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# RELATIONSHIP BETWEEN GROWTH CHARACTERISTICS OF MICROALGAE CULTURE AND AGE-SPECIFIC CELL STATE IN ONTOGENESIS (PROBABILISTIC MODEL)

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The article presents a quantitative model of the dependence of the morphological structure of the continuous microalgae culture on external lighting and species-specific cell parameters. The modeling is based on the concept of two main phases that make up the cell life cycle – interphase and division phase. The interphase is regarded as a light-dependent process during which cell biomass increases. The division phase does not depend on light and occurs when a cell reaches a certain mass equal to (or higher than) the sum of masses of daughter cells. The division stage ends with cytokinesis: a cell splits into daughter cells. The age-specific microalgae cell state is characterized by the value of its biomass, while transitions from one state to another are characterized by the activity (growth and division). The model is represented by a system of differential equations that fully describe the dynamics of ontogenesis. A particular solution of the model for dynamically equilibrium growth of microalgae in the culture at different light intensity is analyzed. As shown, in the continuous microalgae culture under photolithotrophic conditions, the specific growth rate is related to the morphological structure of the cell population by simple directly proportional equations with species-specific coefficients. These coefficients are the maximum growth rate in the interphase (at saturating light intensity) and cell division activity in mitosis.

**Keywords:** microalgae, ontogenesis, age-specific cell state, interphase, mitosis, probabilistic model, growth rate, morphological structure of culture

Considering a microalgae monoculture as a population of individual cells, one can speak about the age population structure, or rather morphological population structure, which is determined by the relationship of age groups (the same as in all plants). The difference between microalgae and higher plants is as follows: in the strict sense, there is no age concept for individual microalgae cells in a population. To characterize age groups and individual cells, the concept of an age-specific state, or ontogenetic state, is applied. The transition from one state to another is one-sided and directed towards growth; it can occur at the same or different rate depending on the actual ontogenetic state and the cell environment.

The microalgae growth in culture is directly related to the growth of each individual cell and the rate of division, *i. e.*, to cell cycle, the duration of which is determined by the properties of the cell environment. The study of ontogenesis of individual microalgae cells is a difficult task since they are microscopic in size. Ideally, ontogenetic investigations can be carried out with a coeval cell population [Helmstetter, 2015]. Methodically, it can be done; the possibility is connected with occurrence of light-dependent

and light-independent phases of microalgae cell development in ontogenesis [Tsoglin, Klyachko-Gurvich, 1980]. By establishing the relationship between durations of light and dark regimes for a particular microalgae culture, the age-specific state for all cells in culture can be synchronized [Tsoglin, 1996; Tsoglin, Klyachko-Gurvich, 1980]. Significant progress in the work with synchronous *Chlorella* cultures is reflected in publications of the researchers [Tsoglin, 1996; Tsoglin, Pronina, 2012].

To date, there are many papers concerning the study of the eukaryotic cell cycle, *inter alia* early works [Winter, 1835] and recent large reviews, such as [Cvrčková, 2018]. The latter publication emphasizes that current understanding of the processes leading to cell division is based on a limited range of concepts, although a lot of hypotheses were proposed earlier.

A similar situation is observed when constructing mathematical models for describing the age-specific cell state in ontogenesis or the cell size distribution within a microbial population [Karlin, 1968; Riznichenko, 2011; Stepanova, 1980]. The most developed kinetic models of eukaryotic regulation of the cell cycle are based on the concept of cyclin-dependent kinases and cyclins [Novák et al., 1999; Sasabe, Machida, 2014]. However, this refers mostly to the very fact of division and is not directly related to the growth processes of an individual cell, especially at the initial stage of the life cycle [Wang, Levin, 2009; Wilkins, Holliday, 2009]. Moreover, the proposed kinetic models include a large number of differential equations, and this ultimately leads to the need for reducing the systems of equations to a small amount [Sible, Tyson, 2007; Tyson, Novák, 2001, 2015].

