

NONLINEAR DYNAMICS OF A CONTROLLED STIRRED TANK BIOREACTOR WITH PREDATOR-PREY RELATIONSHIP

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The paper presents the dynamic characteristics of a continuous tank bioreactor for microbiological process, with a developed predator-prey food chain. The presence of the predator microorganism considerably influences the position and stability character of steady-states. There appears to exist a wide range of unstable steady-states and high-amplitude oscillations of state variables. Without automatic control, the system can operate only in unsteady conditions. From technological point of view, this circumstance is unfavorable. It was shown that oscillations can be removed by employing automatic control with continuous P or PI controllers. Moreover, the use of a controller with integrating element causes removal of the predator from the bioreactor. The paper discusses an application of this phenomenon for practical purposes.

Keywords: predator-prey, dynamics, automatic control, steady states, bioreactor

1. INTRODUCTION

In theoretical works concerning stationary and dynamic properties of microbiological reactors, authors so far have accepted the following kinetic relations between substrates and microorganisms:

- one microbial species and one substrate limiting biomass growth;
- one microbial species and two or more substrates limiting biomass growth, for example, numerous aerobic processes with double-substrate kinetics;
- several microbial species and one limiting substrate, for example, processes occurring with simultaneous participation of heterotrophic and autotrophic microorganisms or prokaryotic and eukaryotic microorganisms in the presence of one carbonaceous substrate;
- several microbial species and two or more substrates limiting biomass growth, they occur, for example, in wastewater treatment plants containing carbonaceous and nitrogen compounds.

Among the works on modelling of microbial processes, those concerning single-substrate processes with one species of microorganisms are the most advanced and the most numerous (Ajbar, 2001a, b; Ajbar and Alhumaizi, 2012; Chi et al., 1974; Dunn et al., 2003; Onysko et al., 2002; Pavlou, 1999; Russo et al., 2008; Tabiś, 1996; Tabiś and Malik, 1996; Yang and Humphrey, 1975).

The smallest group of theoretical and experimental studies on the dynamics and the steady-state analysis of microbiological reactors relate to processes involving two microbial species, forming consecutive links in the food chain. Then predator-prey biocenosis develops in a bioreactor. This phenomenon has a significant impact on the stationary and dynamic characteristics of a bioreactor (Alhumazi and Ajbar., 2005; Butler et al., 1983; El-Owaidy and Moniem, 2003; Li and Kuang, 2000;

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Moghadas and Gumel, 2003; Zhu et al., 2002). The characteristic sustained oscillations have been also observed experimentally (Tsuchiya et al., 1972).

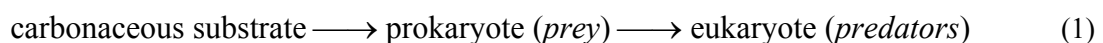
Examples of microbiological processes with kinetic models and microorganisms present in a system are given in Table 1.

Table 1. Examples of microbiological processes following different kinetic models

Reference	Microorganisms	Kinetics
Alhumazi and Ajbar (2005)	predator-prey (<i>Dictyostelium discoideum</i> on <i>E. coli</i>)	single-substrate, Monod model
Onysko et al. (2002)	single-species (<i>Pseudomonas putida</i> Q5)	single-substrate, Lounge model
Olivieri et al. (2011)	single-species (<i>Pseudomonas</i> sp. OX1)	double-substrate, Haldane-Monod model
Russo et al. (2008)	single-species (<i>Pseudomonas</i> sp. OX1)	single-substrate, Haldane model

The first simple description defining relationships between the numbers of prey and predator organisms was proposed by Lotka (1925) and Volterra (1926). This model dates back to the 1920s and belongs to the canons of mathematical ecology (Scudo and Ziegler, 1978). In this work, the term “predator-prey system” is used to analyse a microbiological process occurring in a continuous stirred tank bioreactor.

All continuous bioreactors are thermodynamically open objects. Therefore, they are prone to develop a food chain:



In microbial degradation, bacteria play the role of prokaryotic organisms, and protozoa can occur as eukaryotic microorganisms. Predator-prey biocenosis can take place both in degradation of carbonaceous compounds (Ratsak et al., 1996; Tabiś and Malik, 1998), and nitrification (Moussa et al., 2005).

This work presents the results of research on dynamic properties of bioreactor with a microbiological process following scheme (1). All the above cited papers concern bioreactors without automatic control. For this reason, research program was undertaken, aimed at understanding dynamic properties of such bioreactors, but fitted with an automatic controller. The task of the controller is to stabilise unstable steady-states and remove the oscillations of the state variables. The character of the presented analysis is general.

To ensure that the analysis can be used to real microbiological processes, numerical simulations have been carried out using values of kinetic parameters for selected predator-prey system. The microbial degradation of phenol, as a classical process with substrate inhibition, has been chosen as an example.

2. MATHEMATICAL MODEL OF THE BIOREACTOR

Consider a complex microbiological process occurring in a continuous stirred tank bioreactor according to the scheme (1). The dynamics of the bioreactor is described by a system of three differential equations

$$V \frac{dc_A}{dt} = F_V (c_{A_f} - c_A) - V \cdot r_A(c_A, c_B) \quad (2a)$$

$$V \frac{dc_B}{dt} = -F_V c_B + V \cdot r_B(c_A, c_B, c_D) \quad (2b)$$

$$V \frac{dc_D}{dt} = -F_V c_D + V \cdot r_D(c_A, c_B, c_D) \quad (2c)$$

where c_A , c_B and c_D denote correspondingly the mass concentrations of limiting substrate A, bacteria B (prey) and protozoa (predator).

