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PHYTOPLANKTON PRIMARY PRODUCTIVITY

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Primary productivity is an important integral parameter describing energy potential of aquatic organisms' vital activity. Primary productivity determines the quality of water environment, its self-purifying capacity – from the Global Ocean to various continental ecosystems (Odum 1953, Williams et al. 2002, Bott et al. 2006, Kuehl and Troelstrup 2013).

Primary productivity is a bioenergy process transforming the solar energy into the energy of chemical bonds in organic matter, newly synthesized by the autotrophic link. The autotrophic link is mainly formed by algae from different ecological groups (phytoplankton, phytobenthos, phytoperiphyton) and higher aquatic plants.

As any process of energy production and transition, primary production in aquatic ecosystems is regulated by the laws of thermodynamics: the first law – the Lomonosov-Lavoisier law, the second law – the entropy law (Odum 1953). It is necessary to state clearly, that green plants do not transform the total amount of the Sun's radiant energy, but only a part of it, within the spectral range between 480 and 720 nm (within the wavelength band of photosynthetically active radiation). A simplified equation describing the primary production process can be represented as follows:

$$A = \frac{chlorophyll\ (a,\ b,\ c)\ \times h\vartheta\ (range\ of\ PAR)}{NH_4^+,\ NO_2^-,\ NO_3,\ PO_4^{3-},\ K,\ Na,\ C,\ Mg,\ Mn} + n\ (CO_2)\ +\ n\ (H_2O) \to n\ (CH_2O)\ + \\ + W\ of\ chemical\ bonds\ + n\ O_2$$

Proceeding from the above equation, primary productivity may be considered equivalent to (analogous to) the photosynthesis intensity.

There is a range of various methods for estimating PP: according to algal cell number, according to nutrient dynamic in water, according to diurnal dynamics of dissolved oxygen, according to chlorophyll a content, light-and-dark bottle method in oxygen or radiocarbon modification. With consideration taken of these methods' advantages and disadvantages, researchers will be able to obtain the most reliable and unbiased primary productivity data.

Keywords: *Primary productivity, organic matter destruction, phytoplankton.*

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ПЕРВИННА ПРОДУКЦІЯ ФІТОПЛАНКТОНУ

В.І. Щербак, Н.М. Корнійчук

Первинна продуктивність є важливим інтегральним параметром, що характеризує енергетичний потенціал життєдіяльності гідробіонтів. Первинна продуктивність визначає якість водного середовища, його здатність до самоочищення – від Світового океану до різних континентальних екосистем (Odum 1953, Williams et al. 2002, Bott et al. 2006, Kuehl and Troelstrup 2013).

Первинна продуктивність — це біоенергетичний процес, що перетворює сонячну енергію в енергію хімічних зв'язків в органічній речовині, новосинтезованій автотрофною ланкою. Автотрофну ланку утворюють переважно водорості різних екологічних груп (фітопланктон, фітобентос, фітоперифітон) і вищі водні рослини.

Як і будь-який процес продукування та переходу енергії, первинна продукція у водних екосистемах регулюється законами термодинаміки: перший закон – закон Ломоносова-Лавуазьє, другий закон – закон ентропії (Одум 1953). Необхідно чітко зазначити, що зелені рослини трансформують не всю енергію випромінювання Сонця, а лише її частину, в спектральному діапазоні від 480 до 720 нм (в діапазоні довжин хвиль фотосинтетично активного випромінювання).

Спрощене рівняння, що описує первинну продукцію, можна представити так:

$$A = \frac{\text{хлорофіл } (a,\ b,\ c)\ \times h\vartheta\ (\text{діапазон } \textbf{ФАР})}{NH_4^+,\ NO_2^-,\ NO_3,\ PO_4^{3-},\ K,\ Na,\ C,\ Mg,\ Mn} + n\ (CO_2)\ +\ n\ (H_2O) \rightarrow n\ (CH_2O)\ + \\ +\ W\ \text{хімічних зв'язків}\ +\ n\ O_2$$

Виходячи з наведеного вище рівняння, первинну продуктивність можна вважати еквівалентною (аналогічною) інтенсивності фотосинтезу.

