Role of organomineral detritus in the microbial trophic web

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Received July 18, 2005

The results of investigation of the effect of the mineral suspended matter forming the organomineral detritus due to the organic matter adsorption from the dissolved phase, on productivity characteristics of the plankton entering into the trophic bonds of a microbial web, are presented. It has been found under laboratory conditions that the increase of the phytoplankton chlorophyll concentration (C_{ch}) in samples with adding of suspension runs more intensively and for a longer time period as compared to the control. In the controls, the C_{ch} increase proceeds up to 67 days with a subsequent reaching of a stationary level at a maximum of 220 μg/l. In samples with adding of 100 mg/l suspension, the stationary level has not been achieved up to 80 days of the experiment. The maximum of the chlorophyll concentration equaled to 520 μg/l. In field conditions, it was shown that all parameters connected with the bacterioplankton productivity characteristics and the content of organic matter adsorbed on mineral suspension, considerably influence the productivity characteristics of the phytoplankton. A multiplicative model of the dependence of primary production on the major environmental factors is offered: the phytoplankton chlorophyll content, a specific coefficient of light absorption by the dissolved organic matter, the adsorbed organic matter content, the bacterioplankton production and destruction, the mean size of phytoplankton cells. It follows from the model that at doubling the bacterioplankton productivity (other parameters being constant) the primary production in lake Khanka increases 2.5 times, in the Yenisei –1.9 times, and in the Krasnoyarsk water reservoir –1.4 times.

Recycling of organic and mineral matters is of great importance in vital activity of aquatic ecosystems. The bacterial community of water reservoirs decomposes compound organic matters and returns different inorganic components, earlier entered into their composition, into the dissolved state. Further these components again can be used by the phytoplankton for growth and formation of biomass. This process essentially reduces the limitation effect of the phytoplankton growth rate and can significantly elongate the times of its active growth in waters, where it actively proceeds. The recycling of various components is especially important in conditions, that a considerable amount of organic and inorganic matters is removed from the dissolved state and adsorbed on a mineral suspension.

Recently, serious disadvantages have been revealed in the classical concept of the food chain, in which the matter and energy fluxes are directed from the primary producers to zooplankton and fishes. To correct traditional notions on the trophometabolic structure of water communities, a new concept has been developed, according to which protozoa, bacteria, and phytoplankton form a microbial web on the basis of a linear food chain.[1–7] According to this concept, the bacterioplankton is in the center of the food chain and has similar functions for phytoplankton and protozoa. It is clearly shown, that the bacterioplankton plays a central role in the organic carbon flux in the ecosystem through oxidation of the dissolved organic matters (DOM) and recycling biogenics.

The high assimilatory potential stipulated by small bacteria sizes, provides a fast recycling of biogenous matters, making them repeatedly accessible for phytoplankton.[4,6–8] Thus, the bacterioplankton productivity, undoubtedly, influences the phytoplankton productional characteristics. The organomineral detritus owing to the process of organic matter adsorption on the suspension surfaces affects not only the bacteria growth and spatial distribution, but also stimulates their productivity.[9–11] However, this connection is not always unambiguous because of influence of many factors, for example, a proportion between the organic substrate content and the mineral suspension concentration, the DOM composition and properties, adsorption capacities of mineral detritus, water reservoir temperature regime, and others.

Therefore, based on the concept of microbial web, it is of interest to examine each link of the trophic chain individually, to follow their interrelation, and to estimate qualitatively the influence of functioning of individual links entering into the general scheme of the microbial web, on the phytoplankton productivity.

Matters and methods

According to the suspended mineral matter content, lake Khanka, the Krasnoyarsk water reservoir, and the Yenisei were chosen as contrast objects of the research. The lake Khanka represents a water reservoir of loessial type, in water of which a plenty of terrigenous particles (up to 150 mg/l) are present. Waters of the Yenisei and the Krasnoyarsk water reservoir are characterized by a low suspension content (8 and 5 mg/l, respectively). These reservoirs differ also by the dissolved organic matter content. The research data were obtained in different years and seasons: for the Yenisei and its tributaries in 1994 and 1997, for Khanka and the rivers running into it in 1992–1998, for the Krasnoyarsk water reservoir in 2000 and 2001. Samples for the analysis were taken from the subsurface layer.