After introducing dimensionless state variables

$$\alpha = \frac{c_{Af} - c_A}{c_{Af}}, \quad \beta = \frac{c_B}{c_{Af}}, \quad \gamma = \frac{c_D}{c_{Af}} \quad (3)$$

a reduced form of the model of the reactor dynamics is obtained

$$\frac{d\alpha}{dt} = -\frac{1}{\tau} \alpha + r_A(\alpha, \beta) \quad (4a)$$

$$\frac{d\beta}{dt} = -\frac{1}{\tau} \beta + r_B(\alpha, \beta, \gamma) \quad (4b)$$

$$\frac{d\gamma}{dt} = -\frac{1}{\tau} \gamma + r_D(\alpha, \beta, \gamma) \quad (4c)$$

where $\tau = V/F_{Vf}$ is mean residence time of the liquid in the reactor.

The system of equations (4) was solved numerically using Gear's algorithm. In vector notation, the system of equations (4) is as follows:

$$\frac{dx}{dt} = F(x, \lambda) \quad (5)$$

where $x = (\alpha, \beta, \gamma)$, whereas λ denotes a set of model parameters, or one of the parameters chosen for the determination of steady-state branches. Steady-state of the bioreactor results from solving the system of equations

$$F(x, \lambda) = 0 \quad (6)$$

To obtain steady-state branches, our own computer program based on algorithm of local parameterisation was used. Source codes of all programs were written in Fortran 77 Programming Language and compiled with GNU Fortran.

Uptake rate of the limiting substrate r_A , growth rate of bacteria r_B and growth rate of protozoa r_D are described by the following equations (Tabiś and Malik, 1998)

$$r_A(\alpha, \beta) = \frac{1}{w_{BA}} f(c_A(\alpha)) \cdot \beta \quad (7a)$$

$$r_B(\alpha, \beta, \gamma) = f(c_A(\alpha)) \cdot \beta - \frac{1}{w_{DB}} g(c_A(\alpha), c_B(\beta)) \cdot \gamma \quad (7b)$$

$$r_D(\alpha, \beta, \gamma) = g(c_A(\alpha), c_B(\beta)) \cdot \gamma \quad (7c)$$

The form of the functions $f(c_A)$ and $g(c_A, c_B)$ depends on the kinetic model of a microbiological process. For Haldane kinetics, followed by phenol biodegradation, we have

$$f(c_A) = \frac{kc_A}{K_s + c_A + \frac{c_A^2}{K_{in}}} \quad (8a)$$

$$g(c_A, c_B) = \frac{k_D c_B}{K_{sD} + c_B + \frac{c_A^2}{K_{inD}}} \quad (8a)$$

For a quantitative analysis of the process, the following values of the kinetic parameters have been accepted (Tabiś and Malik, 1998): $k = 0.26$ 1/h, $K_s = 0.0254$ kg/m³, $K_{in} = 0.173$ kg/m³, $w_{BA} = 0.616$ kgB/kgA, $k_D = 0.13$ 1/h, $K_{sD} = 0.050$ kg/m³, $K_{inD} = 0.115$ kg/m³, $w_{DB} = 0.50$ kgB/kgA.

The purpose of applying automatic control is the stabilisation of unstable steady-states. We decided on a closed-loop control system for the sake of considerable industrial experience in the selection of controller settings employed in feedback (Luyben, 1973). The scheme of the bioreactor and control system is presented in Fig. 1.

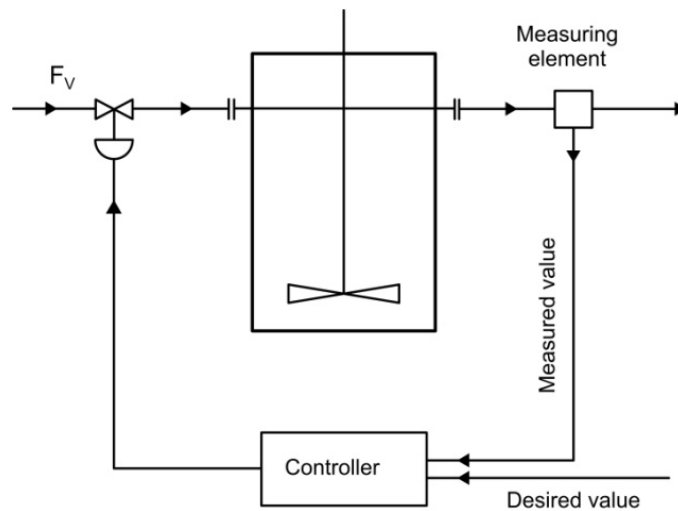


Fig. 1. Scheme of controlled bioreactor

The concentration of carbonaceous substrate has been chosen as a controlled variable. The measurement of this quantity is an easy task, which may be conducted continuously. As the control variable, we have chosen the flow rate of the substrate F_V . The control by flow rate is an easy task as well.

