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QUANTITATIVE RELATIONSHIP BETWEEN SOLAR RADIATION INTENSITY AND AVERAGE DAILY VALUE OF PHOTOSYNTHESIS LIGHT SATURATION FOR PHYTOPLANKTON IN THE DEEP-WATER AREA OF THE BLACK SEA

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According to data obtained during expeditions in the Black Sea (1987–1993), linear relationship between the light flux density incident on the sea surface (E_0) and the starting point of photosynthesis light saturation ($E_{n\ opt}$) is revealed. For calculations, measurements of phytoplankton photosynthesis rate obtained by the radiocarbon method were used. The equation of the relationship between the values reported is presented for the first time for the Black Sea. $E_{n\ opt}$ is the average daily, optimal value of photosynthesis light saturation. The parameters of photosynthesis – light curve, determined in short-period exposures under constant illumination, differ from the parameters obtained in long-term experiments under conditions of variable illumination. This is due to different effects of the intensity and dose on the phytoplankton photosynthesis rate. The values of photosynthetic parameters for a certain time are integrated into a single value which is the optimum for the entire period observed. The approximation of daily data integrated is carried out both separately for seasons and in general for the period of 1987–1993. Using statistical processing of data of average daily values of the intensity of solar radiation incident on the sea surface, slope of the photosynthesis – light curve, and maximum photosynthesis rate, the approximation is determined for the functional dependence of $E_{n\ opt}$ on E_0. The equation is applicable in the range of light intensity 3 to 75 mol quanta·m^{-2}·day^{-1}. It describes with high reliability a change of average daily value of photosynthesis light saturation in the Black Sea during different seasons of the year. The equation includes a parameter easily accessible for measurement. It can be used in analysis of physiological characteristics of phytoplankton and calculation of integrated phytoplankton productivity in euphotic layer with using both satellite and expedition data.

Keywords: phytoplankton, photosynthesis light saturation, photosynthesis rate, photosynthetically active radiation, deep-water area of the Black Sea

It is known that with increasing incident light intensity, the phytoplankton photosynthesis rate increases. Up to some values of photosynthetically active radiation, it grows linearly; then saturation occurs, and the photosynthesis rate becomes constant. A further increase in the light flux density per unit of the surface leads to inhibition of photosynthesis, which can be reversible, while with extremely high light intensity it can become irreversible.

When modeling the photosynthesis – light dependence, the amount of photosynthesis saturation with light (E_n) is an important physiological characteristic showing the light intensity, at which the maximum photosynthesis rate is observed. Studies [9, 14, 18] show that photosynthesis – light parameters in short-period exposures under constant illumination are not equivalent to the parameters if the data are obtained in long-term experiments under conditions of variable solar lighting. These differences often result from different effects of the intensity and dose of the radiation on the phytoplankton photosynthesis rate. The dynamics of photosynthesis during the day or the daylight hours is integrated into a single value, which is the optimum for the entire period observed.

As a rule, a model for calculating phytoplankton primary production includes equations with photosynthetic parameters: the maximum photosynthesis rate, the photosynthesis efficiency, and the amount of light saturation. Depending on the type of the model, different types of parameters are used to calculate the integral primary production [in particular, the values of photosynthesis light saturation both with constant lighting (E_n) and with variable lighting ($E_{n\ opt}$)]. The average daily, or optimal, value of photosynthesis light saturation ($E_{n\ opt}$) deserves special attention. Usually its values are not determined by direct measurements in field studies or remote observations. However, it is convenient to use it when calculating the integral primary production over a long period or evaluating photosynthesis profiles in a water column.

The aim of the research is to determine the relationship between the optimal value of photosynthesis light saturation for phytoplankton and the light incident on the surface in the Black Sea.

MATERIAL AND METHODS

The database formed for the study includes materials of 4 expeditions conducted in 1987–1993 in the Black Sea (Table 1). The basic data set was obtained by D. Sc. Z. Z. Finenko (IBSS RAS) [6, 7] and supplemented by data from the literature [1].

