ISSN 2413-5577, Ecological Safety of Coastal and Shelf Zones of Sea, 2023, No. 4, pp. 87–100.

Original article

A Simulation Growth Model for the Cultured Oyster *Ostrea edulis* L.

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Abstract

Cultivation of the flat oyster *Ostrea edulis* L., which has lost its commercial value due to reduction in abundance, is a relevant task. Simulation models of the flat oyster's growth can be used to improve oyster cultivation methods. The proposed simulation model of the *O. edulis* growth dynamics is based on the principles of dynamic energy balance. The model uses approximations of the oyster's physiological processes (filtration, respiration, excretion, growth, spawning) derived from published observational data. The paper determines functional dependencies of approximation parameters on the environmental conditions. The model was validated using *in situ* data on the linear and weight growth of the oyster *O. edulis* cultured in Donuzlav Bay for 30 months from April 2001 to October 2003. The model allowed us to obtain the dynamics of the energy balance components of the flat oyster at different life-cycle stages. The resulting quantitative distribution of growth energy between generative and somatic tissues of the oyster is confirmed by the qualitative description of the oyster's tissue growth based on *in situ* measurements. The developed model reproduces well the qualitative and quantitative characteristics of the flat oyster functioning processes. The model of the oyster's energy balance can be used as a block of a complex ecological model simulating the cultivation of mollusks on an oyster farm.

Keywords: flat oyster, *Ostrea edulis*, Donuzlav Bay, energy balance model, mariculture

Acknowledgments: The work was performed under state assignment on topic FNNN-2021-0005 "Complex interdisciplinary research of oceanologic processes, which determine functioning and evolution of the Black and Azov Sea coastal ecosystems".

For citation: Filippova, T.A. and Vasechkina, E.F., 2023. A Simulation Growth Model for the Cultured Oyster *Ostrea edulis* L. *Ecological Safety of Coastal and Shelf Zones of Sea*, (4), pp. 87–100.

Имитационная модель роста устрицы *Ostrea edulis* L. в условиях культивирования

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Аннотация

Культивирование плоской устрицы *Ostrea edulis* L., потерявшей свое промысловое значение вследствие сокращения численности, является актуальной задачей. Применение математических имитационных моделей может способствовать развитию технологии выращивания устриц в условиях морской фермы. Предложенная математическая модель динамики роста *O. edulis* построена на принципах динамического баланса энергии. В модели использованы математические аппроксимации физиологических процессов (фильтрация, дыхание, экскреция, рост, нерест), полученные на основе опубликованных данных наблюдений. Установлены функциональные зависимости параметров аппроксимаций от условий среды. Валидация модели выполнена по натурным данным о линейном и весовом росте устрицы *O. edulis*, выращиваемой в заливе Донузлав в течение 30 мес. с апреля 2001 по октябрь 2003 г. Использование модели позволило получить динамику составляющих энергетического баланса плоской устрицы, находящейся на разных стадиях жизненного цикла. Полученное количественное распределение энергии роста между генеративными и соматическими тканями устрицы подтверждается качественным описанием роста тканей устрицы по натурным измерениям. Разработанная модель хорошо воспроизводит качественные и количественные характеристики физиологических процессов плоской устрицы. Модель энергетического баланса устрицы может быть использована в качестве блока комплексной экологической модели, имитирующей культивирование моллюсков на устричной ферме.

Ключевые слова: плоская устрица, *Ostrea edulis*, залив Донузлав, модель энергетического баланса, аквакультура

Благодарности: работа выполнена в рамках государственного задания ФГБУН ФИЦ МГИ по теме: FNNN-2021-0005 «Комплексные междисциплинарные исследования океанологических процессов, определяющих функционирование и эволюцию экосистем прибрежных зон Черного и Азовского морей».

Для цитирования: *Филиппова Т. А., Васечкина Е. Ф.* Имитационная модель роста устрицы *Ostrea edulis* L. в условиях культивирования // Экологическая безопасность прибрежной и шельфовой зон моря. 2023. № 4. С. 87–100. EDN NZYAOP.