Microbial reactors are characterised by slow dynamics. Therefore, proportional P controller and proportional-integral PI controller have been proposed for control by feed flow rate. In further part of the work we evaluate the effects of using these two controllers. The use of the proportional controller leads to the following control rule for volumetric flow rate

$$F_V(t) = F_V^* \cdot [1 + K_p \cdot e(t)] \quad (9)$$

If the proportional-integral controller is used, then volumetric flow rate is controlled by the following rule

$$F_V(t) = F_V^* \cdot \left[1 + K_p \left(e(t) + \frac{1}{T_I} \int_0^t e(t) dt \right) \right] \quad (10)$$

In Equations (9) and (10) F_V^* denotes volumetric flow rate in a given, unstable steady-state under stabilisation. Quantity $e(t)$ is a control error, defined in this work as

$$e(t) = \alpha(t) - \alpha^*(t) \quad (11)$$

where $\alpha^*(t)$ is the desired value of the degree of conversion of the carbonaceous substrate.

3. DYNAMIC CHARACTERISTICS OF THE BIOREACTOR

Analysis of the dynamics of objects, in particular nonlinear systems, is carried out accompanied by the stationary characteristics. Global nonlinear dynamics is determined by the phase trajectories in the neighbourhood of particular steady-states. For this reason, the first step is to determine the effect of the presence of the predator (protozoa) on the structure of steady-states and the character of their linear stability. For this purpose, steady-state branches were determined for a process without the predator, i.e. for $\gamma = 0$, then similar calculations were carried out in the presence of protozoa ($\gamma > 0$). Results of simulations are presented in Fig. 2.

The diagrams in Fig. 2a and 2b show branches of the state variables $\alpha(\tau)$ and $\beta(\tau)$ depending on the residence time in apparatus τ . Solid lines denote stable states, and dashed lines – unstable ones. As we can see, for the process without the predator, i.e. when $\gamma = 0$, one gets a steady-state branch, characteristic for a process with substrate inhibition. There are three ranges of parameter τ , differing in the number of steady-states. With increasing τ we deal with successively a region of single washout steady-states, afterward triple, and for sufficiently high values of τ , a region of double steady-states. In the regions of multiple steady-states, the upper steady-states are stable, which is advantageous from the technological point of view.

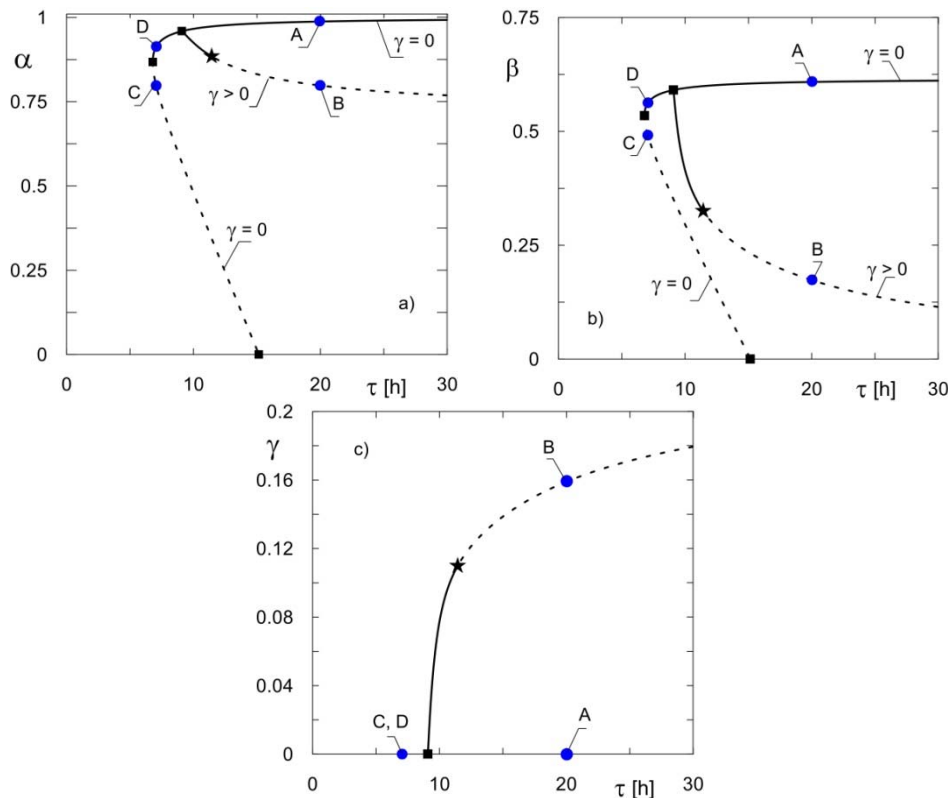


Fig. 2. Steady-state branches of tank bioreactor for microbiological process with substrate limiting biomass growth; $\gamma = 0$ – process without predator presence; $\gamma > 0$ – process according to predator-prey system; — stable steady states; - - - - unstable steady states; * - Hopf bifurcation point; ■ - static bifurcation point

The diagrams placed in Fig. 2 show that the presence of the predator, i.e. when $\gamma > 0$, changes both positions of steady-state branches and the character of their stability. Moreover, of course, there is a non-zero steady-state branch $\gamma(\tau)$. There is a significant decrease of the degrees of conversion values α corresponding to the upper steady states. Furthermore, the states are unstable almost in the whole range of τ . It is an essential consequence of the predator presence. It excludes process guidance in stationary conditions, without automatic control. Points A, B, C, D in Fig. 2 will be used in the further analysis to interpret the results.