Існує низка різних методів оцінки первинної продукції: за кількістю клітин водоростей, за динамікою біогенних елементів у воді, за добовою динамікою розчинного кисню, за вмістом хлорофілу а, склянковий метод у кисневій і радіовуглецевій модифікації. Враховуючи переваги і недоліки цих методів, дослідники можуть отримати надійні та об'єктивні дані щодо первинної продуктивності.

Ключові слова: *первинна продукція, деструкція органічних речовин, фітопланктон.*

Introduction

The UN Sustainable Development Goal No. 6 is to ensure clean water and sanitation for all. The main targets to achieve this goal include, among others, providing access to safe and affordable drinking water, improving water quality, wastewater treatment and safe reuse, implementing integrated water resources management, protecting and restoring water-related ecosystems.

It is well known, that quality of water and its safety for human life and health to a great extent depend on phytoplankton primary productivity, organic matter destruction and their ratio. For example, the production-destruction ratio (A/R) is actually a formalized index, which describes the aquatic ecosystem state, water quality, and may be considered as an indicator of an aquatic ecosystem self-purification or self-pollution. Phytoplankton primary production indices may serve as biological indicators of nutrients or organic matter influx.

In the view of the above, assessing phytoplankton primary productivity is very important for developing scientific basis of protection, sustainable use and management of water resources and ensuring safety and high quality of water for all.

Materials and methods

Primary production (PP) is a complex biological process of energy generation in the aquatic ecosystem. In equations and formulas PP is usually expressed by letter A (from: assimilation), and organic matter destruction (OMD) – by letter R (from: respiration).

PP may be formally divided into several constituents:

A_g – gross primary production (GPP). This is a total amount of photosynthesized energy produced by the autotrophic link (algae, higher aquatic plants, aquatic mosses, green bacteria) in the aquatic ecosystem.

A_e – effective primary production (EPP). This is an amount of photosynthesized energy exclusive of the fraction, which was consumed by the autotrophic link to cover its own energy expenditure ($A_e = A_g - R_a$, where R_a – autotrophic link respiration intensity);

A_n – net primary production (NPP). This is an amount of photosynthesized energy exclusive of the energy fraction, consumed for respiration of the autotrophic link (R_a) and the energy consumed for vital activity (respiration) of aquatic organisms from higher trophic levels: zooplankton (R_{zp}), bacterioplankton (R_b), protists (R_{pr}), bottom macroinvertebrates (R_{bm}) and fish (R_f). The autotrophic link's biomass, which is present in a particular aquatic ecosystem at a particular moment, can be considered NPP (A_n).

The PP may be expressed in any units of energy per unit of volume or area in a unit of time: mg $O_2 \times dm^{-3} \times t$; g $O_2 \times m^{-3} \times t$; g $O_2 \times m^{-2} \times t$; mg C $\times dm^{-3} \times t$; g C $\times dm^{-3} \times t$; g C $\times dm^{-2} \times t$; J $\times dm^{-3} \times t$; kJ $\times m^{-3} \times t$; kJ $\times dm^{-2} \times t$. Time units: from 1 hour to 24 hours (day), month, vegetation season.

24-hour (daily) expositions are the most suitable, if it is necessary to take into account ecological and physiological specifics of primary production and organic matter destruction. Short-term experiments reflect the potential capabilities of autotrophic communities. However, short-term expositions are also justified for measuring PP in eutrophic, hypereutrophic water bodies, as well as during intensive Cyanophyta blooms (Shcherbak, 2001).

To give an integral picture of the aquatic ecosystems' productivity, the $A_g/R \times day^{-1}$ index is often used. It is an important parameter, expressing the ratio between gross primary production (A_g) and organic matter destruction (R).

The A/R ratio can be the following:

A/R ≈ 1. PP and OMD are balanced, the ecosystem is dominated by natural processes, and significant human impact is absent. In accordance with E. Odum (Odum 1953), this condition corresponds to the ecosystem's climax.