Introduction

The oyster *Ostrea edulis* is one of the most valuable species of the Black Sea coast mollusks. However, at present this species has lost its commercial value due to a shell fungal disease. In the second half of the last century, a catastrophic reduction in the habitat of the *Ostrea edulis* species took place in the Black Sea. It caused the work on artificial reproduction of the mollusks, which has been carried out since the 1980s. [1]. Thus, studies devoted to the quantitative description of physiological processes of this species are relevant and can be demanded when developing this mariculture.

In recent years, researchers have invested quite a lot of efforts to create mathematical models that make it possible to simulate the dynamics of oyster growth depending on such environmental parameters as water temperature and feed suspension concentration. This paper is aimed at development of such a model for the oyster *O. edulis* cultured in Donuzlav Bay, a specific area of the Crimean coast. First, let us consider a number of the most interesting models close to our purpose, proposed by other authors [2–8].

In [2], a simulation model of population dynamics of the species *Magallana gigas* is given. The authors analyzed *in situ* data describing the growth of oysters, established functional dependencies of the growth rate on the size of the mollusk, then used the obtained dependencies as parameterizations in the population model. Due to the fact that filtration, respiration and excretion proceed differently in oysters of different stages of development, the researchers introduced separate mathematical functions to describe each stage of the oyster's life cycle and considered them separately from each other. The disadvantage of this approach is the difficulty in describing the continuous growth of individuals in a population.

In [3], a growth model of the Pacific oyster *M. gigas* cultivated in the Thau Lagoon, France, is presented. The control variables of the model are water temperature, concentration of organic matter and chlorophyll a, as well as salinity of waters. The model was verified based on the data concerning the linear and weight growth of two oyster populations grown in the lagoon in 2000–2001. The authors concluded that their model showed good field and simulation data convergence, but better results could be achieved using dynamic energy budget (DEB) models.

Thus, their later work [4] shows the model based on the DEB approach. The results of oyster growth modelling with an empirical model were compared with the results obtained using the DEB model. The latter makes it possible to achieve a better correspondence of the simulation results to the *in situ* data on the weight and linear growth of oysters [3].

In [5], the DEB model of the oyster *M. gigas* growth, which is quite universal for the Atlantic coast marine ecosystems, is presented. The authors applied a unified approach to six different ecosystems and used a nutrition coefficient that takes into account the peculiarities of the nutritional activity of oysters under various external conditions. The model reproduces well the periods of spawning and loss of biomass in the autumn-winter period. The disadvantage is the absence of an explicit dependence of the model variables on water temperature. The authors noted that the water temperature in all the considered areas was approximately the same in winter, and significant differences occurred in summer. Nevertheless, the model uses the same set of parameters for all locations, with the exception of the nutrition coefficient.

A similar model was developed for several Pacific coast marine ecosystems [6]. The oyster *M. gigas* growth DEB model showed good results when compared with measurement data of parameters that determined the growth and spawning processes. However, the authors concluded that three studied locations were characterized by similar external conditions. Therefore, in order to apply this model under conditions other than the specified ones, the model should be detailed by including a number of values that take into account different environmental conditions.

In [7], the DEB model is used to compare the life cycles of two oyster species: *O. edulis* and *M. gigas.* The DEB approach allowed the authors to determine the reaction of the two species to an increase in the average annual water temperature by 2 °C. *M. gigas* demonstrated sufficient resistance to environmental changes, while *O. edulis* changed its life cycle due to the suppression of spawning. Based on the results of the work, the authors were able to estimate the values of environmental parameters necessary to ensure the sustainable growth of the oysters *O. edulis*. The model was developed for regional conditions of the Limfjord, Denmark.

In [8], a mathematical model of the growth of the mussel *Mytilus galloprovincialis* was presented. The model was developed in accordance with the dynamic energy balance principles. The authors considered filtration, respiration, spawning and excretion of mussels in detail. The model was verified with *in situ* data obtained at a mussel farm in the Crimean coastal zone.

The given examples of successful application of DEB models determine our choice of constructing a simulation model of the oyster *O. edulis* based on the energy balance equation. The analysis of literature sources revealed that regional features played an important role in the construction of the model, since they significantly determine the specific type of parameterizations for the main physiological processes. In this regard, it seems relevant to develop a simulation model for the *O. edulis* cultivated in Donuzlav Bay. The model should describe the processes of assimilation of food, excretion, respiration, growth, reproduction. This paper aims at the development of such a model using the approaches described in [2–8] and its verification based on *in situ* observations.