The dissolved organic matter content (DOMC) was estimated from light absorption spectra[12–14] and the DOM fluorescence, the adsorbed organic matter (AOM) – from the difference between the light absorption by non-filtered and filtered samples. The filtration was carried out through filters with a pore diameter of 0.17 μm (the contribution of AOM adsorbed on particles of a smaller diameter made up 2–5%).

Estimation of the mean (effective) diameter of the suspended mineral particles (d, μm) was carried out from the integral light scattering phase functions[13,14] and by the spectrum turbidity method[15]; of the suspended mineral particle concentration (M, mg/l) – from the general light scattering in suspensions.[16]

The concentrating of samples for analysis of the species composition and the phytoplankton population N_{ph} was carried out by the filtration method, the population count – in the Nageotte chamber. The biomass B_{ph} was calculated from the mean volume, equating the shape of cells to a close geometric body. The determination of the primary production P_{ph} and the organic substance destruction D was carried out by the light and dark bottle oxygen method.

The chlorophyll concentration C_{ch} was measured by the fluorimetric and spectrophotometric methods both with pigment extraction from cells and without the extraction.[17]

The bacteria population (N_{b}) was determined via microscope technique, colouring bacteria by fluorescamine at a 1000^{x} magnification by the ML-2B microscope.[18] The generation time and the bacterial production P_{b} were determined by the count-up method from variation of the number of bacteria for a fixed time in two isolated series of water samples. In one of the series the zooplankton was removed by filtration through the track filters with a pore diameter of 4.5 μm.

To pre-estimate the mineral component influence on the development of the natural phytoplankton community, a model experiment has been carried out. As a mineral suspension, the kaolin was used, taken from bottomset beds of the Krasnoyarsk water reservoir, from water samples of which the phytoplankton was taken. The medium of Knopp was added to all experiment samples. The kaolin concentrations in the experiment were 0 mg/l (control), 50, and 100 mg/l.

Results and discussion

It was revealed during the model experiment that the bacterioplankton growth in samples with doping of suspension was more intensive as compared to the control. On the 4th day of the experiment the bacteria population in samples with suspension several times exceeded that in the control.

The increase of the chlorophyll concentration C_{ch} during 20 days proceeded practically with the same rate in all samples. An insignificant excess of the chlorophyll concentration was observed in samples free of suspension. The growth of photosynthetic activity of the phytoplankton was recorded on the 20th day. In the control, the C_{ch} increase proceeded up to 67 days having reached a stationary level at a maximum of 220 μg/l. In samples with 50 mg/l dope of suspension C_{ch} reached its maximum of 400 μg/l. The stationary level has not been achieved up to 80 days of experiment for samples with 100 mg/l doping of suspension. The maximal chlorophyll concentration was 520 μg/l. Thus, the doping of suspension made the growth of the chlorophyll concentration more intense and long.

To the end of the experiment the species composition and cell size of algae were considered. In the control, the development of two blue-green algae taxons (*Synechocystis* and *Synechococcus*), mainly in the form of colony was recorded. In samples with doping of suspension the taxon number achieved 9 and the cells were in a non-aggregated state. This points out to the fact that the presence of suspension creates conditions for conservation and development of species composition of phytoplankton cells.

In the field experiment, the main attention was paid, first of all, to the bacterioplankton (its production and destruction), the dissolved organic matter, and the organomineral detritus. The measurement data on the phytoplankton production depending on the sum of DOM production and destruction ($A = P_{\text{b}} + R$) by bacterioplankton, obtained from the Yenisei, the Krasnoyarsk water reservoir, and Khanka, are presented in Fig. 1.

There is a great number of factors affecting the primary production, therefore, the observed strong scattering of points relative to the regression line allows us to say only about a tendency. The regression interrelation $P_{\text{ph}} = 0.91A – 0.02$ (correlation coefficient $r = 0.55$; 74 samples) confirms the increase of the phytoplankton production as the DOM assimilation by the bacterioplankton increases. To average the influence of various factors, a smoothing procedure was used. The variation series was divided by the principle of equal quantity of points in classes (by elevens points in the first 6 classes, and only 8 points fell into the last 7th class). The linear regression for this smoothing version $P_{\text{ph}} = 0.93A–$

0.004 ($r = 0.98$) is close to the regression immediately from measurements (Fig. 1). High correlation coefficients between the parameters allow us to say about a rise of the primary production with an increase of the bacterioplankton functional characteristics.