A/R > 1. PP prevails in the ecosystem and exceeds energy consumption for OMD considerably. This ratio is typical for eutrophic water bodies with Cyanophyta blooms.

A/R < 1. PP is less intensive than OMD. Such phenomenon is possible in two major cases: 1) autotrophic link has low productivity, which may be observed in early spring – late autumn, during seasonal succession of species, when there is a lack of nutrients. It is one of possible temporal stages in seasonal periodicity, depending upon natural processes; 2) the aquatic ecosystem has been exposed to significant human impact, inhibiting PP. Volley discharge of unpurified sewage can serve as an example.

Along with a daily ratio ($A/R \times day^{-1}$), it is possible (and even justified) to use a larger time interval in order to evaluate an extended human impact upon the aquatic ecosystem, which may last for ten days, a month, a season, or a year. It will allow assessing the share of PP in the aquatic ecosystem's bioproductivity potential in a more unbiased way.

The A_n/B (P/B) index is equally important. It expresses the ratio between NPP and biomass during a particular time interval.

Actually, $A_n/B \times day^{-1}$ corresponds to specific primary production of the aquatic ecosystem. It is acknowledged that the average $A_n/B \times day^{-1}$ ratio for phytoplankton is equal to 2. Such ratio is observed in water bodies with natural intrabasin processes prevailing, devoid of any significant human impact.

Chlorophyll a is the major pigment present in all green plants and determining the solar energy assimilation during the photosynthetic process. That is why several important production indices are based on chlorophyll a: assimilation number (AN):

$$AN = \frac{GPP\ (A_g)}{chlorophyll\ a} \times t\ (1\ hour);$$

daily assimilation number (DAN):

$$DAN = \frac{GPP\ (A_g)}{chlorophyll\ a} \times t\ (24\ hours).$$

Assimilation numbers fluctuate within quite a wide range. For example, for marine phytoplankton the AN index varies between 0.1 and 57.5 mg C × mg Ch a^{-1} × 1 hour.

The main factors making effect upon PP:

Biological: a) size characteristics of autotrophic organisms; b) the S/V index, which is a ratio between the cell surface area (S) and its volume (V); c) the amount of active chlorophyll a and additional pigments.

Abiotic: a) amount of PAR-range energy; b) albedo value (the ratio between the solar radiation falling upon the water surface and the portion of such radiation reflected by the water surface); c) water temperature (t°C); d) salinity (S‰); e) water transparence (Secchi depth, m); f) water turbidity (mg × dm^{-3}); g) absolute concentration of inorganic nitrogen and phosphorus (mg × dm^{-3}) (Jørgensen, 1980); h) N : P ratio (an optimal N : P ratio for phytoplankton PP is equal to 16–20 : 1; i) availability of other chemical elements indispensable for photosynthesis.

A well-known English chemist Joseph Priestley laid the foundation of methods for measuring PP. As far back as in 1770s he discovered, that oxygen bubbles appeared on stems of Vallisneria spiralis L., when flasks with plants were exposed to sunlight and, on the contrary, the "bubble effect" was absent, when the plant was in darkness.

Proceeding from the equation of photosynthesis, the choice of methods is rather wide and depends upon the particular variable to be measured and the goals pursued by the researcher. A short list of methods for measuring PP applied in hydroecology is the following:

- According to algal cells number. The method consists in calculating the number of algal cells, forming in isolated cylinders within a definite time interval. Since phytoplankton's growth gain can be easily transformed into its biomass, this method shows the NPP value (A_n);

- According to nutrients dynamics in water, i. e. the difference in nutrient content (inorganic nitrogen, phosphorus) in the test and control flasks. The major disadvantages of this method include quick regeneration of nutrients during decomposition (lysis) of algal cells and their adsorption on the cell wall surface. This is especially true for phosphates.