Phase portraits, i.e. sets of phase trajectories on state planes, are a source of information about global dynamics of nonlinear objects. On the basis of phase portraits, one can conclude about the number of steady-states, their stability and the dynamics of state variables around particular steady-states. The phase portraits of an uncontrolled bioreactor are the basis for a quantitative and qualitative evaluation of effects of using automatic control. Fig. 3 presents such portraits in the coordinate system (β, α) for a chosen value of the residence time of the liquid τ .

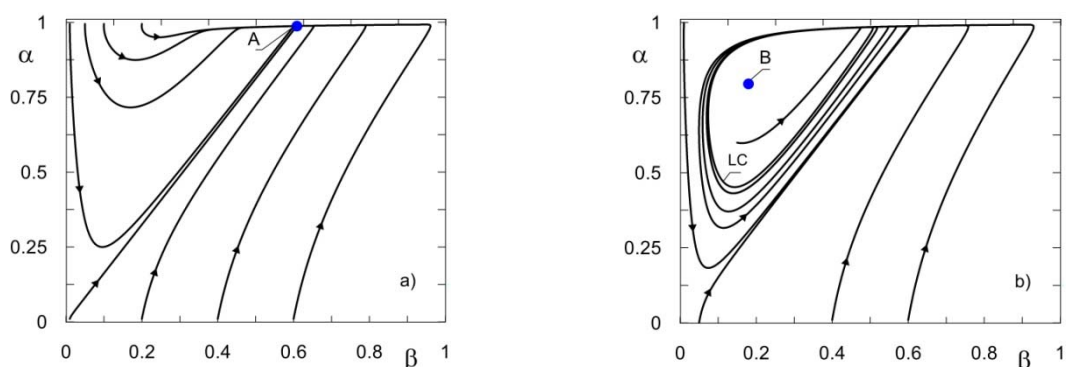


Fig. 3. Phase trajectories of uncontrolled bioreactor;
 a) process without predator; b) process in predator-prey system;
 LC – limit cycle; A, B – points at steady-state branches in Fig. 2

Fig. 3a illustrates the bioreactor dynamics with one microbial species, i.e. without predator ($\gamma = 0$). All trajectories converge to upper steady-state, marked with point A in this diagram and Fig. 2. For the chosen value of the residence time τ , it is the only stable state. If we take into account the predator presence, then not only the steady-state characteristics (Fig. 2), but also the dynamics of this object are altered diametrically. The dynamic characteristics of the bioreactor for the process following scheme (1) is presented in Fig. 3b. Point B in this figure corresponds to point B in steady-state branches presented in Fig. 2. Point B is an unstable focus surrounded by stable limit cycle (LC). The trajectories shown in the phase plane tend to achieve this limit cycle over time. A stable limit cycle is characterised by considerable amplitudes of state variables. Limit cycle means sustained oscillation of all state variables i.e. α , β and γ .

Taking into consideration the stationary characteristics presented in Fig. 2 and dynamic properties of the bioreactor shown in Fig. 3b, it was decided to analyse the nonlinear dynamics of the bioreactor with automatic control.

Representative results illustrating effects of using the proportional controller are presented in Fig. 4. In this Figure, phase portraits of the bioreactor are placed in the plane (β, α) , (γ, β) and (γ, τ) for three values of the gain coefficient of the controller $K_P = \{0.2; 0.4; 0.8\}$. Because the bioreactor volume is constant, variations of volumetric flow rate F_V , caused by controller work, result in variation of mean residence time τ , according to previously given relationship (Equations (4)). For comparison, the dashed line (LC-0) was used to represent a stable limit cycle for the bioreactor without automatic control, i.e. $K_P = 0$. Simulations of the bioreactor dynamics with automatic control were started

according to quantities of state variables on limit cycle for a chosen value of residence time $\tau = 20$, which can be seen in Fig. 4c, f, i.