To establish the relationship between the microalgae growth characteristics in culture and its morphological structure, it is necessary to know the effect of the environment on the life cycle (the age-specific state of individual cells). This relationship can be quantified in various ways. In this work, the age-specific cell state and its transitions during the life cycle are modeled by probabilistic methods.

**Basic provisions.** The life cycle of a microalgae cell, or cell cycle, consists of several periods, which are combined into two distinct phases – interphase and mitosis or meiosis [Cvrčková, 2018; Tyson, Novák, 2015]. During the interphase, a cell grows; then, the processes of DNA replication begin, and a cell enters the division stage; it ends with cytokinesis – a cell splits into daughter cells. During mitosis, two distinct daughter cells are formed. During meiosis, which can be considered as a sequence of several mitoses (or autospores), cytokinesis ends with the formation of several daughter cells [Tsoglin, Pronina, 2012; Wilkins, Holliday, 2009], with their abundance depending on the quantity of mitoses according to an exponential law.

To characterize the age-specific cell state, various parameters can be applied. Cell biomass (b) can be considered as the most appropriate quantitative characteristic of the age-specific microalgae cell state. Indeed: in order for a cell to divide into daughter cells (d), its biomass in the interphase must increase to a value ($b_m$) higher than or equal to the sum of masses of daughter cells ($b_0$):

$$b_m \geq db_0,\ d = 2, 4, 8, 16...$$

This inequality may be due to the fact that the process of cell division is accompanied by the internal energy consumption and, consequently, by the mass loss [Pederson, 2003; Tsoglin, 1996]. Moreover, the mass loss can result from a cell wall destruction, flagella shedding, *etc.*

The cell biomass structural form seems to be a more accurate characteristic [Trenkenshu et al., 2018] if we consider the mass loss during division to be insignificant. In this case, it becomes possible to assess the biomass structural form by measuring chlorophyl concentration, which is proportional to the cell

biomass structural form [Trenkenshu et al., 2018]. At the same time, a key point in terms of methodology is the ability to measure pigments and biomass optically – without damage to the cell structural integrity.

The growth of microalgae in culture is characterized by the rate of change in its density (biomass B or cell abundance N) over time t. For relatively long constant external conditions, the specific growth rate μ remains constant:

$$\mu = \frac{dB}{Bdt} = \frac{dN}{Ndt}.$$

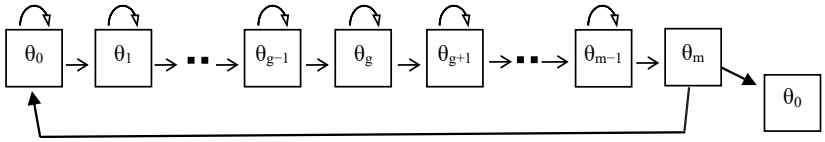
If, as a result of cytokinesis, an individual cell is divided into d daughter cells, the duration of the life cycle is related to the specific growth rate of the culture by a simple ratio:

$$\tau_z = \frac{\ln d}{\mu}.$$

Distinguishing two time periods in the life cycle [the growth stage (interphase $\tau_g$) and the division stage (mitosis $\tau_m$)], we state that their sum is equal to the duration of the life cycle:

$$\tau_z = \tau_g + \tau_m.$$

**Probabilistic model of ontogenesis.** The life cycle of an individual microalgae cell can be represented as a graph of the age-specific states in which the cell can be. To do this, we express the probability that a cell is in one of its growth states through $\theta_g(t)$, and the probability that it is in the division stage, through $\theta_m(t)$.