Materials and methods

There are several marine farms in Donuzlav Bay where oysters and mussels are grown. Basically, all farms are concentrated in the central Donuzlav Bay. Many years of marine farming experience in this bay indicate the suitability of this water area for the cultivation of oysters and mussels [9]. With this in mind, the central Donuzlav Bay was selected for the test calculation as a possible location for oyster *O. edulis* mariculture.

Dynamic energy balance model. The main physiological processes that determine oyster growth are filtration, food consumption, respiration, excretion and spawning. The model below describes mathematically these processes for oysters that have already passed the larval stage and are fixed on a solid substrate. The model is built in accordance with the concept of dynamic energy balance. The quantitative characteristics of the processes are expressed in energy units: calories or joules. To switch from mass units to energy ones, the coefficients of caloric content of oyster tissues are used.

The energy balance is formed and then changes depending on physiological processes of the oyster, which, in their turn, depend on its weight, age, water temperature, salinity, period of year, availability of resources and individual characteristics. When using this approach in practice, in the mollusk life cycle simulation model, it is necessary to describe mathematically all the physiological processes for a particular species as accurately as possible. This requires data from *in situ* observations and laboratory experiments. In this paper, we used approximations obtained from in situ data (Table) presented mainly in the thesis [1)] and the works of N.A. Sytnik [10, 11].

Morphometric relations. The wet weight of the oyster W (g) is represented as the sum of the shell W_{sh} (g) and soft tissues W_{soft} (g) weights. The wet and dry weight of the mollusk soft tissues is related by the ratio $W_d = 0.11 W_{soft}$ [12].

As the oyster grows, the height of the shell also increases. Based on the *in situ* data presented in work [1)], we proposed the following approximation of the dependence of the shell height on the wet weight of the mollusk:

$$\text{if } W_{soft} \le 0.35 \text{ г} \quad H = 154.67 W_{soft}^2 - 32.40 W_{soft} + 2.39,$$

$$\text{if } W_{soft} > 0.35 \text{ г} \quad H = -0.013 W_{soft}^2 - 1.88 W_{soft} + 17.70.$$

Food consumption. The oyster receives all the nutrients, i. e. the energy spent on maintaining the structure and growth, from seawater containing a feed suspension – phytoplankton and detritus. During the filtration process, the mollusk consumes the energy of diet I (cal/h), but assimilates only a part of it: $A = I - E_a$, where E_a – undigested part of the diet. The mollusk spends the assimilated energy on respiration R with the release of metabolites E_x, growth of soft tissues P_{som}, gonads P_{gen} and increase of the shell P_{sh}:

$$A = R + P + E_x;$$

$$P = P_{som} + P_{gen} + P_{sh},$$

where P – productive energy, cal/h; R – respiration cost, cal/h; E_x – excreted energy, cal/h. Thus, the distribution of energy costs of a flat oyster can be simplified in the form of the balance equation:

$$I = P + R + E_a + E_x. \tag{1}$$

Let us consider the components of balance (1) in more detail. The consumed energy (or diet) depends on the filtration rate F (L/h), concentration of feed suspension in water C (mg/L) and caloric content of the suspension K_c (cal/mg): $I = F \cdot K_C \cdot C$. The amount of assimilated energy depends on the efficiency of digestion, traditionally described with the assimilation coefficient: $A = A_e \cdot F \cdot K_C \cdot C$. Then, the total energy release can be considered as follows: $E = F \cdot K_C \cdot C\,(1 - A_e) + E_x$.