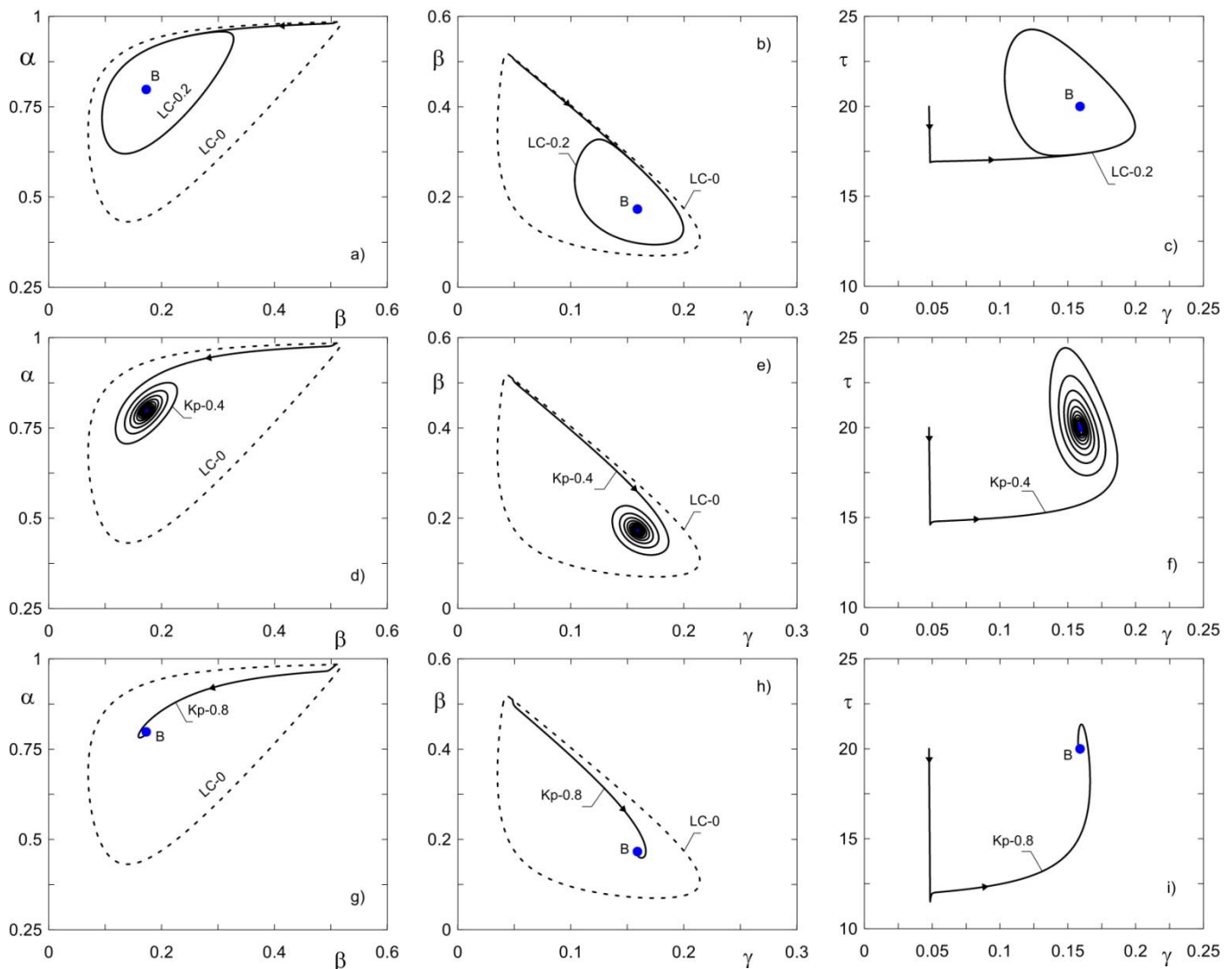


Fig. 4. Phase portraits of bioreactor controlled with proportional controller for three chosen values of the gain coefficient $K_p = \{0.2, 0.4, 0.8\}$; LC-0 limit cycle for uncontrolled bioreactor; LC-0.2 limit cycle for controlled bioreactor with $K_p = 0.2$; B – point at unstable steady-state branch for $\gamma > 0$ in Fig. 2

On the basis of the analysis of phase portraits presented in Fig. 4, one can draw the following conclusions:

- gradual increase of the gain coefficient of the proportional controller causes a decrease of amplitude of limit cycles, at a certain value of K_p stabilisation of unstable steady-state occurs. It is consistent with the theory of automatic control;
- after stabilisation of an unstable steady-state, the bioreactor reaches a stable steady-state, corresponding to point B at steady-state branches presented in Fig. 2a, b, c;
- after stabilisation of a steady-state the biocenosis predator-prey is maintained as well as the initial value of mean residence time of the liquid in the reactor.

The use of the proportional-integral controller gives different as well as surprising results. The bioreactor dynamics with imposed PI control is illustrated as phase trajectories in Fig. 5. It was proved that the use of PI control also leads to stabilisation of steady-state, but in a completely different manner. The addition of an integrating element makes the controller change the volumetric flow rate in such a

way that its position on steady-state branches changes. After stabilisation of unstable steady-state, the bioreactor reaches steady-state marked with point C in Fig. 2. However, point C is present at steady-state branches corresponding to washout of the predator, i.e. $\gamma=0$. The addition of the integrating element, therefore, changes the biocenosis in the bioreactor. Point C also corresponds to the value of mean residence time of the liquid τ varying from the initial value, which in this case was $\tau=20$ h.