- According to diurnal dynamics of dissolved oxygen. This method is based upon the difference in the amount of oxygen emitted in the photosynthetic process during the day. The PP intensity will be equal to the difference between the dissolved oxygen's maximal and minimal concentrations. The results obtained correspond to GPP. However, the method has the following disadvantages. Firstly, this method can be used during the periods of maximal photosynthetic activity (spring, summer), but it is rather difficult to take into account the temperature effect; secondly, it is methodically difficult to distinguish between the amount of oxygen, emitted into water due to photosynthesis, and the amount of oxygen, dissolving in water due to normal diffusion.

- According to chlorophyll a content. The biological essence of this method is the following: the PP intensity is proportional to chlorophyll a amount. There are methodical approaches to measuring chlorophyll a concentration: measuring chlorophyll a via pigment extraction; extraction-free spectrophotometric method.

The chlorophyll method (especially its extraction-free variant) is widely used in up-to-date hydroecological studies, and its findings are close to net primary production (A_n);

Light-and-dark bottle method in oxygen or radiocarbon modification. The light-and-dark-bottle method in oxygen modification has been the most widely used method starting from G. G. Vinberg's research conducted as far back as in the 30s of the 20th century

(Vinberg, 1960). After the radiocarbon modification of the light-and-dark bottle method was proposed (Steemann-Nielsen, 1952), this method became even more widespread, especially for measuring PP in seas, oceans and oligotrophic water bodies. Since the light-and-dark bottle method in both modifications is well-known and is often explained in detail in scientific literature, it makes no sense to describe it here.

The main advantages of the light-and-dark bottle method include its simplicity, availability, and possibility to apply it in field conditions. Moreover:

- in oxygen modification – along with GPP, one can estimate OMD;
- in radiocarbon modification – high sensitivity, making it possible to conduct observations in low-productive oligotrophic aquatic ecosystems. It has been shown (Shcherbak and Klenus 1982) that radiocarbon modification gives results which are close to NPP;
- Fluorescence method. Today this method is widely used internationally. No statistically significant difference has been found between the data obtained by the fluorescence method and those obtained by the light-and-dark bottle method (Mineyeva, 2009).

Thus, today there is a range of various methods for estimating PP, and each of them has both advantages and disadvantages. With consideration taken of their advantages and disadvantages, researchers will be able to obtain the most reliable and unbiased primary productivity data.

Results and discussions

PP is an integral energy flow formed by the autotrophic link in an aquatic ecosystem. The particular components of autotrophic link make different contributions to the total productivity (Reynolds, 1984). In the Global Ocean, especially in its deep-water part (from 400 m and deeper), phytoplankton is the main component of the autotrophic link, which forms the largest share of PP. In the shelf area the significance of phytobenthos, epiphytic algae, and higher aquatic plants increases, however phytoplankton still plays a dominant part.

As regards continental water bodies, the following example of the Kyiv Water Reservoir (the Dnieper River, Ukraine) illustrates the contribution of different plant communities to the total primary production (Shcherbak, 1999).

The major share of energy flow is formed by phytoplankton, which is also distinguished by the highest specific production (table 1). Less important parts are played by phytobenthos, filamentous algae and higher aquatic plants.

Table 1

Structure of autotrophic link's primary production in the Kyiv Water Reservoir, kJ × m^{-2} (Shcherbak, 1999)

Autotrophic link elements	A_g	A_n	Share of each component in the total production, %	A_n/B	R	A_g/R
Phytoplankton	8985	6992	51	42	1993	4,5
Phytobenthos	4271	3203	24	35	1068	4,0
Filamentous algae	3471	2604	19	16	867	4,0
Higher aquatic plants	1005	804	6	1	201	5,0

Note. The total primary production of the Kyiv water reservoir is taken for 100%; A_g – gross primary production, A_n – net primary production, R – organic matter destruction, B – biomass.

The recent studies of production parameters pertaining to particular components of the autotrophic link in the Kyiv Water Reservoir have shown the role of another component – epiphytic algae (Semenyuk and Shcherbak, 2017).

Therefore, while in the Global Ocean phytoplankton plays a leading role in PP, in the continental water bodies the contribution of other autotrophic organisms is also very important.

