + \gamma_{xc}) dx_{eaten}/dt = ((C_0 - \gamma_{yc}y - C_m)/x) dx_{eaten}/dt, \\ dN_{yb}/dt &= ((N_0 - \gamma_{xn}x - \gamma_{yn}y - N_m)/x + \gamma_{xn}) dx_{eaten}/dt = ((N_0 - \gamma_{yn}y - N_m)/x) dx_{eaten}/dt. \end{aligned}$$

Using Liebig's law, one can obtain

$$dx_{eaten}/dt = x \cdot \min \left(\frac{1}{C_0 - \gamma_{yc}y - m} dC_{yb}/dt, \frac{1}{N_0 - \gamma_{yn}y - N_m} dN_{yb}/dt \right). \quad (2)$$

Bacteria need for vital activity not only biogenic elements but also energy. Part of consumed organic matter is used for growing bacterial biomass, and the rest part is degraded by bacteria releasing inorganic nutrients and obtaining energy. This process is known as mineralization. It can be described as follows

$$\begin{aligned} dC_{yb}/dt &= \mu_{yc,max} \nu(C_{yb}) y = \gamma_{yc} dy_p/dt + dC_{ym}/dt, \\ dN_{yb}/dt &= \mu_{yn,max} \nu(N_{yb}) y = \gamma_{yn} dy_p/dt + dN_{ym}/dt, \end{aligned} \quad (3)$$

where $\mu_{yc,max}$, $\mu_{yn,max}$ — maximal specific consumption rate of carbon and nitrogen, respectively; dy_p/dt — specific growth rate of heterotrophic bacteria without regard for mortality; dC_{ym}/dt , dN_{ym}/dt — rates of mineralization of carbon and nitrogen. It is proved in the Appendix that if condition (A2) is satisfied then

$$dy_p/dt = \mu_{y,max} \cdot \min(\nu_y(C_{yb}), \nu_y(N_{yb})) y. \quad (4)$$

Algae consume mineral forms of carbon and nitrogen independently. Then

$$\begin{aligned} dC_{xm}/dt &= \gamma_{xc} \mu_{x,max} \nu_x(C_m) x, \\ dN_{xm}/dt &= \gamma_{xn} \mu_{x,max} \nu_x(N_m) x, \end{aligned} \quad (5)$$

where dC_{xm}/dt , dN_{xm}/dt — consumption rates of inorganic carbon and nitrogen in water. Using Liebig's law and (5), one can obtain specific growth rate of algae without regard for mortality dx_p/dt as follows

$$dx_p/dt = \min((1/\gamma_{xc})dC_{xm}/dt, (1/\gamma_{xn})dN_{xm}/dt) = \mu_{x,max} \min(\nu_x(C_m), \nu_x(N_m)) x \quad (6)$$

Using (2), (4), (6) and (A3), specific growth rates of algae and bacteria are written in the form

$$\begin{aligned} dx/dt &= dx_p/dt - d_x x - dx_{eaten}/dt, \\ dy/dt &= dy_p/dt - d_y y, \end{aligned} \quad (7)$$

where d_x , d_y — specific mortality rates of algae and bacteria, respectively. Using (3)–(5), the rate of concentration change of mineral forms of carbon and nitrogen is described as follows

$$\begin{aligned} dC_m/dt &= dC_{ym}/dt - dC_{xm}/dt, \\ dN_m/dt &= dN_{ym}/dt - dN_{xm}/dt. \end{aligned} \quad (8)$$

Considering (7) and (8), the following system of differential equations is finally obtain

$$\begin{aligned} d\mathbf{s}_2/dt &= \mathbf{f}_2(\mathbf{s}_2), \\ \mathbf{s}_2 &= (x, y, C_m, N_m)^T, \quad \mathbf{f}_2(\mathbf{s}_2) = (f_{2,1}(\mathbf{s}_2), \dots, f_{2,4}(\mathbf{s}_2))^T. \end{aligned} \quad (9)$$

5. Steady states of closed laboratory microecosystem «Chlorella-Pseudomonas sp»

Results of experimental studies of various closed microecosystems were presented [8]. For example, microecosystem that contains algae *Chlorella 219* and heterotrophic bacteria *Pseudomonas sp* was studied. Biocenosis was illuminated for 24 hours at 28–30°C. Concentrations of

biomass of living algae cells, bacteria cells, dead algae cells and concentration of detritus were determined.