Table 1. Years of the expeditions and number of measurements included in the database

Year	Month	Number of measurements	Year	Month	Number of measurements
1987	12	12	1989	4, 5, 6	52
1988	1	10	1993	4	14
1988	3	48			

The database contains information on the time (year, month, and day) and location (longitude, latitude, and depth) of sampling. The measurements were carried out in the water area of 41° to 46° Northern latitude and 28° to 35° Eastern longitude for the depths of the euphotic zone, which ranged 12 to 100 m in different months at individual stations. The database also includes the parameters measured:

- the solar radiation intensity incident on the sea surface, E_0 (mol quanta·m^{-2}·day^{-1});
- maximum photosynthesis rate, P^B_{opt} (mgC·mgChl^{-1}·day^{-1});
- slope of the photosynthesis – light curve reflecting the photosynthesis efficiency, α (mgC·mgChl^{-1}·(mol quanta·m^{-2})$^{-1}$).

The optimal photosynthesis light saturation, $E_{n\ opt}$ (mol quanta·m^{-2}·day^{-1}), is calculated as the ratio: $E_{n\ opt} = P^B_{opt} / \alpha$.

Phytoplankton photosynthesis rate was measured by the radiocarbon method during the first or second half of daylight hours [6]. To obtain daily production, the values were doubled, since the phytoplankton photosynthesis rate is a function of light, and the total solar radiation flux on clear days during the first and second half of the day is approximately the same. The flasks were filled with water from the depths where 0.5 to 100 % of surface light penetrated. Then radioactive carbon was added, and the flasks were exposed on the ship deck under natural light which was weakened by neutral filters to the light conditions observed at the depths from which the samples were taken. Lighting was measured with a Yu116 light meter from dawn to sunset with an interval of one hour. Values in luxes were converted to energy units (1 klx = 20 μE·m^{-2}·s^{-1}; 1 mol quanta·m^{-2}·s^{-1} = 10^{6} μE·m^{-2}·s^{-1}) [5].

RESULTS

For all the parameters studied, the sample for each month of 1987–1993 was averaged. The measured values of E_0 have high variability, especially in summer and spring (Fig. 1). Therefore, for calculations, we used the integral average daily values determined for each specific month in the considered period.

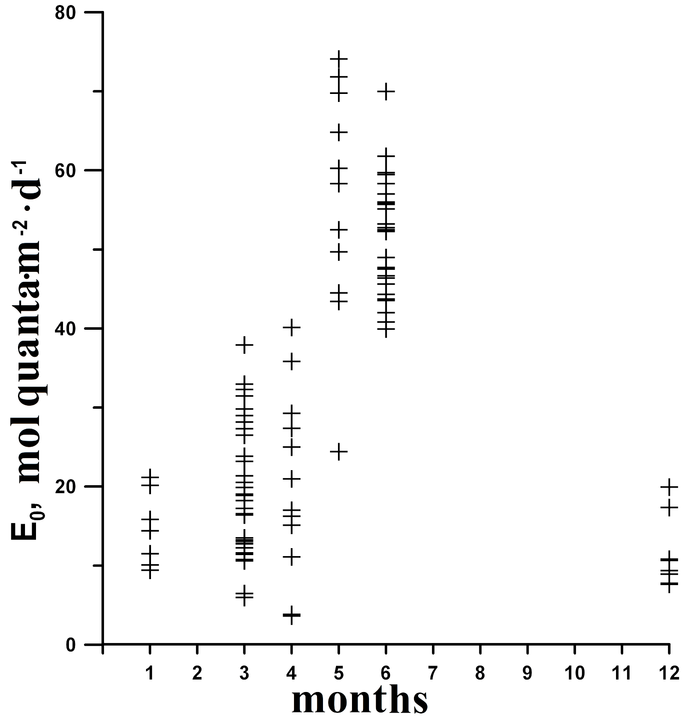

Fig. 1. Variability of solar radiation intensity incident on the sea surface (E_0) in different months of 1987–1993 in the Black Sea

The approximation of daily data was carried out by seasons and in general for the period of 1987–1993. The integration of average daily values of the solar radiation intensity incident on the sea surface, the slope of the photosynthesis – light curve, and the maximum photosynthesis rate for each month in a single year made it possible to determine the best approximation for the functional dependence of $E_{n\,opt}$ on E_0 (Fig. 2).