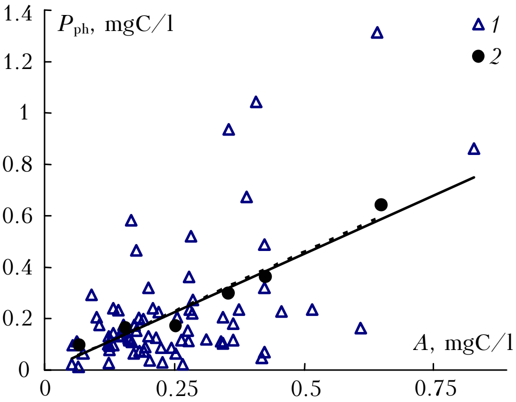

Fig. 1. Dependence of phytoplankton production on the food energy assimilated by bacteria: measured data (*1*); averaged values over 11 measurements in each point (*2*).

The variational series can be divided by the A values into classes with a 0.1 mgC/l step; then we can calculate mean values of P_{ph} and A in each class (since after $A = 0.5$ mgC/l there are only 4 points, we unite them in one class with 0.5–0.9 mgC/l). The regression relation according to this smoothing version is $P_{ph} = 0.79A + 0.03$ ($r = 0.96$).

The dependences are clearly seen, if the smoothing procedure is conducted for individual water reservoirs. Note that for the loess lake Khanka the regression coefficient is 3 times higher than for the Yenisei and the Krasnoyarsk water reservoir. Probably, it is connected with a great amount of fine-dispersed mineral suspension in Khanka, on the boundary surface of which about 90% of organic matter from the dissolved phase is adsorbed. It is well-known, that the particle boundary surfaces influence the activity of the detritus (organic and organomineral) incorporation into the biological cycle[9] and favor a more powerful additional feeding of phytoplankton by biogenic elements for the sacrifice of active mineralization of the adsorbed OM on particles by bacteria.

Since the primary production depends on a great number of environmental factors, it is clear that the demonstrated dependences, in principle, reflect only a tendency. Therefore, a multifactor mathematical models are required. In the absence of necessary information, we can choose an adequate multifactor model based only on the trial and error method. In practice, to describe the results of some multifactor experiment, we often would have to use a mathematical model without pre-testing its adequacy.

For example, it is known from the experience of various sciences that the most part of already received formulas looks like the product of quantities to various degrees (multiplicate model):

$$y = a_0 x_1^{a_1} x_2^{a_2} \ldots x_k^{a_k}, \tag{1}$$

where a_1, ..., a_k can be integral and fractional, positive and negative.

Such a model is in a wide use for description of multifactor dependences due to its simplicity: at k factors only $k + 1$ coefficients must be defined. It is desirable to avoid redundant terms or, especially, factors in the model. Therefore, we introduce in our model functional characteristics of bacterioplankton as two factors – production and destruction (respiration).

It would be naturally to think that the natural factor affecting the primary phytoplankton production is its available biomass, but it turns out, that a large amount of algae biomass does not guarantee this (according to our data received for various water reservoirs and seasons, the correlation coefficient between the phytoplankton biomass and its production is practically zero). The absence of interrelation between the biomass and production results in decreasing phytoplankton P_{ph}/B_{ph} – coefficient (specific production) as the biomass growth. The relation between the P/B and the phytoplankton biomass is approximated by the exponential function $P_{ph}/B_{ph} = 0.16B_{ph}^{-0.98}$ ($r = 0.82$).

The specific production of phytoplankton also depends on a share of small-cell species in the total algae biomass or on sizes (volume) of a mean cell ($V_c = V_{ph}/N_{ph}$). If to include in the small-cell species the cells with $V_c \le 100$ μm^3, the relation is approximated by the exponential function $P_{ph}/B_{ph} = 239V_c^{-0.72}$ with $r = 0.56$.