We denote the activity of transitions from one state to another with subscripts corresponding to the probabilities from which the transition occurs. Thus, the growth transition activity is $\mu_g$ ($0 \le g \le m - 1$), and the activity of complete cell division into daughter cells is $\mu_m$. Analytically, such a graph can be outlined by a system of differential equations that completely describes the change in the cell state over time:

$$\begin{cases} \frac{d\theta_0(t)}{dt} = -\mu_0\theta_0(t) + \mu_m\theta_m(t), \\ \frac{d\theta_1(t)}{dt} = -\mu_1\theta_1(t) + \mu_0\theta_0(t), \\ \ldots\ldots\ldots\ldots \\ \frac{d\theta_g(t)}{dt} = -\mu_r\theta_g(t) + \mu_{g-1}\theta_{g-1}(t);\ [0 \le g \le m-1], \\ \ldots\ldots\ldots\ldots \\ \frac{d\theta_m(t)}{dt} = -\mu_m\theta_m(t) + \mu_{m-1}\theta_{m-1}(t). \end{cases}$$

Normalization condition for all the states is as follows:

$$\theta_m + \sum_{g=0}^{m-1} \theta_g = 1.$$

By integrating the obtained system of equations, one can completely describe the dynamics of cell ontogenesis for any moment of time. However, an exact formal description of cyclic graphs is mathematically difficult due to integration problems [Karlin, 1968]. Nevertheless, some particular solutions are possible, and those can be used in assessing the morphological structure of microalgae populations.

**Stationary case.** Of particular interest is the solution of the system of equations for the stationary case. In a stationary (dynamically equilibrium) process, the state probabilities are equal to their limits:

$$\lim_{\Delta t\to 0}\theta_g(t)=\theta_g;\ 0\le g\le m-1),\ \lim_{\Delta t\to 0}\theta_m(t)=\theta_m,$$

and the derivatives of the probabilities in terms of time are equal to zero:

$$\frac{d\theta_g(t)}{dt}=0;\ (0\le\ g\le\ m-1),\ \frac{d\theta_m(t)}{dt}=0.$$

The system of differential equations turns into an algebraic one:

$$\begin{cases}\frac{d\theta_0}{dt}=0=-\mu_0\theta_0+\mu_m\theta_m,\\ \frac{d\theta_1}{dt}=0=-\mu_1\theta_1+\mu_0\theta_0,\\ \ldots\ldots\ldots\\ \frac{d\theta_g}{dt}=0=-\mu_g\theta_g+\mu_{g-1}\theta_{g-1};\ [0\le g\le m-1],\\ \ldots\ldots\ldots\\ \frac{d\theta_m}{dt}=0=-\mu_m\theta_m+\mu_{m-1}\theta_{m-1}.\end{cases}$$

We express the required probabilities for the interphase in terms of the probability of the initial state:

$$\theta_1=\frac{\mu_0}{\mu_1}\theta_0,\ \theta_2=\frac{\mu_0}{\mu_2}\theta_1=\frac{\mu_0}{\mu_2}\frac{\mu_0}{\mu_1}\theta_0,\ \ldots,\ \theta_g=\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}\theta_0.$$

The probability of the age-specific cell state in the division stage is as follows:

$$\theta_m=\frac{\mu_0}{\mu_m}\theta_0.$$

Condition for normalization over all the states is:

$$\frac{\mu_0}{\mu_m}\theta_0+\sum_{g=0}^{m-1}\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}\theta_0=1.$$

Hence, we obtain the dependences of the probability density of cell being in the growth state ($\Theta_g$) and in the division stage ($\Theta_m$):

$$\Theta_g=\frac{\theta_g}{\frac{\mu_0}{\mu_m}\theta_0+\sum_{g=0}^{m-1}\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}\theta_0}=\frac{\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}}{\frac{\mu_0}{\mu_m}+\sum_{g=0}^{m-1}\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}};$$

$$\Theta_m = \frac{\theta_m}{\frac{\mu_0}{\mu_m}\theta_0 + \sum_{g=0}^{m-1} \frac{(\mu_o)^g}{\prod_{g=0}^{m-1}\mu_g}\theta_0} = \frac{\frac{\mu_0}{\mu_m}}{\frac{\mu_0}{\mu_m} + \sum_{g=0}^{m-1} \frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}}.$$