Spatial and Temporal Dynamics of Primary Production. Vertical distribution. Analysis of the long-term data series obtained from the Dnieper water reservoirs has shown that PP can be distributed in the water column according to three main types. The type of the PP vertical distribution usually depends upon the water body's trophic state and phytoplankton dominant complex structure (fig. 1).

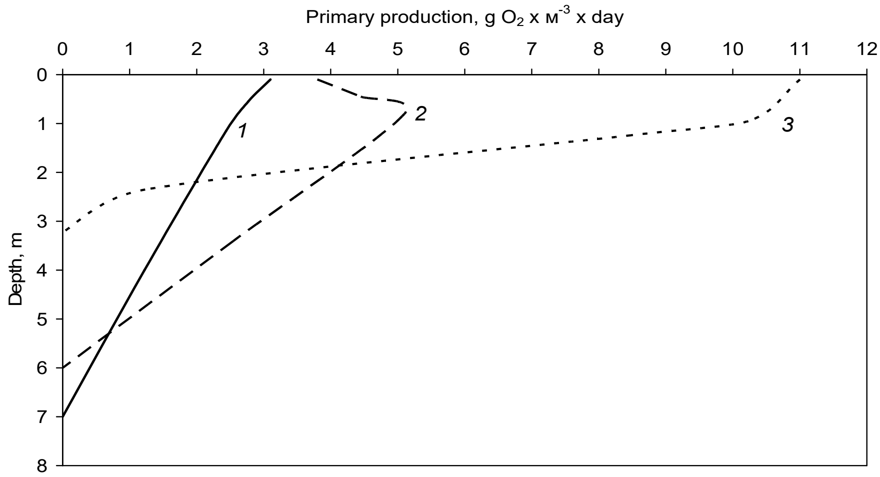

Fig. 1. Vertical distribution of primary production intensity depending upon the water body's trophic state and dominant complex structure (unpublished field data of V.I. Shcherbak).

Mesotrophic type. Phytoplankton structure is polydominant and represented by Bacillariophyta, Chlorophyta, Cryptophyta, Chrysophyta. The PP values are the highest in surface layers, gradually decreasing with depth. The photic layer is within the threefold Secchi depth.

Mildly-eutrophic type. Phytoplankton is dominated by Bacillariophyta. Most diatoms are shade-requiring species (Shcherbak and Kuz'menko, 1987); therefore the photosynthetic curve reaches its peak at a 0.5–1.2 m depth. The photic layer capacity is approximately equal to the doubled Secchi depth.

Hypereutrophic type. Cyanophyta are monodominant and intensive water bloom is observed. The photosynthetic curve peak occurs in surface layers, the photic layer capacity does not exceed the Secchi depth.

Presence of suspended particulate matter in the water column is an important abiotic factor, making effect upon the PP intensity and the photic layer capacity. It has been shown (Shcherbak et al., 1987), that the minimal PP and, respectively, minimal photic layer capacity in the Danube river were recorded in spring – during high water, when suspended mineral particulate matter amount in water was the highest. And, on the contrary, when the amount of suspended particulate matter in water was the lowest (in autumn), PP and the photic layer capacity were the highest.

Diurnal dynamics. Experiments on PP measuring within 4-hour intervals (at one and the same sampling site) in summer (when daylight hours are the longest) have shown, that the diurnal dynamics of PP is expressed by a unimodal curve with a peak within an interval from 9 a. m. to 1 p. m. (table 2).

Table 2

Diurnal dynamics of phytoplankton primary production (A, mg C × cell^{-1} × 4 hours) in shallow areas of the Kremenchug Water Reservoir (the Dnieper River, Ukraine) (Shcherbak, 1982)

Exposition period, time o'clock	*A*, mg C × cell^{-1} × 4 hours		Percentage shares	
	min-max	$\overline{\Sigma}$	min-max	$\overline{\Sigma}$
9 p. m. – 5 a. m.	6.24–31.80	14.36	1–9	5
5 a. m. – 9 a. m.	18.35–124.19	65.31	7–30	21
9 a. m. – 1 p. m.	51.24–242.94	116.52	31–58	40
1 p. m. – 5 p. m.	30.80–109.26	55.93	11–32	19
5 p. m. – 9 p. p.	7.43–104.16	43.52	9–26	15

Thus, the above examples evidently demonstrate that the PP process has a well-marked spatial and temporal dynamics.