To take into account the specific production or the unit of the biomass activity, we introduce also the mean cell volume as an environmental factor into the model. In addition, this factor reflects the total phytoplankton biomass amount, since with the biomass growth, as a rule, the portion of large-sized algae species increases, which just leads to the increase of the average cell volume. The relation between the biomasses of small-sized ($V_c \le 100$ μm^3) and large-sized species of the plankton algae can vary, depending on the total biomass amount, from thousandth to a unit. Therewith, with increase of the total biomass of phytoplankton, the biomass of small species, varying from sample to sample within substantial range, practically does not grow (although insignificantly increasing in total according to the regression relation).

It is revealed also that as the algae biomass grows, a significant reduction in ratio between bacterioplankton and phytoplankton biomasses is observed (at large algae biomass, a smaller portion of the bacteria biomass relates to each its unit). This fact also leads to weakening of the role of recycling biogenic elements realized by bacterioplankton, and, respectively, to reduction of additional feeding of phytoplankton (Fig. 2).

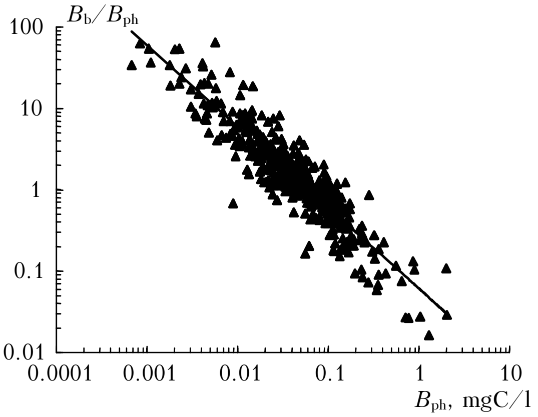

Fig. 2. The relation between biomasses of bacterioplankton and phytoplankton (B_b/B_{ph}).

Naturally, factors affecting the productive characteristics of bacterioplankton must be introduced into the model as well. This is, first of all, the content of easily oxydizable organic matter (EOM) as a feeding resource for bacterioplankton. The EOM content can be estimated by the oxygen biochemical consumption (OBC). Unfortunately, we did not estimated OBC in all points, where the bacterio- and phytoplankton functional characteristics were measured. However, this factor can be taken into account via using a specific parameter of light absorption by the dissolved organic matter ($\kappa_s = \kappa(\lambda)/C_{DOM}$, where $\kappa(\lambda)$ is the light absorptance), which to a certain degree reflects the DOM qualitative composition and, in particular, characterizes the EOM content variations in the total content of the dissolved organic matter (Fig. 3).

Besides, with the problem in mind (on effect of the organomineral detritus on matter and energy fluxes along the microbial web), we introduced into the model the adsorbed organic matter content C_a, which is connected both with the content of the mineral suspended matter (the total boundary surface of the suspension particles) and the specific parameter of light absorption (Fig. 4).

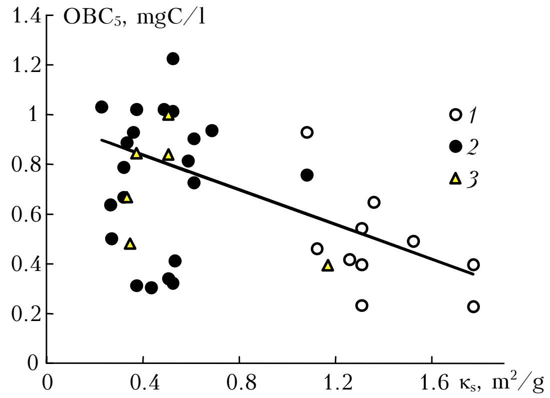

Fig. 3. Dependence of biochemical consumption of oxygen for 5 days (OBC_5) on the specific parameter of light absorption: lake Khanka (*1*); the Yenisei (*2*); the Krasnoyarsk water reservoir (*3*).

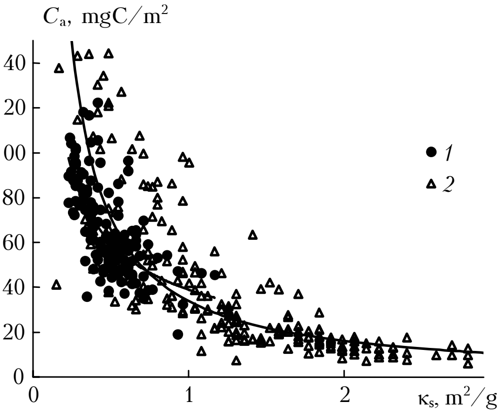

Fig. 4. Relation of the adsorbed organic matter content calculated to a unit surface of the mineral suspension to the specific parameter of light absorption: the Yenisei and the Krasnoyarsk water reservoir (*1*); lake Khanka (*2*).