It is possible to use the model obtained for describing age or size cell distribution in a microalgae culture, only if we know the relationship between the probabilistic coefficients of the ontogenesis model and the kinetic characteristics of the culture. First of all, we take into account that the last equations were obtained for continuous dynamically equilibrium conditions. Thus, the equations can be applied to continuous microalgae cultures. This means that probability densities of cells being in a growth state and division stage will show the quantitative ratio of growing cells ($n_g$/N) and the ratio of dividing cells ($n_m$/N) in their total abundance (N):

$$n_g + n_m = N,$$

$$\frac{n_g}{N} = \Theta_g = \frac{\frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}}{\frac{\mu_0}{\mu_m} + \sum_{g=0}^{m-1} \frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}}; \frac{n_m}{N} = \Theta_m = \frac{\frac{\mu_0}{\mu_m}}{\frac{\mu_0}{\mu_m} + \sum_{g=0}^{m-1} \frac{(\mu_0)^g}{\prod_{g=0}^{m-1}\mu_g}}.$$

The ontogenetic state of cells is described by a set of probabilistic coefficients that determine transitions from one state to another. Interestingly, this process is cyclic: in the interphase, it is directed towards growth; in the division phase, it returns the cell to its initial state. The rate of transitions is taken into account by activity factors which generally determine the life cycle. As established, there are two phases in the microalgae life cycle – light-dependent and light-independent [Tsoglin, Klyachko-Gurvich, 1980; Tsoglin, Pronina, 2012]. The first relates to the interphase while the second relates to mitosis.

The continuity of growth, both for a microalgae culture and an individual cell, is characterized by a constant specific rate, in other words, by an exponential increase in the culture density (biomass concentration) and the cell biomass. The continuity of biomass growth under constant light allows simplifying the equation for the probability density of cell being in the growth state and mitosis:

$$\mu_0 = \mu_g = \text{const}, \ \mu_m = \text{const},$$

$$\Theta_g = \frac{\theta_g}{\frac{\mu_g}{\mu_m} + \sum_{g=0}^{m-1} \frac{(\mu_g)^g}{\prod_{g=0}^{m-1}\mu_g}} = \frac{1}{1+\mu_g/\mu_m}, \ \Theta_m = \frac{\theta_m}{\frac{\mu_g}{\mu_m} + \sum_{g=0}^{m-1} \frac{(\mu_g)^g}{\prod_{g=0}^{m-1}\mu_g}} = \frac{\mu_g/\mu_m}{1+\mu_g/\mu_m},$$

$$\Theta_g = \frac{\mu_m}{\mu_g+\mu_m}, \ \Theta_m = \frac{\mu_g}{\mu_g+\mu_m}.$$

**The effect of light on the age-specific cell state.** With continuous photolithotrophic [Stukolova, Trenkenshu, 2020] microalgae growth, the duration of the interphase depends on a light intensity at which cell grows. This means that the activity of transitions of age-specific states in the interphase is also dependent on light conditions under which the cell is. The effect of light on the biomass specific growth rate in the interphase can be described by the equation [Lelekov, Trenkenshu, 2019]:

$$\mu_g = \begin{cases} \mu_{gmax}(i - i_{cp}), \ i_{cp} \le i \le 1; \\ \mu_{gmax}, \ i - i_{cp} \ge 1. \end{cases}$$

There, $\mu_{gmax}$ is the maximum specific rate of the cell mass growth at saturating light intensity;

i is the light intensity normalized relative to saturating one;

$i_{cp}$ is the compensation point of photosynthesis in normalized units.