Productive energy. When growing, the oyster increases the mass of the shell and of soft tissues. Let us assume that the weight of the shell can increase or remain unchanged, while the mass of soft tissues can both increase and decrease depending on the periods of life (the spawning state or nutrient deficiency can lead

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[1)] Sytnik, N.A., 2015. [*Functional Ecology of the flat oyster (Ostrea edulis L., 1758, Ostereidae, Bivalvia) of the Black Sea.* Extended Abstract of Doctoral Dissertation]. Sevastopol, 23 p. (in Russian).

to weight loss). The change in body weight of the oyster depends on the amount of energy spent by the body when growing:

$$K_d \frac{dW_d}{dt} = P_{som} + P_{gen},$$

where K_d = 5307 cal/(g DW) – caloric content of the dry weight of oyster soft tissues; W_d – dry weight of the soft tissues, g. According to [10], the energy costs for the shell growth P_{sh} amount on average to 12% of the total productive energy available to a mollusk, based on energy balance equation (1). Taking into account these observations, we assumed that $P_{som} + P_{gen} = 0.88P$ in the model

Spawning. The growth of oysters is closely related to the spawning process. To start spawning, a number of conditions must be met. As a rule, oysters spawn at a shell height of more than 35 mm and a mass of generative tissues of more than 0.015 g dry weight. The researchers note that in different regions, the beginning of *O. edulis* oyster spawning can occur at different water temperature. Thus, in Galicia (Spain), oysters spawn at a temperature of 12–13 °C, in the Northern Adriatic (Italy) – at a temperature of 13–17 °C, in the Norwegian fjords – at a temperature of 25 °C [1, 13, 14]. For the Black Sea, *in situ* data on the intensity of spawning processes show that the temperature range of spawning is 17–25 °C [1, 10]. This range of water temperature was adopted in the model. The distribution of energy spent on the growth of somatic and generative tissues can be estimated using the empirical energy costs ratio P_{gen}/P_{som}. According to [15], this ratio increases linearly with the mollusk size, and for the oyster *O. edulis* it can be expressed by the following equation:

$$\frac{P_{gen}}{P_{som}} = 0.013\ W_d + 0.09. \tag{2}$$

The model assumes the condition according to which positive productive energy is distributed between P_{som} and P_{gen} in accordance with equation (2), and P_{gen} is assumed to be zero with negative one (nutrient deficiency).

Filtration. The European oyster filtration intensity depends on the age and size of the mollusk, water temperature, concentration of feed suspension and its caloric content, and the time of day. With an increase in water temperature from 7 to 23 °C, the intensity of mollusks filtration increases, and with a further increase in water temperature, it decreases. At a temperature of 7 °C and below, the vital activity of the mollusk is suppressed [11]. The filtration rate, like some other vital functions of a mollusk, can be approximated by a power function of dry body weight – an allometric dependence. Also, taking into account the dependence of the filtration rate on water temperature, we write the following:

$$F_T = a_f(T) W_d^{b_f(T)},$$

$$\text{if } T < 23\ °\text{C} \quad a_f(T) = 0.1161T - 0.2678,$$

$$\text{if } T \geq 23\ °\text{C} \quad a_f(T) = -0.1T + 4.67,$$

$$b_f(T) = 10^{-4}\,T^2 + 0.0046\,T + 0.38.$$

where T – water temperature, °C; $a_f(T)$ and $b_f(T)$ – empirical coefficients obtained from *in situ* data (Table).

Coefficients of allometric dependencies of the form aW_d^b for the main physiological processes (based on the works of N. A. Sytnik and R. Mann)

Process	Temperature, °C	Coefficient		Work
		a	*b*	
Filtration	7	0.54	0.443	[11]
	10	0.88	0.435	
	13	1.20	0.583	
	16	1.69	0.512	
	20	2.05	0.602	
	23	2.37	0.487	
	27	1.97	0.606	
Respiration	6	0.112	0.617	Work 1)
	11	0.291	0.773	
	13	0.320	0.813	
	18	0.491	0.688	
	19	0.475	0.721	
	23	0.725	0.737	
Excretion	12	10.92	0.601	[16]
	15	13.88	0.501	
	18	12.71	0.796	
	21	11.73	0.874	

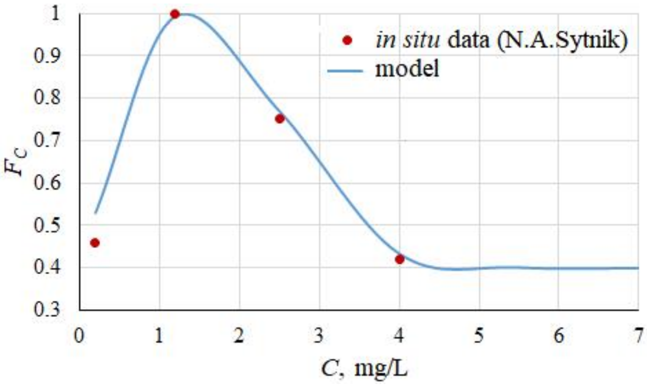
Note: The estimates were derived from *in situ* data.