The chlorophyll content in phytoplankton must be also introduced into the model as a factor determining the absorption of solar energy. The sample irradiance was not controlled at determining the primary production, which has led to a certain extra scattering of points relative to the model regression, though the main measurements were carried out in sunny (and at insignificant cloudiness) days.

As a factor reflecting a specific productive activity of algae cells, let us introduce the mean volume of cells of phytoplankton communities.

Thus, the following parameters are introduced into the model (1): $x_1 = C_{ch}$; $x_2 = \kappa_s$; $x_3 = C_a$; $x_4 = P_b$; $x_5 = D$; $x_6 = V_c$. The calculation of the model coefficients is presented in Table 1.

Table 1. Coefficients of model (1) at chosen environmental factors

Reservoir	a_0	a_1	a_2	a_3	a_4	a_5	a_6
Lake Khanka	0.107	−1.97	2.11	0.43	1.3	0.35	0.17
The Yenisei	0.174	−1.50	1.60	0.45	0.90	0.40	0.17
Krasnoyarsk water reservoir	0.032	−1.18	1.90	−0.13	0.48	0.11	0
Total	0.188	−1.50	1.50	0.20	0.90	0.30	0.10

Further we estimate the most significant factors of the chosen model by the method of serial exception of each term of the model one by one and step-by-step determination of the multiple correlation coefficient r. This coefficient reflects the magnitude of the relative variance σ_x^2 of the model points in comparison with the variance σ_y^2 of the response values, because $\sigma_x^2/\sigma_y^2 = 1 - r^2$. Hence, to estimate the significance in the model of each of its members, it is convenient to use the coefficient in the form $r_\Sigma^2 - r_i^2$.

The calculation results for the multiple correlation coefficients are presented in Table 2.

Table 2. The calculation results for multiple correlation coefficients and estimates of significance of various model parameters

Reservoir	At all x_i	In the absence of					
		x_1	x_2	x_3	x_4	x_5	x_6
Lake Khanka	$r^2 = 0.854$	0.023	0.471	0.639	0.409	0.756	0.823
	$r^2_\Sigma - r^2_i$	0.831	0.383	0.161	0.445	0.098	0.031
	Place by the significance	1	3	4	2	5	6
The Yenisei	$r^2 = 0.813$	0.631	0.048	0.618	0.141	0.725	0.293
	$r^2_\Sigma - r^2_i$	0.182	0.765	0.195	0.672	0.088	0.520
	Place by the significance	5	1	4	2	6	3
Krasnoyarsk water reservoir	$r^2 = 0.582$	0.017	−0.262	0.531	0.486	0.559	0.582
	$r^2_\Sigma - r^2_i$	0.564	0.844	0.050	0.096	0.023	0.000
	Place by the significance	2	1	4	3	5	6
Total	Place by the sum of places of individual reservoirs	3	1	4	2	6	5
General model	$r^2 = 0.650$	0.095	0.104	0.433	0.181	0.552	0.644
	$r^2_\Sigma - r^2_i$	0.553	0.545	0.216	0.468	0.097	0.005
	Place by the significance	1	2	4	3	5	6

The negative connection of the primary production with the adsorbed organic matter content in the Krasnoyarsk water reservoir ($a_3 = -0.13$; see Table 1) is of interest. Possibly, this is stipulated by the fact that for the reservoir water, we did not determine parameters of the dissolved OM adsorption on the mineral suspension particles. The constant of the adsorbed balance (k, m^2/mg) and the maximum possible AOM concentration ($C_{\text{a max}}$, mg/m^2) for the AOM calculation in waters of the reservoir were taken the same as for Yenisei waters. They were determined experimentally.

It is also seen from Table 1 that the dependence of the primary production on mean size of algae cells is absent for the Krasnoyarsk water reservoir. Apparently, the bond between these parameters for the reservoir waters is not obvious at variation of other parameters because of small ratio of the mean maximal volume to the mean minimal one for the investigated samples ($V_{\text{c max}}/V_{\text{c min}} = 8$). For comparison, this ratio is 28 for Khanka, and 39 for the Yenisei.