As a result, the probability density of cell being in the growth state or mitosis will depend on non-saturating light intensity according to the equation:

$$\Theta_g = \frac{\mu_m}{\mu_{gmax}(i - i_{cp}) + \mu_m},\ (i_{cp} \le i \le 1);\ \Theta_m = \frac{\mu_{gmax}(i - i_{cp})}{\mu_{gmax}(i - i_{cp}) + \mu_m},\ (i_{cp} \le i \le 1).$$

At light intensities equal to or higher than saturating intensity:

$$\Theta_g = \frac{\mu_m}{\mu_{gmax} + \mu_m}, (i - i_{cp}) \ge 1;\ \Theta_m = \frac{\mu_{gmax}}{\mu_{gmax} + \mu_m}, (i - i_{cp}) \ge 1.$$

Given that the maximum transition activities during growth and division are species-specific constants, their ratio ($\mu_{gmax}/\mu_m$) is also a species-specific constant. This allows writing the above equations in the form:

$$\begin{cases} \Theta_g = \frac{1}{1+\mu_{gmax}(i-i_{cp})/\mu_m},\ (i_{cp} \le i \le 1);\ \Theta_m = \frac{\mu_{gmax}(i-i_{cp})/\mu_m}{1+\mu_{gmax}(i-i_{cp})/\mu_m},\ (i_{cp} \le i \le 1), \\ \Theta_g = \frac{1}{1+\mu_{gmax}/\mu_m},\ (i - i_{cp}) \ge 1;\ \Theta_m = \frac{\mu_{gmax}/\mu_m}{1+\mu_{gmax}/\mu_m},\ (i - i_{cp}) \ge 1. \end{cases}$$

The obtained equations are graphically illustrated in Fig. 1.

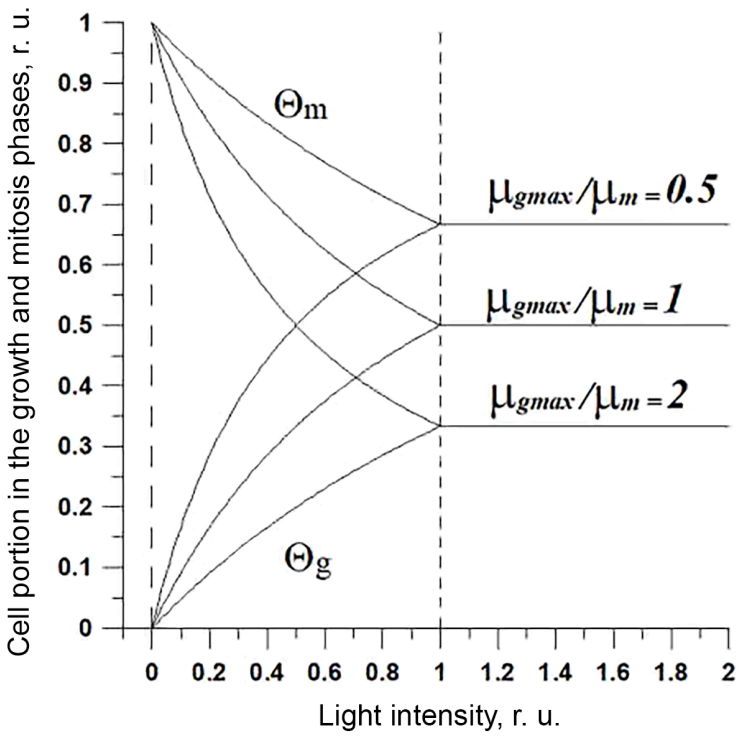



**Fig. 1.** Dependence of the cell proportion in the interphase ($\Theta_g$) and in the mitosis phase ($\Theta_m$) on light intensity at different species-specific ratios (shown by numbers) of specific growth rate of the cell mass and mitosis rate ($\mu_{gmax}/\mu_m$)

Fig. 2 clearly shows how the morphological structure of the microalgae population at saturating light intensity depends on the species-specific ratio $\mu_{gmax}/\mu_m$.