As a result of the analysis, a linear equation was obtained for the optimal value of photosynthesis light saturation in the absence of inhibition for the deep-water area of the Black Sea. The general equation relating the average daily values of $E_{n\,opt}$ and E_0 is:

$$E_{\text{nopt}} = a \times E_0 + b \,, \tag{1}$$

where $E_{n\,opt}$ is measured in mol quanta·m^{-2}·day^{-1};

a and b are constant coefficients (a = 0.12; b = 1.92).

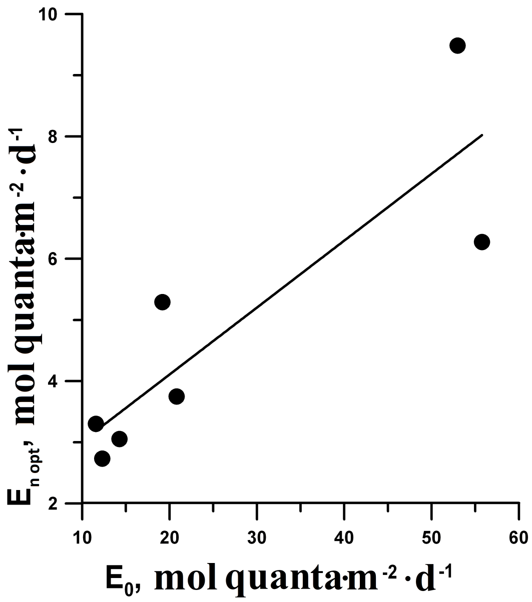

Fig. 2. Variability of optimal value of photosynthesis light saturation ($E_{n\,opt}$) depending on intensity of the solar radiation incident on the sea surface (E_0) in 1987–1993 in the Black Sea

The equation (1) is significant at $p < 0.0001$, $r^2 = 0.76$. The value of $E_{n\,opt}$ is determined for the euphotic zone. The dependence found is applicable in the illumination range 3 to 75 mol quanta·m^{-2}·day^{-1}. The equation (1), obtained from empirical data, has a regional character and is calculated for the first time for the deep-water area of the Black Sea.

DISCUSSION

In our studies, we used empirical data on the values of the optimal maximum photosynthesis rate and the slope of the photosynthesis – light curve integrated over the day for the period of 1987–1993 [1, 6, 7]. Unfortunately, regular measurements of these parameters, which could be used in modeling in the Black Sea for other years, were not carried out. Many studies have estimated the photosynthesis light saturation. This characteristic was used when modeling the photosynthesis rate and the integral primary production of phytoplankton [2, 9, 10, 11, 12, 13, 14, 15, 16, 17]. E_n or $E_{n\,opt}$ parameters were usually determined empirically for various regions of the World Ocean. A detailed analysis of the difference between these two parameters was made by M. Behrenfeld and P. Falkowski [9]. Empirically, they determined relationship between E_0 and the optimal value of light photosynthesis saturation E^*_n in the absence of inhibition; linear relationship was obtained. This function was used in modeling the integral primary production for the analysis of optical depths and vertical profiles of photosynthesis rate [3], since it gave similar results to the Black Sea data [7]. However, for the Black Sea, there was no such mathematical dependence that allowed one to determine $E_{n\,opt}$ using one parameter that is easily accessible for measurements, such as E_0. Previously, we examined the maximum value of photosynthesis light saturation; according to the model calculations, we estimated the greatest influence of the factors on E_n [4]. As a result, a multiple regression was obtained for E_n; it was determined that the maximum E_n values are observed at low chlorophyll concentrations and high P^B_m values, while minimum values are observed at high chlorophyll concentration and low photosynthetic activity. It is indicated that E_n values are more dependent on the maximum photosynthesis intensity than on the chlorophyll concentration. E_n differs from $E_{n\,opt}$, but such an influence of factors qualitatively reflects the change in $E_{n\,opt}$, especially if we take into account the vertical heterogeneity of the phytoplankton distribution in a water column. We found a linear dependence of $E_{n\ opt}$ on E_0. For the dependence (1) obtained empirically, the vertical uniformity of the phytoplankton distribution is assumed. Consequently, the photosynthesis profile in a water column without photoinhibition is presented on the surface by the area of light saturation, and at depth – by the area of light limitation. Such a change in the photosynthesis profile is usually observed in the deep-water area of the Black Sea [7, 8].