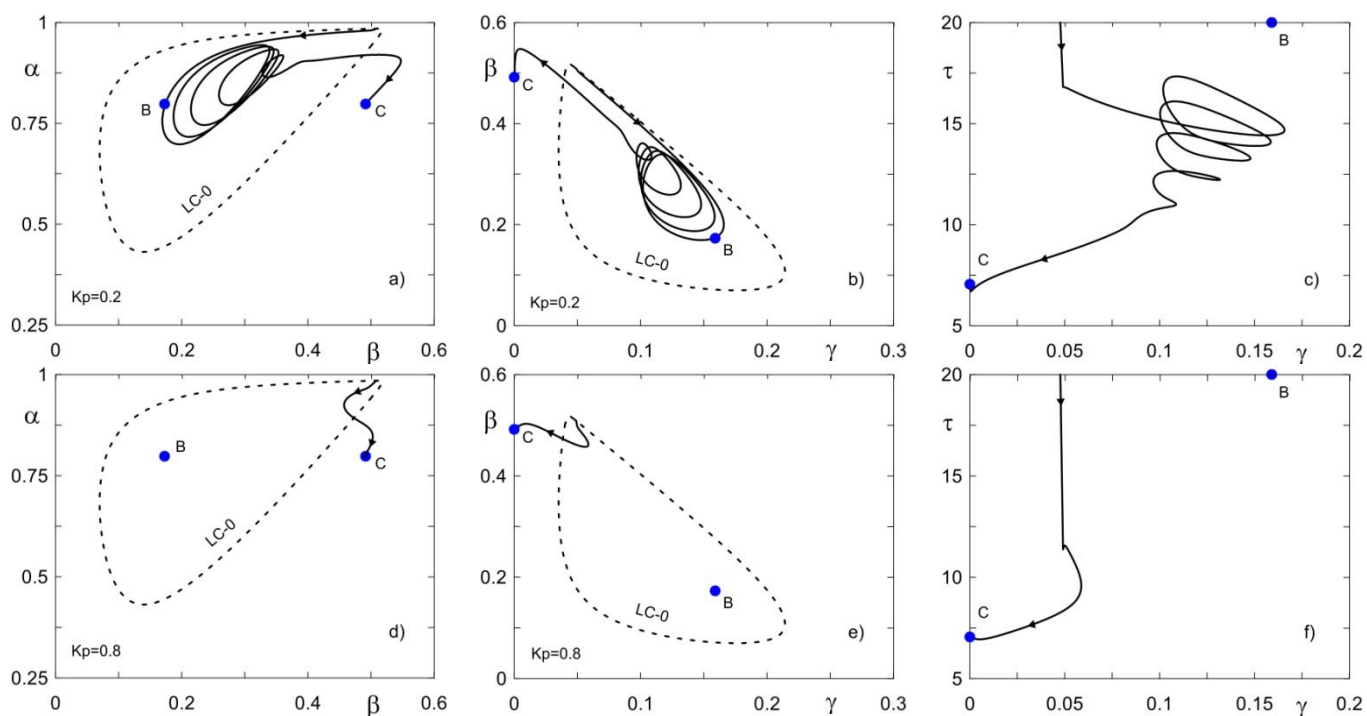


Fig. 5. Phase portraits of bioreactor controlled using the proportional-integral controller for two values of the gain coefficient $K_P=\{0.2, 0.8\}$; LC-0 limit cycle of uncontrolled bioreactor; B, C – points at steady-state branches in Fig. 2

Fig. 5 demonstrates different operations of the proportional and the proportional-integral controller. The explanation of the PI controller performance is presented in Fig. 6 for two values of K_p . Time trajectories $\tau(t)$ have a different shape when using the proportional controller, and another when applying the proportional-integral controller. The PI controller causes a change in the residence time of the liquid in the apparatus by changing the volumetric flow rate F_V in such a way, that finally one reaches a steady-state on the branch corresponding to washout of the predator, i.e. for $\gamma=0$ in Fig. 2.

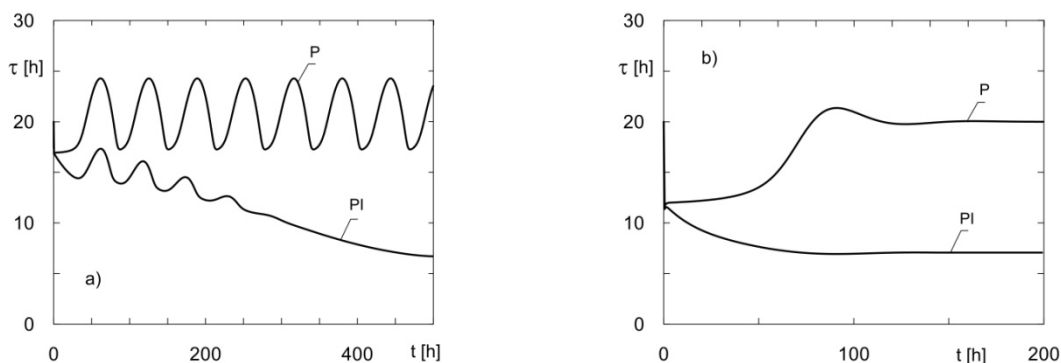


Fig. 6. Control method by mean residence time of liquid in bioreactor using the proportional and the proportional-integral controllers ($T_I=20$ h); a) $K_P=0.2$; b) $K_P=0.8$

The described phenomenon may be used in practice for operation of a bioreactor. After removal of the predator, it is possible, by switching off the automatic control, to restore the bioreactor to any upper steady-state specified by branches $\gamma=0$ in Fig. 2. The effect of such a procedure is shown in Fig. 7. Fig. 7a presents the results of the bioreactor dynamics, corresponding to automatic control off, after reaching point C in Fig. 2. Then, the trajectories of state variables $\alpha(t)$ and $\beta(t)$ tend to achieve upper stable steady-state marked by point D in Fig. 2. If after switching off the automatic control, one will change simultaneously the mean residence time in the apparatus, e.g. to value $\tau=20$ h (Fig. 7b), then trajectories of state variables $\alpha(t)$ and $\beta(t)$ will tend to achieve upper steady-state denoted in Fig. 2 by point A, which corresponds to the stable character of bioreactor work, with high conversion degree of the carbonaceous substrate.