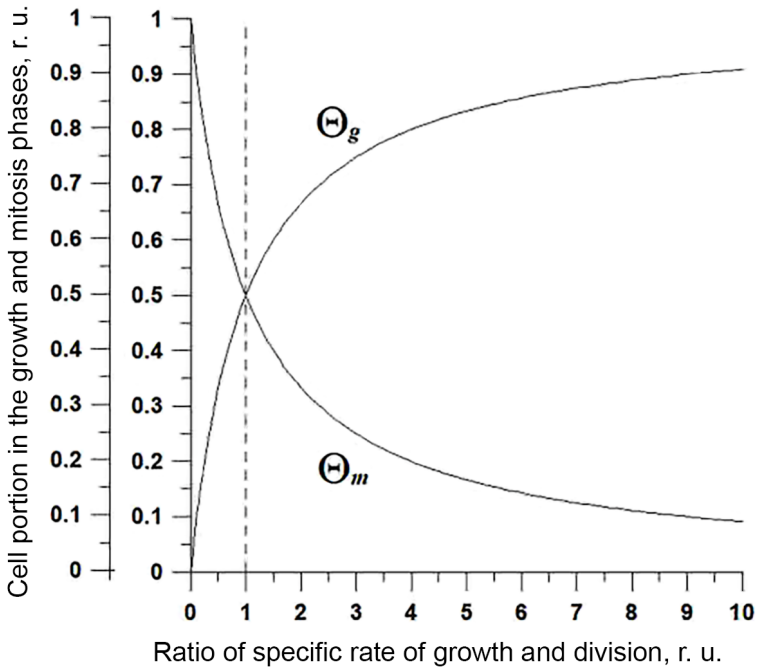



**Fig. 2.** Dependence of the cell proportion in the interphase ($\Theta_g$) and in the mitosis phase ($\Theta_m$) on the species-specific ratio of specific growth rate of the cell mass and mitosis rate ($\mu_{gmax}/\mu_m$) at saturating light intensity

There is an important corollary of the obtained equations. As the last equation shows, it is possible to experimentally find the quantitative value of the species-specific ratio $\mu_{gmax}/\mu_m$. To do this, it is necessary to identify the distribution of growing or dividing cells in a continuous microalgae culture at saturating light intensity:

$$(i - i_{cp}) \geq 1,$$

$$\frac{\mu_{gmax}}{\mu_m} = \frac{1 - \Theta_g}{\Theta_g}; \; \frac{\mu_{gmax}}{\mu_m} = \frac{\Theta_m}{1 - \Theta_m}.$$

**Relationship between specific growth rate in a culture and probability density of the age-specific cell state.** First, we determine the relationship between the specific growth rate and the activities of cell transitions from one state to another. This requires some transformations:

$$\tau_z = \tau_g + \tau_m, \;\; \frac{\ln d}{\mu} = \frac{\ln d}{\mu_g} + \frac{\ln d}{\mu_m}, \;\; \frac{1}{\mu} = \frac{1}{\mu_g} + \frac{1}{\mu_m}, \;\; \mu = \frac{\mu_g \mu_m}{\mu_g + \mu_m}.$$

Comparing this result with the obtained probability density of age-specific cell states, we finally get:

$$\Theta_g = \frac{\mu_m}{\mu_g + \mu_m}, \;\; \Theta_m = \frac{\mu_g}{\mu_g + \mu_m},$$

$$\mu = \frac{\mu_g \mu_m}{\mu_g + \mu_m} = \mu_g \Theta_g = \mu_m \Theta_m.$$

The obtained relationship equations allow assessing the morphological structure of a microalgae cell population at different specific growth rates of a microalgae culture. This value is determined by a simple formula:

$$\frac{n_g}{N} = \Theta_g = \frac{\mu}{\mu_g};\ \frac{n_m}{N} = \Theta_m = \frac{\mu}{\mu_m}.$$

**Conclusion.** Based on the concept of two main phases that make up the cell life cycle – interphase and division phase, a probabilistic model of the dynamics of changes in the age-specific microalgae cell state in ontogenesis is developed.

The age-specific microalgae cell state is characterized by its biomass value, while transitions from one state to another are characterized by the activity of growth and division. For photolithotrophic conditions of microalgae cultivating, the interphase is regarded as a light-dependent process during which cell biomass grows. The division phase does not depend on light and starts after a cell reaches a certain mass.