Let us consider time evolution of microecosystem «*Chlorella vulgaris* - *Pseudomonas sp*» that is described by system of equations (1). It is assumed that microecosystem is kept at optimal illumination and pH at 29°C. Functions $f_{2,x}(T)$ and $f_{2,y}(T)$ are given in [4]. Stoichiometric coefficients, parameters r and parameters of functions for specific substrate consumption rate for *Chlorella vulgaris* and *Pseudomonas sp* are also presented in [4]. The following stationary solution was obtained

$$\begin{aligned} \mathbf{s}_1^a &= (x, y, C_b, C_m, N_b, N_m)|_{t \rightarrow \infty} = (x^a, y^a, C_b^a, C_m^a, N_b^a, N_m^a) = \\ &= (0.02465, 0.00647, 0.0906, 0.00273, 0.0002, 0.00048). \end{aligned}$$

Consider now stationary solution for model 2 that follows from system of equations (9). In stationary state $d\mathbf{s}_2/dt = 0$. Then

$$\begin{cases} 0 = dx_{born}/dt - d_x x - dx_{eaten}/dt, \\ 0 = dy_{born}/dt - d_y y, \\ 0 = \beta_C \mu_{y \max} \nu(C_0 - \gamma_{yC} y - C_m) y - \gamma_{yC} c dy_{born}/dt - \gamma_{xC} \mu_{x \max} \nu(C_m) x, \\ 0 = \beta_N \mu_{y \max} \nu(N_0 - \gamma_{yN} y - N_m) y - \gamma_{yN} c dy_{born}/dt - \gamma_{xN} \mu_{x \max} \nu(N_m) x. \end{cases} \quad (10)$$

Parameters d_x and d_y follow from the first two equations of (10)

$$\begin{aligned} d_x &= \mu_{x \max} \min(\nu(C_m), \nu(N_m)) - \mu_{y \max} y \min\left(\frac{\beta_N \nu(N_0 - \gamma_{yN} y - N_m)}{N_0 - \gamma_{yN} y - N_m}, \frac{\beta_C \nu(C_0 - \gamma_{yC} y - C_m)}{C_0 - \gamma_{yC} y - C_m}\right), \\ d_y &= \mu_{y \max} \min(\nu(C_0 - \gamma_{yC} y - C_m), \nu(N_0 - \gamma_{yN} y - N_m)). \end{aligned}$$

It is assumed that *Chlorella* contains 50 % of proteins, 10 % of fats and 40% of carbohydrates. Using average formulae for proteins, fats, carbohydrates and energy values for them [9], estimates of parameters Q_C and Q_N can be obtained: $Q_C = 12.182$ kJ/g and $Q_N = 0.595$ kJ/g.

Four possible stationary solutions were found

1. $C_m < C_{\max}, N_m < N_{\max}$

$$C_m = 0.00049, N_m = 0.01794, x = 0.023, y = 0.004, C_b = 0.06, N_b = 0.001.$$

2. $C_m < C_{\max}, N_m > N_{\max}$

$$C_m = 0.0000468, N_m = 0.06776, x = 0.02, y = 0.001, C_b = 0.01, N_b = 0.001.$$

3. $C_m > C_{\max}, N_m < N_{\max}$

$$C_m = 0.827, N_m = 0.013, x = 0.021, y = 0.002, C_b = 0.01, N_b = 0.001.$$

4. $C_m > C_{\max}, N_m > N_{\max}$

$$C_m = 0.3987, N_m = 0.0333, x = 0.019, y = 0.004, C_b = 0.01, N_b = 0.001.$$

Solution 1 corresponds to the conditions of the experiment. Specific mortality rates are determined from relations (21), using stationary solution 1. They are

$$d_x = 0.0285, d_y = 0.0588.$$

Organic form of carbon C_b and nitrogen N_b were not immediately determined in the experiment. Biomass concentration of dead chlorella cells (0.12 g/l) and concentration of detritus (0.12g/l) were determined. It was assumed that dead chlorella cell is chemically identical to living chlorella cell, and detritus contains 35–50 % of carbon and 1–4 % of nitrogen. Then parameters C_b and N_b can be estimated for the experiment. Calculated parameters of the microecosystem are shown in comparison with experimental results in Tab. 1.