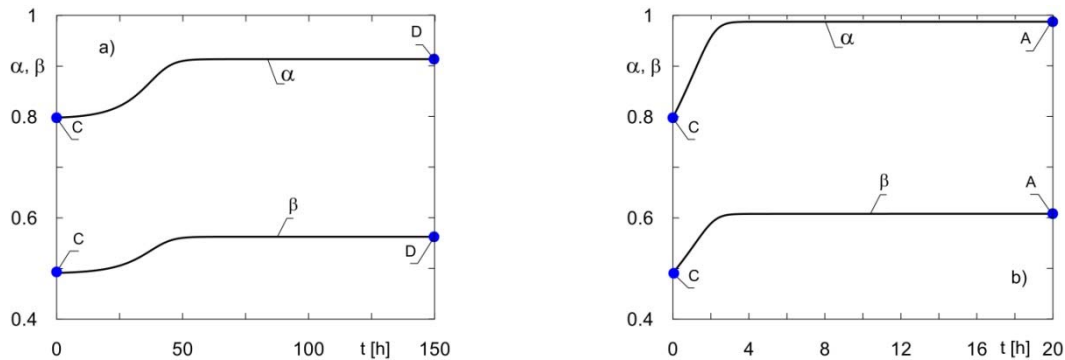


Fig. 7. Dynamics of bioreactor after reaching steady-state C in Fig. 2 and after switching off the automatic control; a) without changing the value of τ corresponding to point C in Fig. 2, the bioreactor will obtain stable steady-state D; b) after changing τ to value corresponding to point A in Fig. 2, the bioreactor will obtain stable steady-state A

4. CONCLUSIONS

This work presents dynamic characteristics of a continuous bioreactor with automatic control. Microbiological process in the bioreactor occurs with substrate inhibition according to the predator-prey scheme. The introduction of a microorganism acting as a predator results in fundamental changes in stationary and dynamic characteristics of the bioreactor. Such a system without automatic control can work only in transient conditions. Then, the productivity is periodically changing, according to dynamics of a stable limit cycle. From the technological point of view, this circumstance is unfavourable, because there are time intervals when the unreacted substrate flows out of the bioreactor. It was demonstrated that oscillations can be removed by employing automatic control with continuous P or PI controllers. Moreover, the use of the controller with an integrating element removes the predator from the bioreactor. In this work, we proposed control by volumetric flow rate, and the conversion degree of carbonaceous substrate is a controlled variable.

The dynamic properties of the controlled bioreactor were determined based on analysis of phase portraits. Closed-loop control system evaluation was performed, as well as two continuous controllers, i.e. proportional and proportional-integral.

It was pointed out that both controllers can lead to stabilisation of unstable steady states in the bioreactor. However, the controllers produce different effects from the point of view of biotechnology.

The performed analysis revealed that the use of P controller for sufficiently large values of gain coefficients allows for stabilisation of unstable steady-state. However, the predator is still in the

bioreactor, precluding obtaining higher degrees of carbonaceous substrate. Additionally, the initial value of τ is maintained.

The effect of PI controller operation is different than that of P controller, although for both types of controllers, volumetric flow rate was used as a control variable. Interestingly, an unknown phenomenon was discovered. It was demonstrated that the use of PI control changes volumetric flow rate and eliminates the predator from the system. Thanks to this, when there is no predator in the bioreactor, it is possible to obtain any upper steady-state with a high degree of conversion of the substrate, i.e. as for a process without the predator. Technological importance of this solution is high due to the necessity of thorough biodegradation of wastewater containing toxic compounds, like e.g. phenol. It is also significant from the technological point of view, that the removal of the predator from the system can be performed without stopping the operation of the bioreactor.

Obtained results can be the basis for future analysis of dynamics and control of other ecosystems with predator-prey interaction.

SYMBOLS

A	limiting substrate
B	bacteria (prokaryote)
c_A, c_B, c_D	mass concentration of limiting substrate, bacteria and protozoa, kg/m^3
c_{Af}	concentration of limiting carbonaceous substrate in a feed stream, kg/m^3
D	protozoa (eukaryote)
F_V	volumetric flow rate through the reactor, m^3/h
k, k_D	constants in kinetic equations, $1/\text{h}$
K_s, K_{in}	constants in kinetic equations, kg/m^3
K_I, K_P	settings of the controllers, h
r_A, r_B, r_D	substrate consumption rate, growth rate of bacteria and protozoa, $\text{kg}/(\text{m}^3 \cdot \text{h})$
t	time, h
V	volume of the bioreactor, m^3
w_{BA}, w_{DB}	yield coefficients, $\text{kg B}/(\text{kg A}), \text{kg D}/(\text{kg B})$
x	state vector

Greek symbols

α	degree of conversion of the limiting substrate
β	dimensionless concentration of bacteria
γ	dimensionless concentration of protozoa
λ	vector of model parameters or selected model parameter
τ	mean residence time of liquid, h

Subscripts

A, B, D	refers to limiting substrate, bacteria and protozoa, respectively
f	refers to feed stream

REFERENCES

- Ajbar A., 2001a. Classification of stability behaviour of bioreactors with wall attachment and substrate-inhibited kinetics. *Biotechnol. Bioeng.*, 72, 166-176. DOI: 10.1002/1097-0290(20000120)72:2<166::AID-BIT5>3.0.CO;2-R.