A particular solution of the model is found for the dynamically equilibrium microalgae growth in culture at different light intensities. As shown, the activities of cell transitions from the growth state to the cytokinesis stage are species-specific microalgae culture parameters, and their quantitative ratio is constant at saturating light intensity.

It is shown that in a continuous microalgae culture under photolithotrophic conditions, the specific growth rate is related to the morphological structure of a cell population by simple directly proportional equations with species-specific coefficients. These coefficients are the maximum growth rate in the interphase (at saturating light intensity) and cell division activity in mitosis.

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## REFERENCES

1. Karlin S. Determinirovannyi rost populyatsii s raspredeleniem po vozrastam. In: Karlin S. *Osnovy teorii sluchainykh protsessov*. Moscow : Mir, 1968, pp. 387–395. (in Russ.)
2. Lelekov A. S., Trenkenshu R. P. Modeling of photosynthesis light curves by linear splines. *Ekologiya gidrosfery*, 2019, no. 2 (4), pp. 20–29. (in Russ.). https://doi.org/10.33624/2587-9367-2019-2(4)-20-29
3. Riznichenko G. Yu. *Lektsii po matematicheskim modelyam v biologii.* Moscow : Izd-vo RKhD, 2011, 560 p. (in Russ.)
4. Stepanova N. V. Matematicheskie modeli nepreryvnoi kul'tury mikroorganizmov, raspredelennykh po vozrastam i razmeram. In: *Matematicheskie modeli v ekologii*. Gorky : Izd-vo GGU, 1980, pp. 95–113. (in Russ.)
5. Stukolova I. V., Trenkenshu R. P. The main types of algae nutrition (short glossary). *Voprosy sovremennoi algologii*, 2020, no. 1 (22), pp. 34–38. (in Russ.). https://doi.org/10.33624/2311-0147-2020-1(22)-34-38
6. Trenkenshu R. P., Lelekov A. S., Novikova T. M. Linear growth of marine microalgae culture. *Morskoj biologicheskij zhurnal*, 2018, vol. 3, no. 1, pp. 53–60. (in Russ.). https://doi.org/10.21072/mbj.2018.03.1.06
7. Tsoglin L. N. *Tsikly razvitiya kletok i fiziologicheskie svoistva populyatsii mikrovodoroslei* : avtoref. dis. … d-ra biol. nauk : 03.00.12. Moscow, 1996, 77 p. (in Russ.)
8. Tsoglin L. N., Klyachko-Gurvich G. L. Changes in functional activity of the chloroplast in the chlorella cell cycle. *Fiziologiya rastenii*, 1980, vol. 27, no. 6, pp. 1172–1179. (in Russ.)
9. Tsoglin L. N., Pronina N. A. *Biotekhnologiya mikrovodoroslei.* Moscow : Nauchnyi mir, 2012, 184 p. (in Russ.)