Table 1. Stationary state of closed microecosystem «Clorella Pseudomonas sp»

Parameter	Model 1	Model 2	Experiment [9]
$x_r = x/r, g/l$	0.049	0.046	0.05
$y_r = y/r, g/l$	0.011	0.007	0.015
$C_b, g/l$	0.091	0.06	0.097 – 0.115*
$N_b, g/l$	0.0002	0.001	0.007 – 0.01*

* estimate

6. Stability of steady states of closed microecosystem «Chlorella-Pseudomonas sp»

Now turn to investigate the stability of the obtained steady states. First consider the method that allows one to determine whether the equilibrium of the nonlinear system is asymptotically stable or unstable based on the analysis of the linearized system about this equilibrium. This method is sometimes known as Lyapunov indirect method.

Lyapunov indirect method. Let $ds/dt = \mathbf{A}s$ be the linearisation of non-linear system $ds/dt = \mathbf{f}(s)$ about the equilibrium point of non-linear system. Let $\lambda_n, n = 1, \dots, N$ denote the eigenvalues of matrix \mathbf{A} . If $Re(\lambda_n) < 0$ for all n then the equilibrium of non-linear system is asymptotically stable. If there exists n such that $Re(\lambda_n) > 0$ then the origin is unstable.

Real parts of eigenvalues of matrix \mathbf{A} for model 1 are

$$(-724.77, -0.236, -0.128, -0.067, 0, 0).$$

Real parts of eigenvalues of matrix \mathbf{A} for model 2 are

$$(-0.0025, -775.8166, -0.0001, 0).$$

Hence, there are zero eigenvalues. In this case Lyapunov wrote [10] "...one can come to conclusion that ...problem on stability is resolved by the sign of the minimal characteristic number. Consequently, only cases when this number is equal to zero remain open to question. Then the problem can not be resolved until higher then linear terms are taken into account in differential equations". Alternatively, one can use Lyapunov direct method.

Lyapunov direct method. Let $s = 0$ be an equilibrium point for $ds/dt = \mathbf{f}(s)$ where $\mathbf{f} : D \rightarrow \mathbf{R}^n$ is locally Lipschitz on domain $D \subset \mathbf{R}^n$. Assume there exists a continuously differentiable function $V(s) : D \rightarrow \mathbf{R}$ such that

1. $V(0) = 0$ and $V(s) > 0$ for all $s \in D$ not equal to zero,
2. $\frac{dV}{dt}(s) = \sum_{n=1}^N \frac{\partial V}{\partial s_n} \mathbf{f}_n(s) \leq 0$ for all $s \in D$.

Then $s = 0$ is stable in the sense of Lyapunov.

To study stability of steady state for model 1 the folloing Lyapunov function is proposed

$$V(s_1) = \sum_{n=1}^6 (\mathbf{f}_{1,n}(s_1))^2$$

For model 2 Lyapunov function has similar form:

$$V(s_2) = \sum_{n=1}^4 (\mathbf{f}_{2,n}(s_2))^2$$

Hence the first condition is fulfilled in D . To study stability of nonzero stationary state one should use change of variables $\mathbf{s}^* = \mathbf{s} - \mathbf{s}^a$, where \mathbf{s}^a is nonzero stationary state.

Analytical study of the derivative of the Lyapunov function in the vicinity of stationary states was performed for both models using Maple software. Then as a result conditions were established whereby $dV/dt \leq 0$. In the case of model 1 the derivative of the Lyapunov function is non-positive for

$$x < 0.135, N_m < 0.0085, N_b < 0.0495.$$

In the case of model 2 appropriate conditions were established for every stationary state:

$$1. C_m < C_{\max}, N_m < N_{\max}$$

$$x < 0.035, y < 0.0105.$$

$$2. C_m < C_{\max}, N_m > N_{\max}$$

$$x < 0.08, y < 0.0065.$$

$$3. C_m > C_{\max}, N_m < N_{\max}$$

$$0.008 < N_m < 0.01335, 0.0009 < y < 0.0029, 0.015 < C_m.$$

$$4. C_m > C_{\max}, N_m > N_{\max}$$

$$N_m > 0.03165, y < 0.035.$$

By this means the stability of obtained stationary states is proved.

Conclusions

Two models of closed microecosystem «algae-heterotrophic bacteria» were considered in this paper. Mathematical models are the Cauchy problem for system of non-linear ordinary differential equations. The Liebig's law of the minimum and the Andrew model for the specific rate of biomass growth were used to develop these models. Both models predict stationary state of microecosystem «*Clorella vulgaris Pseudomonas sp.*» that is in reasonable agreement with experimental data. To study stability of the obtained stationary state Lyapunov indirect method and Lyapunov direct method were used. The form of Lyapunov function that is used in Lyapunov direct method was proposed. Methodology developed in this paper can be used to study stability of stationary states of various closed microecosystems that include algae and heterotrophic species.