- Ajbar A., 2001b. On the existence of oscillatory behavior in unstructured models of bioreactors. *Chem. Eng. Sci.*, 56, 1991-1997. DOI: 10.1016/S0009-2509(00)00423-1.
- Ajbar A., Alhumazi K., 2012. *Dynamics of the chemostat. A bifurcation theory approach*. CRC Press, London – New York.
- Alhumazi K., Ajbar A., 2005. Dynamics of predator-prey interactions in continuous cultures. *Eng. Life Sci.*, 5, 139-147. DOI: 10.1002/elsc.200420062.
- Butler G.J., Hsu S.B., Waltman P., 1983. Coexistence of competing predators in chemostat. *J. Math. Biol.*, 17, 133-151. DOI: 10.1007/BF00305755.
- Chi C.T., Howell J.A., Pawlowsky U., 1974. The regions of multiple stable steady states of a biological reactor with wall growth, utilising inhibitory substrates. *Chem. Eng. Sci.*, 29, 207-211. DOI: 10.1016/0009-2509(74)85046-3.
- Dunn I.J., Heinzle E., Ingham J., Prenosil J.E., 2003. *Biological reaction engineering. Dynamic modelling fundamentals with simulation examples*. Wiley-VCH Verlag, Weinheim.
- El-Owaidy H.M., Moniem A.A., 2003. On food chain in a chemostat with distinct removal rates. *Appl. Math. E-Notes*, 3, 183-191.
- Li B., Kuang Y., 2000. Simple food chain in a chemostat with distinct removal rates. *J. Math. Anal. Appl.*, 242, 75-92. DOI: 10.1006/jmaa.1999.6655.
- Lotka J.A., 1925. *Elements of physical biology*, Williams & Wilkins, Baltimore.
- Luyben W.L., 1999. *Process modeling, simulation and control for chemical engineers*. McGraw-Hill, Inc., New York-Toronto.
- Moghadas S.M., Gumel A.B., 2003. Dynamical and numerical analyses of a food-chain model. *Appl. Math. Comp.*, 142, 35-49. DOI: 10.1016/S0096-3003(02)00282-5.
- Moussa M.S., Hooijmans C.M., Lubberding H.J., Gijzen H.J., Loosdrecht M.C.M., 2005. Modelling nitrification, heterotrophic growth and predation in activated sludge. *Water Res.*, 39, 5080-5098. DOI: 10.1016/j.watres.2005.09.038.
- Onysko K.A., Robinson C.W., Budman H.M., 2002. Improved modelling of the unsteady-state behavior of an immobilized-cell, fluidized-bed bioreactor for phenol biodegradation. *Can. J. Chem. Eng.*, 80, 239-252. DOI: 10.1002/cjce.5450800209.
- Olivieri G., Russo M. E., Marzocchella A., Salatino P., 2011. Modeling of an aerobic biofilm reactor with double-limiting substrate kinetics: Bifurcational and dynamical analysis. *Biotechnol. Progress*, 27, 1599-1613. DOI: 10.1002/btpr.690.
- Pavlou S., 1999. Computing operating diagrams of bioreactors. *J. Biotechnol.*, 71, 7-16. DOI: 10.1016/S0168-1656(99)00011-5.
- Ratsak C.H., Maarsden K.A., Kooijman S.A.L.M., 1996. Effects of protozoa on carbon mineralization in activated sludge. *Water Res.*, 30, 1-12. DOI: 10.1016/0043-1354(95)00096-4.
- Russo M.E., Maffettone P.I., Marzocchella A., Salatino P., 2008. Bifurcation and dynamical analysis of a continuous biofilm reactor. *J. Biotechnol.*, 135, 295-303. DOI: 10.1016/j.jbiotec.2008.04.003.
- Scudo F.M., Ziegler J.R., 1978. *The golden age of theoretical ecology: 1923-1940*. Springer-Verlag, Berlin, Heidelberg, New York.
- Tabiś B., 1996. Investigation of parametric dependency and linear stability of a cascade of stirred tank bioreactors. *Inż. Chem. Proc.*, 17, 279-294 (in Polish).
- Tabiś B., Malik J., 1996. Steady states multiplicity in a cascade of stirred tank bioreactors for phenol degradation. *Inż. Chem. Proc.*, 17, 645-651 (in Polish).
- Tabiś B., Malik J., 1998. Stability characteristics of a biochemical reactor with predator-prey relationship. A substrate inhibition case. *Chem. Eng. J.*, 70, 179-188. DOI: 10.1016/S1385-8947(98)00094-1.
- Tsuchiya M.M., Drake J.F., Jost J.L., Fredrickson A.G., 1972. Predator-prey interactions of *Distyostelium discoideum* and *Escherichia coli* in continuous culture. *J. Bacteriol.*, 110, 1147-1153.
- Volterra V., 1926. Variazione e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. Accad. Nazion. Lincei*, 2, 31-113.
- Yang R.D., Humphrey A.E., 1975. Dynamics and steady state studies of phenol biodegradation in pure and mixed cultures. *Biotechnol. Bioeng.*, 17, 1211-1235. DOI: 10.1002/bit.260170809.
- Zhu H., Campell S.A., Wolkowicz G.S.K., 2002. Bifurcation analysis of a predator-prey system with nonmonotonic functional response. *SIAM J. Appl.*, 63, 636-682. DOI: 10.1137/S0036139901397285.

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