Observations show that the filtration rate depends on the concentration of feed suspension in the water. There is a kind of optimal concentration, above and below which the filtration rate decreases. To record these features, it is necessary to introduce a modulating function varying from 0 to 1 [8]. The filtration rate *in situ* data given in [11], were approximated by the following function (Fig. 1):

$$F_C = 0.4 + 0.65\,C\exp(-0.18\,C^{2.3}).$$

Thus, the filtration rate is determined as $F = F_T F_C$, and the diet (consumption) – as $I = K_C F_T F_C C$.

According to [11], oysters filter water only during a certain part of the day. The minimum filtration time is 6 hours for small oysters. With the growth of an individual, it increases to 18 hours. To record the duration of filtration, an empirical function was introduced into the model, which made it possible to calculate the number of filtration hours: $h = 6 + 14t/(t + 50)$, where t – time since the oyster was attached to the substrate.



F i g. 1. Dependence of the normalized to maximum filtration rate on the feed suspension concentration in water

Respiration. Bivalves spend part of the assimilated energy on metabolic processes, namely, respiration. The intensity of respiration is determined by water temperature and size of the oyster. Based on the *in situ* data presented in Table, the following approximation was obtained:

$$R_{\mathrm{O}} = a_r(T) W_d^{b_r(T)}$$
$$a_r(T) = 0.0357T - 0.1161,$$
$$b_r(T) = 0.0042T + 0.642,$$

where R_{O} – oxygen consumption rate, mL O_2/h. The oxycaloric coefficient $K_{ox} = 4.74$ cal/mL O_2 (the ratio of the amount of energy in calories released during the oxidation of matter to the mass of oxygen consumed by the hydrobiont) was used for the conversion into energy units. Therefore, the respiration costs are $R = R_{\mathrm{O}} K_{ox}$.

Excretion. The energy assimilated by the oyster is also spent on excretion of metabolites from the body. The main excreted substance is ammonium. The rate of excretion depends on the water temperature and size of the mollusk, which can be expressed by an allometric equation. The maximum excretion rate of the oyster *O. edulis* is observed at a temperature of about 15 °C. Above and below this value, the rate decreases slightly [16]. Table shows the coefficients of the allometric excretion equation obtained under laboratory conditions at different water temperatures. Based on these values, the approximation was performed and an allometric excretion equation was derived, which is a function of two variables (water temperature and dry weight of the oyster):