• Primary Production of Particular (Dominant) Species

The above data on PP of oceanic and continental ecosystems describe the main patterns of the autotrophic link. However, the cause-and-effect mechanisms sustaining autotrophic communities' production are determined by dominant species' contribution. Production parameters at the population and species levels can be measured by autoradiography method, suggested almost simultaneously and independently by Maquire and Nell (1971) and Watt (1971).

The principle of the autoradiography method consists in measuring the algal cells radioactivity, which is proportional to the number of ^{14}C atoms, assimilated in the photosynthetic process from the introduced "tracer" ($NaH^{14}C_3$; $Na_2{}^{14}CO_3$).

The higher is the algal cell's photosynthetic activity, the larger amount of ^{14}C will be uptaken. The radioactivity (primary production) of a separate cell is measured by a number of traces ("tracks") made by β-particles of ^{14}C, which reduce silver grains of the emulsion covering permanent slides with radioactive algae.

The autoradiography method has made it possible to prove (Shcherbak 1998a, 1998b), that the absolute PP value (A, pg C × cell^{-1} × day) increases with cell volume. At the same time, the specific PP (A/B × day^{-1}) follows an opposite relation: the less is the cell volume, the higher is the specific production (table 3).

Table 3

Cell volume (V, mcm^3), production rate (A, pg C × cell^{-1} × day) and specific production (A/B × day^{-1}) of algae relating to major divisions of phytoplankton in continental water bodies of Ukraine (Shcherbak, 1998b)

Divisions of algae	Number of species	V		A		P/B	
		min-max	$\overline{\Sigma}$ V	min-max	$\overline{\Sigma}$ A	min-max	$\overline{\Sigma}$ P/B
Cyanophyta	86	2–268	72.3±19.3	1.4–163.3	18.7±3.9	0.3–19.7	3.0±0.64
Bacillariophyta	97	47–3846	963.3±6.4	7.8–698.5	119.3±21.3	0.3–10.1	1.8±0.32
Chlorophyta	132	77–400	438.9±50.1	21.4–580.3	133.4±10.1	0.6–9.4	3.8±0.41

Note. The table contains the upper and lower limits of (min-max), average ($\overline{\Sigma}$) cell volumes and their production parameters.

The dominant algal species dynamics is an essential mechanism sustaining phytoplankton seasonal periodicity.

A case-study of the Kyiv Water Reservoir shows that there is a temporal delimitation of dominant algae's production within a vegetation season. For example, the maximal primary production of green algae (fig. 2) is recorded in spring and early autumn. Respectively, at that time the role of these algae in phytoplankton production is the most significant (Shcherbak, 1999).

Diatoms differ by more complex seasonal dynamics of primary production (fig. 3). The photosynthesis maximum of a spring-autumn species Cyclotella meneghiniana Kütz. is recorded when the water temperature varies between 12 and 15°C, at the same period this species prevails in the phytoplankton. The summer increase in the water temperature up to 23–25°C is the main factor causing a rise in the photosynthetic activity of Melosira italica (Ehr.) Kütz. and M. granulata (Ehr.) Ralfs.

Blue-green algae (fig. 4) have the maximal production in summer (when the water temperature is the highest), synthesizing the major part of the phytoplankton biomass to the water blooms level.

So, following an environmental factor change one population of microscopic algae is replaced with another. Thus, primary production of different populations is characterized by discrete temporal patterns, while the phytoplankton's total production retains its continuity. This is an essential specific trait of autotrophic link functioning, which makes it possible for ecosystems to reach high trophic level and sustain resistance to external impacts.