Conclusion. According to the results of the analysis of the data obtained during expeditions in the Black Sea (1987–1993), a quantitative relationship between the optimal value of photosynthesis light saturation for phytoplankton and the average daily light incident on the sea surface is obtained. This relationship is considered important in a number of modern studies, since the optimal value of photosynthesis light saturation is one of the fundamental characteristics used in modeling the phytoplankton productivity. For the first time for the Black Sea, an equation is obtained that allows one to determine $E_{n\ opt}$ in the surface layer, having the measurement data of E_0. This is especially convenient when using a large array of satellite observation data.

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КОЛИЧЕСТВЕННАЯ СВЯЗЬ ИНТЕНСИВНОСТИ СОЛНЕЧНОЙ РАДИАЦИИ И СРЕДНЕСУТОЧНОЙ ВЕЛИЧИНЫ НАСЫЩЕНИЯ ФОТОСИНТЕЗА ФИТОПЛАНКТОНА ПО СВЕТУ ДЛЯ ГЛУБОКОВОДНОЙ ЧАСТИ ЧЁРНОГО МОРЯ

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По данным экспедиционных исследований, проведённых в Чёрном море в 1987–1993 гг., установлена линейная зависимость между плотностью светового потока, достигающего поверхности моря (E_0), и началом светового насыщения фотосинтеза фитопланктона ($E_{n\,opt}$). Для расчётов использованы измерения скорости фотосинтеза фитопланктона, полученные радиоуглеродным методом. Уравнение связи между указанными величинами представлено впервые для Чёрного моря. $E_{n\,opt}$ — среднесуточная, оптимальная величина насыщения фотосинтеза по свету. Параметры кривой фотосинтез — свет, определяемые в короткопериодных экспозициях при постоянном освещении, отличаются от параметров, полученных в длительных опытах в условиях переменного освещения. Это обусловлено разным действием интенсивности и дозы облучения на скорость фотосинтеза фитопланктона. Величины фотосинтетических параметров за определённое время интегрируются в единственное значение, которое является оптимумом за весь наблюдаемый период. В работе проведена аппроксимация интегрированных суточных данных отдельно за сезоны и в целом за 1987–1993 гг. С помощью статистической обработки данных среднесуточных значений интенсивности солнечной радиации, падающей на поверхность моря, тангенса угла наклона кривой фотосинтез — свет и величины максимальной скорости фотосинтеза определена аппроксимация для функциональной зависимости $E_{n\,opt}$ от E_0. Уравнение с высокой достоверностью описывает изменение среднесуточной величины светового насыщения фотосинтеза в Чёрном море в различные сезоны года, оно применимо в диапазоне освещённостей от 3 до 75 моль квантов·м$^{-2}$·сут$^{-1}$. Эта зависимость включает легко доступный для измерения параметр и может использоваться при анализе физиологических характеристик фитопланктона и расчёте интегральной продуктивности фитопланктона в эвфотическом слое как по спутниковым наблюдениям, так и по экспедиционным данным.

Ключевые слова: фитопланктон, световое насыщение фотосинтеза, скорость фотосинтеза, фотосинтетически активная радиация, глубоководная часть Чёрного моря