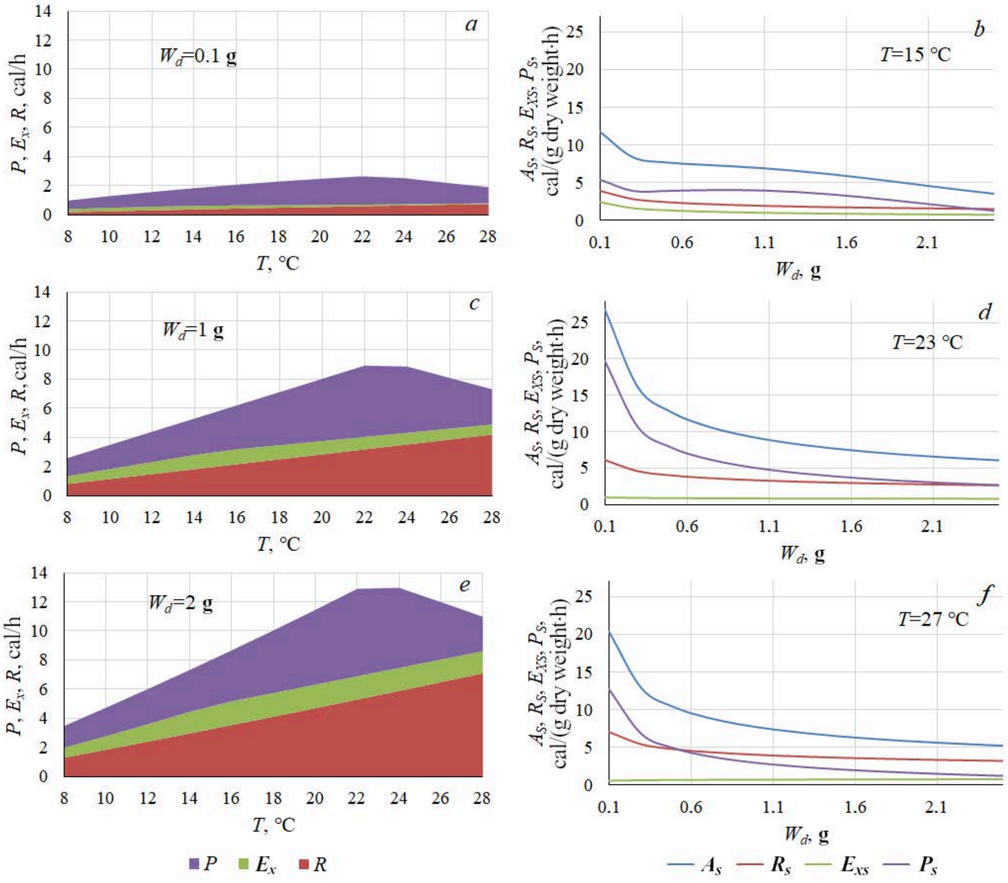
$$A_m = a_{ex}(T) W_d^{b_{ex}(T)},$$
$$\text{при } T < 15\ {}^\circ\mathrm{C} \quad a_{ex}(T) = 0.9867\,T - 0.92,$$
$$\text{при } T \geq 15\ {}^\circ\mathrm{C} \quad a_{ex}(T) = -0.3583\,T + 19.22,$$
$$b_{ex}(T) = 0.0371\,T + 0.0803,$$

where A_m – excretion rate, μg NH_4/h. Taking into account the caloric content of oyster tissues and the percentage of nitrogen in the dry weight of soft tissues of the mollusk (7 % according to data from [16]), the excretion energy costs E_x (cal/h) can be calculated using the following formula:

$$E_x = 0.0758\,A_m,$$

where E_x – energy costs for excretion, cal/h.

Energy balance components. A graphical description of the energy balance variations depending on water temperature and marine suspension concentration is of interest. Fig. 2 shows the model dependencies of the oyster energy balance components presented in absolute and specific terms. Fig. 2, *a*, *c*, *e* shows the distribution of assimilated energy among growth, excretion and respiration processes depending on temperature in oysters of various sizes. The larger the mollusk is, the more energy it is able to assimilate. The maximum values of assimilated energy are fixed at an ambient temperature of 22–24 °C, which takes place due to the maximum filtration rate in this temperature range (the most comfortable conditions for this species).

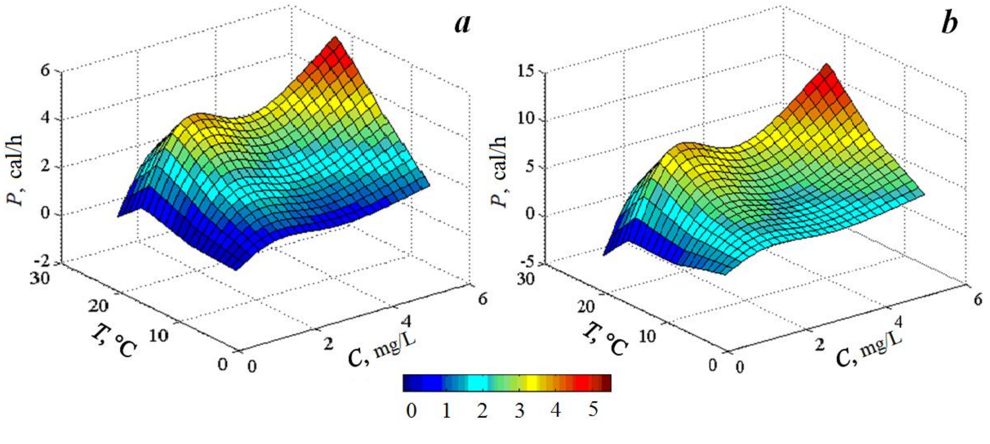


F i g. 2. Dependence of the energy balance components on water temperature T (*a*, *c*, *e*) and oyster dry weight W_d (*b*, *d*, *f*). P – productive energy; E_x – excretion energy; R – respiration costs; A – assimilated energy. The S indices denote specific quantities

In small oysters, more than half of the assimilated energy is spent on growth, while in larger mollusks, the growth and respiration energy costs are almost equal. At the same time, the size of the oyster has almost no effect on the amount of excreted energy, which accounts for 10–15% of the assimilated energy.