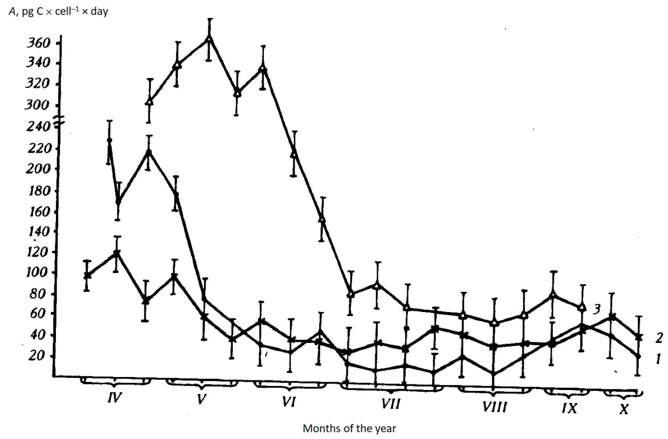

Fig. 2. Seasonal dynamics of the dominant green algae production: 1 – Monoraphidium contortum, 2 – Desmodesmus communis, 3 – Chlamydomonas reinhardtii (Shcherbak, 1999).

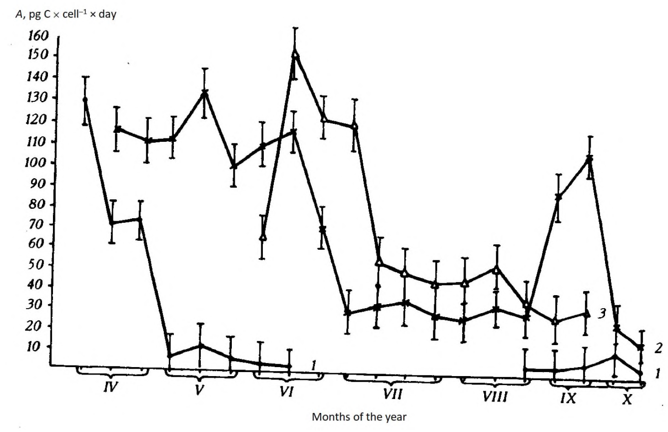

Fig. 3. Seasonal dynamics of the dominant diatoms production: 1 – Cyclotella meneghiniana, 2 – Aulacoseira italica, 3 – Aulacoseira granulata (Shcherbak, 1999).

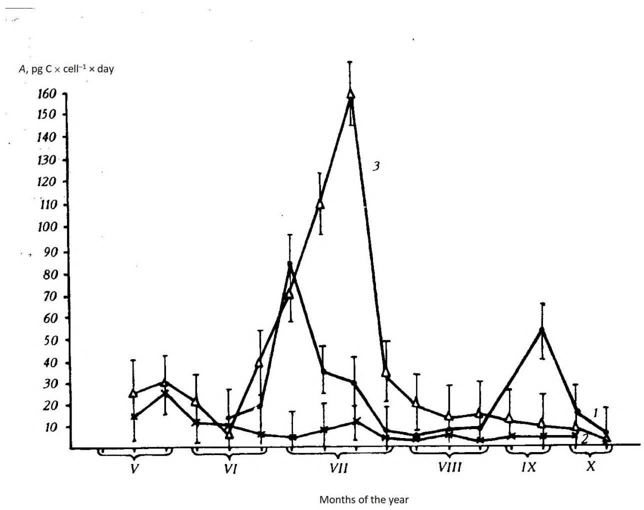

Fig. 4. Seasonal dynamics of the dominant blue-green algae production: 1 – Aphanizomenon flos-aquae, 2 – Microcystis pulverea, 3 – Microcystis aeruginosa (Shcherbak, 1999).

Conclusions

Thus, primary production is one of the most important bioenergy processes, determining biodiversity, trophic state, self-purification, water quality – from the Global Ocean and seas to various lotic and lentic continental aquatic ecosystem of the Earth.

There is a range of various methods for estimating PP, and with consideration taken of their advantages and disadvantages, researchers will be able to obtain the most reliable and unbiased primary productivity data. Assessing phytoplankton primary productivity is very important for developing scientific basis of achieving the UN Sustainable Development Goal No. 6 – ensuring safety and high quality of water for all.

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