Appendix

Energy that bacteria can spend on biomass growth can not exceed energy obtained during the process of degradation of organic matter by bacteria and releasing inorganic nutrients:

$$Q_C dC_{ym}/dt + Q_N dN_{ym}/dt \geq Q_y dy_p/dt \quad (A1),$$

where Q_C , Q_N – energy values of carbon and nitrogen, respectively; Q_y – energy needed to support vital activity of bacteria. Bacterial growth efficiency e introduced in model 1 can be represented as follows

$$e = dy_p/(dC_{yb} + dN_{yb}) = dy_p/(dY + dC_{ym} + dN_{ym}) = \frac{1}{1 + dC_{ym}/dy_p + dN_{ym}/dy_p}$$

Then maximal value of e is

$$e_{\max} = \frac{1}{1 + dC_{ym,\max}/dy_{p,\max} + dN_{ym,\max}/dy_{p,\max}} \text{ and } dC_{ym,\max}/dy_{p,\max} + dN_{ym,\max}/dy_{p,\max} = 1/e_{\max} - 1$$

Because $Q_C > Q_N$ one can assume that e_{\max} has the following form

$$e_{\max} = \frac{1}{1 + dC_{ym}(e_{\max})/dy_p(e_{\max})} \text{ and } dC_{ym}(e_{\max})/dY_p(e_{\max}) = 1/e_{\max} - 1.$$

If growth is limited by carbon then maximal growth of bacterial biomass is achieved when $e = e_{\max}$. Then

$$Q_C dC_{ym}(e_{\max})/dt = Q_y dy_p(e_{\max})/dt.$$

Let us express Q_y and obtain

$$Q_y = Q_C(1/e_{\max} - 1).$$

Then

$$\mu_{yc,\max} y = \gamma_{yc} y_p(e_{\max})/dt + C_{ym}(e_{\max})/dt = \gamma_{yc} dy_p(e_{\max})/dt + (1/e_{\max} - 1) dy_p(e_{\max})/dt = dy_p(e_{\max})/dt (\gamma_{yc} + (1/e_{\max} - 1)).$$

Taking into account that $dY_p/dt = \mu_y(e_{\max})y$ when $e = e_{\max}$, one can obtain expression for $\mu_{yc,\max}$:

$$\mu_{yc,\max} = (\gamma_{yc} + (1/e_{\max} - 1)) \mu_y(e_{\max})$$

Expression for $\mu_{yn,\max}$ can be obtained in analogous way:

$$\mu_{yn,\max} = (\gamma_{yn} + (Q_C/Q_N)(1/e_{\max} - 1)) \mu_y(e_{\max}).$$

When $e = e_{\max}$ inequality (A1) becomes

$$Q_C dC_{ym}/dt + Q_N dN_{ym}/dt = Q_C (1/e_{\max} - 1) dY_{p,\max}/dt. \quad (A2)$$

Let us express bacterial biomass growth that follows from energy requirements

$$dy_e/dt = \frac{Q_C (\gamma_{yc} + (1/e_{\max} - 1)) \nu(C_{yb}) + Q_N (\gamma_{YN} + (Q_C/Q_N)(1/e_{\max} - 1)) \nu(N_{yb})}{Q_C \gamma_{yc} + Q_N \gamma_{yn} + Q_C (1/e_{\max} - 1)} \mu_y(e_{\max}).$$

Maximal specific growth rate of bacterial biomass $\mu_{y,\max}$ is achieved when $\nu(C_{yb}) = \nu(N_{yb}) = 1$, ($\mu_y(e_{\max}) = \mu_{y,\max}$). Then

$$dy_e/dt = \frac{Q_C (\gamma_{yc} + (1/e_{\max} - 1)) \nu(C_{yb}) + Q_N (\gamma_{YN} + (Q_C/Q_N)(1/e_{\max} - 1)) \nu(N_{yb})}{Q_C \gamma_{yc} + Q_N \gamma_{yn} + 2Q_C (1/e_{\max} - 1)} \mu_{y,\max} Y,$$

$$dy_{yb}/dt = (\gamma_{yc} + (1/e_{\max} - 1)) \frac{Q_C \gamma_{yc} + Q_N \gamma_{yn} + Q_C (1/e_{\max} - 1)}{Q_C \gamma_{yc} + Q_N \gamma_{yn} + 2Q_C (1/e_{\max} - 1)} \mu_{y,\max} \nu(C_{yb}) Y = \quad (A3)$$