Fig. 2, *b*, *d*, *f* shows specific (normalized for dry weight) components of the energy balance depending on the dry weight of soft tissues of the oyster for different temperatures. Some special features of the energy balance variations of oysters should be noted. At temperatures of 22–24 °C, assimilation and production take on maximum values. The growth energy costs are determined by the difference between assimilation and metabolic costs (respiration and excretion). In small-sized mollusks, productive energy exceed excretion and respiration, and less energy is spent on growth with increasing body weight. With the growth of a mollusk, the specific values of assimilated energy, growth energy and respiration decrease, while the excreted energy remains the same. In too warm water (27 °C), the respiration costs of oysters exceed the productive energy.

Fig. 3 shows the dynamics of changes in productive energy due to the combined action of two variables (feed suspension concentration and temperature) for oysters of two sizes: W_{soft} = 4.5 g, H = 26 mm and W_{soft} = 27 g, H = 59 mm. For oysters of both sizes, it is possible to identify areas of lack of growth due to nutrient deficiency at low feed suspension concentrations in sufficiently warm water. The growth of oysters begins at a feed suspension concentration above 1 mg/L and a temperature greater than 8 °C. Maximum growth rates are observed at a maximum feed suspension concentration and a temperature of 23 °C.



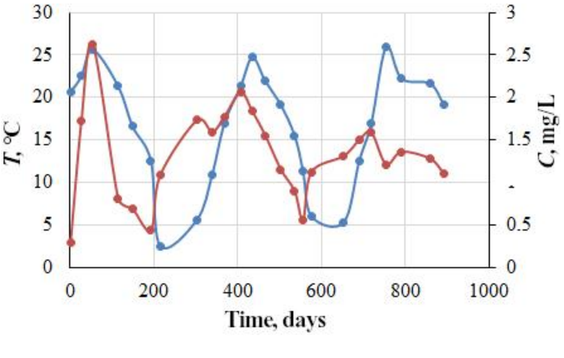
F i g. 3. Dependence of the productive energy on water temperature and feed suspension concentration for oysters with a shell height of 26 mm (*a*) and 59 mm (*b*)

Discussion of results

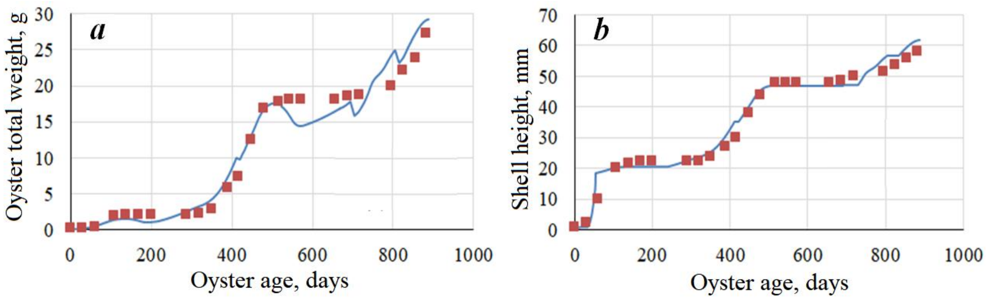
Model validation. The study [1)] presents *in situ* data on the linear and weight growth of oysters *O. edulis* cultured in Donuzlav Bay for 30 months from April 2001 to October 2003. The intervals between successive measurements of the average weight and height of oysters vary from 1 to 2 months. The model was validated by comparing the simulation results with these data. The model integration step was one day. The time of the model experiment was 30 months. The experiment began on 19 April 2001 and ended on 29 October 2003. The series of control variables for the model (water temperature and suspension concentration) were also taken from work [1)] (Fig. 4). They corresponded to the average characteristics of the central Donuzlav Bay during the study of the mollusks growth .