10. Cvrčková F. A brief history of eukaryotic cell cycle research. In: *Concepts in Cell Biology – History and Evolution* / V. P. Sahi, F. Baluška (Eds). Cham, Switzerland : Springer, 2018, pp. 67–93. (Plant Cell Monographs (CELLMONO ; vol. 23)). https://doi.org/10.1007/978-3-319-69944-8_4
11. Helmstetter Ch. E. A ten-year search for synchronous cells: Obstacles, solutions, and practical applications. *Frontiers in Microbiology*, 2015, vol. 6, art. no. 238 (10 p.). https://doi.org/10.3389/fmicb.2015.00238
12. Novák B., Tóth A., Csikász-Nagy A., Györffy B., Tyson J. J., Nasmyth K. Finishing the cell cycle. *Journal of Theoretical Biology*, 1999, vol. 99, iss. 2, pp. 223–233. https://doi.org/10.1006/jtbi.1999.0956
13. Pederson T. Historical review: An energy reservoir for mitosis, and its productive wake. *Trends in Biochemical Sciences*, 2003, vol. 28, iss. 3, pp. 125–129. https://doi.org/10.1016/s0968-0004(03)00030-6
14. Sasabe M., Machida Y. Signaling pathway that controls plant cytokinesis. In: *Signaling Pathways in Plants* / Y. Machida, C. Lin, F. Tamanoi (Eds). London ; San Diego ; Oxford : Academic Press, 2014, chap. 6, pp. 145–165. (The Enzymes ; vol. 35). https://doi.org/10.1016/B978-0-12-801922-1.00006-3
15. Sible J. C., Tyson J. J. Mathematical modeling as a tool for investigating cell cycle control networks. *Methods*, 2007, vol. 41, iss. 2, pp. 238–247. https://doi.org/10.1016/j.ymeth.2006.08.003
16. Tyson J. J., Novák B. Regulation of the eukaryotic cell cycle: Molecular antagonism, hysteresis, and irreversible transitions. *Journal of Theoretical Biology*, 2001, vol. 210, iss. 2, pp. 249–263. https://doi.org/10.1006/jtbi.2001.2293
17. Tyson J. J., Novák B. Temporal organization of the cell cycle. *Current Biology*, 2008, vol. 18, iss. 17, pp. R759–R768. https://doi.org/10.1016/j.cub.2008.07.001
18. Tyson J. J., Novák B. Models in biology: Lessons from modeling regulation of the eukaryotic cell cycle. *BMC Biology*, 2015, vol. 13, iss. 1, art. no. 46 (10 p.). https://doi.org/10.1186/s12915-015-0158-9
19. Wang J. D., Levin P. A. Metabolism, cell growth and the bacterial cell cycle. *Nature Reviews Microbiology*, 2009, vol. 7, iss. 11, pp. 822–827. https://doi.org/10.1038/nrmicro2202
20. Wilkins A. S., Holliday R. The evolution of meiosis from mitosis. *Genetics*, 2009, vol. 181, iss. 1, pp. 3–12. https://doi.org/10.1534/genetics.108.099762
21. Winter A. W. Ueber die Vermehrung der Pflanzen-Zellen durch Theilung. [dissertation]. Tübingen : L. F. Fues, 1835. 20 S.

## СВЯЗЬ РОСТОВЫХ ХАРАКТЕРИСТИК КУЛЬТУР МИКРОВОДОРОСЛЕЙ С ВОЗРАСТНЫМ СОСТОЯНИЕМ КЛЕТОК В ОНТОГЕНЕЗЕ (ВЕРОЯТНОСТНАЯ МОДЕЛЬ)

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В работе представлена количественная модель зависимости морфологической структуры непрерывной культуры микроводорослей от внешнего освещения и видоспецифических параметров клеток. В основе моделирования лежит представление о двух ключевых фазах, составляющих жизненный цикл клетки, — интерфазе и фазе деления. Интерфаза рассматривается как светозависимый процесс, при котором происходит рост биомассы клетки. Фаза деления не зависит от света и наступает после достижения клеткой определённой массы, равной (или большей) сумме масс дочерних клеток. Заканчивается стадия деления цитокинезом — полным разделением клетки на дочерние. Возрастное состояние микроводорослевой клетки характеризуется

величиной её биомассы, а переходы из одного состояния в другое — активностью (роста и деления). Модель представлена системой дифференциальных уравнений, полностью описывающих динамику процесса онтогенеза. Проанализировано частное решение модели для динамически равновесного роста микроводорослей в культуре при различной интенсивности света. Показано, что в непрерывной культуре микроводорослей, растущей фотолитотрофно, удельная скорость роста связана с морфологической структурой популяции клеток простыми прямо пропорциональными уравнениями с видоспецифическими коэффициентами — максимальной скоростью роста в интерфазе (при насыщающей интенсивности света) и активностью деления клеток при митозе.

**Ключевые слова:** микроводоросли, онтогенез, возрастное состояние, интерфаза, митоз, вероятностная модель, скорость роста, морфологическая структура культуры