The dependence of the phytoplankton production, calculated by the model (1) and measured, is plotted in Fig. 5.

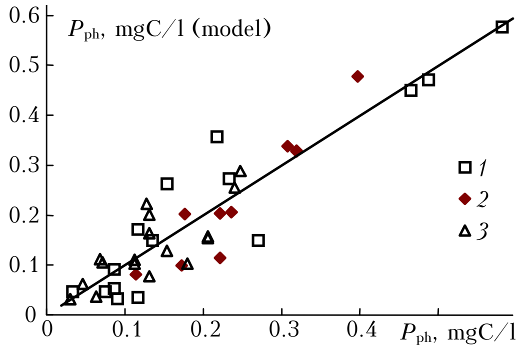

Fig. 5. Regression dependence between the measured primary production and calculated by the model (1): lake Khanka (*1*); the Yenisei (*2*); the Krasnoyarsk water reservoir (*3*).

The regression line in Fig. 5 ($y = x$) expresses the relation between the production amounts in each reservoir individually and the relation by the general model. A noticeable deflection from the regression line of individual points of lake Khanka is seen. Apparently, it is connected with the fact that when measuring points at this lake, the most significant irradiation variations were observed.

Conclusion

According to significance of factors for the model calculated without dividing into individual reservoirs (general), and the lake Khanka model, the first is the chlorophyll content (see Table 2), because it is the energy source for the primary producing of organic matter in aquatic ecosystems. The next two are parameters connected with the bacterioplankton production (immediately with the P_{b} production and the bacteria feeding resource). A special attention should be paid to the AOM content (the parameter C_{a} taking the 4th place by the significance for all reservoirs) as a factor, determining the organomineral detritus importance for functioning of ecosystems. Note, that the DOM fraction, easily assimilable by bacteria, is adsorbed on the surface of mineral particles in the greater degree than the conservative fraction. Probably, it is due to a smaller molecular weight of EOM. The organic matter destruction by the bacterioplankton influences the primary production to a lesser extent, than the bacteria production (buildup of their biomass).

Significance of some factors for the Yenisei and the Krasnoyarsk water reservoir somewhat differs from the above data. The decrease in significance of the phytoplankton chlorophyll content for these reservoirs is due to low C_{ch} variability in comparison with other factors. So, the ratios of the maximal C_{ch} values to the minimally recorded during the measurements were 8 and 4 for the Yenisei and the Krasnoyarsk water reservoir, respectively, while for the mean volume of algae cells these ratios were 39 and 8.

The different $P_{\rm ph}$ increase at an identical initial bacterioplankton production (and its identical increase) for the investigated reservoirs is caused, to our opinion, by distinctions in size distribution of algae cells. So, the mean phytoplankton cell size in lake Khanka is 157 μm^3, in the Yenisei – 396 μm^3 and in the Krasnoyarsk water reservoir – 727 μm^3. The area of the boundary cell surface increases at a decrease of their sizes (at equal biomass). And the greater surface area is equivalent to increase of the biogenics concentration in the medium since the algae cells are fed via their surface (the contact area increases).

Thus, it is possible to state that all parameters connected with productivity characteristics of bacterioplankton and the organic matter content adsorbed on the mineral suspension considerably affect the productivity characteristics of phytoplankton. If the bacterioplankton productivity doubles (at other parameters constant), the primary production in the Khanka increases 2.5 times, in the Yenisei –1.9 and in the Krasnoyarsk water reservoir –1.4 times. For the model calculations without division into individual reservoirs (general), doubling of $P_{\rm b}$ will lead approximately to a 1.9 time increase of the primary production. The same increase of the organic matter destruction according to this model increases $P_{\rm ph}$ only by 20%. The lesser influence of the OM destruction is connected either with a lesser yield of biogenics (the greater yield of fragments of organic molecules) caused by the bacteria respiration, or with a change of the quality composition of biogenics under destruction (the biogenic elements are excreted, which are less necessary for the phytoplankton growth).

Hence, we can make a conclusion that the organomineral detritus plays an essential role in the productivity of aquatic ecosystem. Besides, it is a nutrient substrate not only for bacteria, but also for protozoa and can be considered as an individual link in the general scheme of the trophic microbial web.

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