Fig. 5 shows modelling results compared with *in situ* data. Linear and weight growth indicators demonstrate good convergence with *in situ* data. However, there are some differences. The model graph of oyster weight dynamics shows some peculiarities corresponding to the beginning of spawning periods. Such features are not recorded in the *in situ* data due to their large discreteness, which makes it impossible to record such rapid changes in the physiological state of oysters. During 30 months of model integration, oyster spawning was recorded three times: in June 2002, April and July 2003. Thus, the oysters spawned 15, 25 and 28 months after their attachment to a solid substrate.

The simulation results allow detailed studying the dynamics of the energy balance components of cultivated oysters. Fig. 6 shows how much energy the oyster assimilates daily and how this energy is distributed among the processes of growth, respiration and excretion during 30 months of cultivation. Assimilated energy maxima correspond to feed suspension concentration maxima, which are usually followed by spawning periods. Productive energy is positive for a long time, and a mollusk grows. However, as a result of spawning, mass of a mollusk decreases, the assimilated energy is not enough to cover the costs of respiration and excretion, and growth is inhibited.



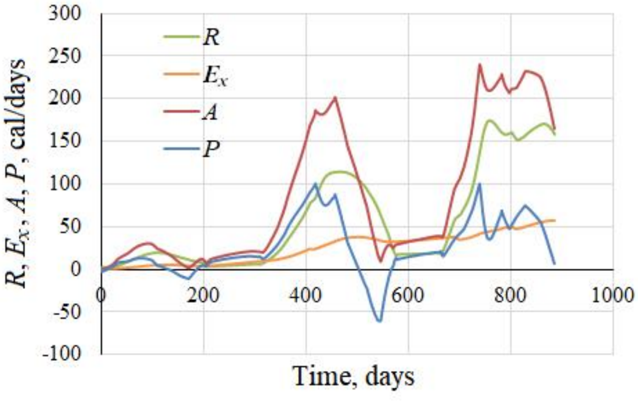
F i g. 4. Environmental parameters of the central Donuzlav Bay which affect the oyster cultivation. The red curve is water temperature; the blue curve is feed suspension concentration



F i g. 5. Simulation results (curve) compared with *in situ* data (squares) on the oyster growth at a farm in Donuzlav, 2001–2003: *a* – total fresh weight; *b* – linear size

Two periods of mollusk growth inhibition, which are not related to spawning, are recorded during the cultivation. They are determined by a sharp decrease in the feed suspension concentration (negative values P in Fig. 6). Similar conclusions were drawn from *in situ* experiments given in study $^{1)}$ and [17].

The distribution of growth energy between generative and somatic tissues is of interest. In the first year of cultivation, P_{gen}/P_{som} increases from 10 to 16%, the mollusk develops to an adult state, increasing mainly somatic tissues. In the second year, P_{gen}/P_{som} increases from 16 to 33%, the oyster is already quite large, most of the productive energy is spent on the growth of generative tissues needed to ensure reproduction. During the third year of observations, the energy costs for growth of generative tissues increase to 47 %. These modelling results confirm the qualitative conclusions on the flat oyster growth made in study $^{1)}$ and [17].



F i g. 6. Dynamics of the energy-balance components distribution during 30 months of cultivation

Conclusion

The study presents the simulation model of flat oyster growth. The model makes it possible to calculate the energy of respiration, filtration, excretion, reproduction processes. The paper examines the processes of functioning of the oyster *O. edulis* in detail and identifies factors (temperature, feed suspension concentration, age of an individual) that affect these processes and their relationship. Approximations of such vital functions of the oyster as respiration, filtration, excretion, spawning are proposed.

The model was validated using *in situ* data obtained during the study of the oyster *O. edulis* cultured in Donuzlav Bay in 2001–2003. The simulation results show good qualitative and quantitative correspondence to the *in situ* data on linear and weight growth, distribution of energy costs, ratio of the energy spent on growth of generative tissues to the energy of structural growth. The model can be used as a block of a complex ecological model simulating the cultivation of mollusks on an oyster farm.

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Submitted 3.07.2023.; accepted after review 29.07.2023;
revised 11.10.2023; published 20.12.2023

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