$$= \beta_C \mu_{y,\max} \nu(C_{yb}) Y,$$

$$dN_{yb}/dt = (\gamma_{yn} + (Q_C/Q_N)(1/e_{\max} - 1)) \frac{Q_C \gamma_{yc} + Q_N \gamma_{yn} + Q_C (1/e_{\max} - 1)}{Q_C \gamma_{yc} + Q_N \gamma_{yn} + 2Q_C (1/e_{\max} - 1)} \mu_{y,\max} \nu(N_{yb}) Y = \beta_N \mu_{y,\max} \nu(N_{yb}) Y.$$

Finally, using Liebig's law, one can obtain

$$dy_p/dt = \mu_{y,\max} y \min(\nu(C_{yb}), \nu(N_{yb}), (dy_e/dt)(1/t)) =$$

$$= \mu_{y,\max} y \min \left(\nu(C_{yb}), \nu(N_{yb}), \frac{Q_C (\gamma_{yc} + (1/e_{\max} - 1)) \nu(C_{yb}) + Q_N \left(\gamma_{yn} + \frac{Q_C}{Q_N} (1/e_{\max} - 1) \right) \nu(N_{yb})}{Q_C \gamma_{yc} + Q_N \gamma_{yn} + 2Q_C (1/e_{\max} - 1)} \right).$$

Let us transform given above expression

$$dy_p/dt = \mu_{y,\max} y \min \left(\nu(C_{yb}), \nu(N_{yb}), \frac{Q_C \gamma_{yc} + Q_C (1/e_{\max} - 1)}{Q_C \gamma_{yc} + Q_C (1/e_{\max} - 1) + Q_N \gamma_{yn} + Q_C (1/e_{\max} - 1)} \nu(C_{yb}) + \frac{Q_C \gamma_{yn} + Q_C (1/e_{\max} - 1)}{Q_C \gamma_{yc} + Q_C (1/e_{\max} - 1) + Q_N \gamma_{yn} + Q_C (1/e_{\max} - 1)} \nu(N_{yb}) \right).$$

Let us note that this expression has the form

$$dy_p/dt = \mu_{y,\max} y \min (\nu(C_{yb}), \nu(N_{yb}), a\nu(C_{yb}) + (1-a)\nu(N_{yb})).$$

Then

$$dy_p/dt = \mu_{y,\max} y \min (a\nu(C_{yb}) + (1-a)\nu(C_{yb}), (1-a)\nu(N_{yb}) + a\nu(N_{yb}), a\nu(C_{yb}) + (1-a)\nu(N_{yb})).$$

Taking into account that

$$\begin{aligned} a\nu(C_{Yb}) + (1-a)\nu(C_{Yb}) &< a\nu(C_{Yb}) + (1-a)\nu(N_{Yb}), \\ (1-a)\nu(N_{Yb}) + a\nu(N_{Yb}) &< a\nu(C_{Yb}) + (1-a)\nu(N_{Yb}), \end{aligned}$$

one can finally obtain (15).

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Устойчивость стационарного состояния замкнутой микроэкосистемы «одноклеточная водоросль – гетеротрофная бактерия»

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Аннотация. В работе предлагаются две модели замкнутой микроэкосистемы «одноклеточная водоросль–гетеротрофная бактерия». Математическая модель формулируется в виде задачи Коши для системы нелинейных обыкновенных дифференциальных уравнений. Для построения модели последовательно использовался закон минимума Либиха, как для описания скорости роста биомассы элементов микроэкосистемы, так и для описания скорости отмирания клеток водоросли и бактерии. Для описания удельной скорости потребления биогенных элементов водорослью и бактерией использовалась функция Эндрюса (ингибирование избытком субстрата). Предполагается, что биогенными элементами являются углерод и азот. Вычисленные с использованием предложенных моделей концентрации биомассы микроэкосистемы «*Clorella vulgaris*-*Pseudomonas* sp» в стационарном состоянии хорошо согласуются с данными эксперимента. Устойчивость стационарного состояния исследуется с использованием метода первого приближения и метода функций Ляпунова.

Ключевые слова: математическое моделирование экосистем, замкнутая экосистема, одноклеточная водоросль, гетеротрофная бактерия, стационарное состояние, устойчивость, метод первого приближения, метод функций Ляпунова.