A Hundred Years of the “Living Matter” Concept: 
Its Amount, Quality, and Distribution in the Ocean

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Abstract—The paper discusses advances and failures in solving the problems posed by V.I. Vernadsky 100 years ago. The quantity and quality of “living matter” along with its distribution on Earth are analyzed. In accordance with the competence of the author, the paper is focused on the most voluminous biogeochemical reservoir of the planet, i.e., the World Ocean. In a number of cases, the presented literature and original data demonstrate a progress in the solution of V.I. Vernadsky problems: the estimation of the quantity and the description of the distribution of living matter. In particular, new data on the role and distribution of the living matter in the oceansphere are presented. In other cases such as the analysis of the amount of homogeneous living matter and its biogeochemical role, there is no visible progress over the past decades but possible solutions to the problem are suggested.

Keywords: ocean biogeochemistry, living matter, organic carbon, plankton

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Even more important questions are associated with the study of marine plankton. In our analyses, we do not study real ocean water, but a totally ideal composition—an aqueous solution. This aqueous solution is the only one we take into consideration in all our discourses about oceanic chemical processes, and obviously must lead—and leads—to wrong conclusions [1].

Exactly 100 years have passed since the end of the cycle of works united by V.I. Vernadsky under the title “Living Matter in the Earth’s Crust and Its Geoch- 
emical Significance” (1916–1922) [1]. One hundred years ago biogeochemistry was born and since that time represents a branch of geochemistry that studies the chemical composition of living matter and geochemical processes in the biosphere of the Earth with the participation of living organisms. The headstone of this complex science is the concept of “living matter,” “the totality of plant and animal organisms, including humans” [2].

Vernadsky posed a number of problems that have not been solved and, partially, have not been understood until now. According to Vernadsky, a possible reason is that “unfortunately, biologists pay very little attention to the phenomena associated with living matter... Biologists forget that the organism they study is an inseparable part of the Earth’s crust, is a mechanism that changes it, and can be separated from it only in our abstraction” [1]. On the other hand, classical geochemists and even biogeochemists do not try to get into the problems of biological sciences, forgetting that biogeochemistry, as it was understood by its founder, is an interdisciplinary science, solving general problems of biology, ecology, and geochemistry. The purpose of this work is to come back to the questions posed by Vernadsky a century ago, to show where we have progressed in solving them and where we have stay at the same position, and to outline possible pathways of solving problems. This will be done on the example of the living matter of the World Ocean, the most voluminous biogeochemical reservoir of the planet, the study of which is the key problem of biogeochemistry. The stock and cycling processes of organic carbon ($C_{org}$) in living matter of the ocean determines, in many respects, the parameters necessary for the occurrence of oil and gas, the gas exchange between geospheres (and, therefore, the climate), and the fluxes of almost all chemical elements, many of which are functionally related to the fluxes of $C_{org}$.

THE STOCK OF LIVING MATTER ON THE PLANET AND IN THE OCEANS AND ITS PERSISTENCE

To consider the geochemical effect of the accumulation of living matter..., it is necessary to take all living homogeneous organisms from all classes and groups of organisms [1]. The real object of geochemistry is a living organism, with all the water that permeates it entirely while it is alive [2].
A HUNDRED YEARS OF THE "LIVING MATTER" CONCEPT

The carbon of living matter is only a minor part of the total carbon content of our planet (100 × 10^6 Gt in total). Planetary carbon is generally contained in sedimentary rocks in the form of carbonates and organic compounds (65 × 10^6 Gt and 16 × 10^6 Gt); is dissolved in seawater as CO_2, HCO_3^−, and CO_3^{2−} (38.5 × 10^3 Gt); and finally, is accumulated in sediments of large lakes (19.5 × 10^3 Gt), fossil fuels (5.2 × 10^3 Gt), soils (2.2 × 10^3 Gt), and the atmosphere as CO_2 (850 Gt), as well as in the ocean in the form of dissolved (1000 Gt) and suspended (50 Gt) organic matter.

What about the carbon of living matter? According to modern concepts based on a generalization of a large database the total biomass of living matter of our planet is estimated as 547 Gt C (Table 1). The value of 5 × 10^{−4}% of the total C seems to be negligible; however, the biogeochemical cycles of this particular component determine the key processes of the biosphere of the Earth. If we use the coefficient, linking the C_{org} mass with the wet weight of an organism equal to 0.05, the mass of all living matter may be assessed 1.1 × 10^{13} t. The conditionality of the transition coefficient allows us to speak only about an order of magnitude (10^{13} t). This point of view is shared by many researchers. Other authors considered that the mass of living matter increased over geological time owing to the biological activity of plants. However, most likely, the change in the amount of living matter was not monotonous. Before the higher plants conquered the land, the main biogeochemical processes occurred in the ocean, where, depending on the conditions of macro-scale stratification, the ocean depths were either enriched or depleted of life (scenarios are discussed in detail in [5]). The stock of living matter in the biosphere varied accordingly. With a decrease in the amount of living matter, part of C_{org} was transferred and/or buried in sediments. The significant increase in the amount of living matter owing to the presence of terrestrial ligneous plants occurred in the Late Paleozoic. Since that time living matter was mainly concentrated on the land. Assuming that 70% of the biomass of terrestrial plants is the biomass of woody stems and trunks, which are metabolically and biogeochemically inert [6], a decrease in the share of the oceanic living matter in the Paleozoic hardly resulted in a proportional decrease in its role in the planetary biogeochemical cycles.

Indeed, the basic value for assessing the biogeochemical cycles of carbon is the value of primary production, i.e., new C_{org} generated by producers. Of the two main types, chemosynthesis or photosynthesis, photosynthesis currently dominates on the planet. The contribution of chemosynthesis to primary production seems to be insignificant and ranges from 0.02 to 10%
According to various estimations [3, 7]. However, in the early stages of the biosphere, the role of chemosynthesis was higher. Currently, we can estimate relatively confidently only the value of the photosynthetic production (in the range of 40−103 Gt C/yr). We know that its total value is approximately the same in the terrestrial and oceanic parts of the biosphere [3, 8]. The first consequence of such a balance is the lower value of the primary production and, consequently, the lower amount of living matter on the planet before the development of plants on the land. The second consequence is that comparable flows of energy (values of primary production) are concentrated in 470 Gt of living matter on the land and in 6 Gt of living matter in the ocean (Table 1). Therefore, biogeochemical processes in the ocean are almost 80 times more intense than on the land. Thus, the living matter of the World Ocean merits a special attention.

Only 1% (6 Gt C) of 547 Gt C of the planetary living matter is harbored by the ocean [6]. Would it be worth focusing on such a small quantity? Of course, yes.

First, the World Ocean represents over 95% of the inhabited volume of the biosphere [9] and, accordingly, is a crucial biogeochemical reservoir on the planet where basic processes occur.

Secondly, in terms of metabolism and biochemical processes, the living matter of the ocean is orders of magnitude more active than the living matter of other areas of the biosphere: it has been shown above that the biogeochemical processes in the ocean are nearly 80 times more intense than those on the land. The biomass of the most mobile and metabolically active animal kingdom in the ocean (2 Gt C, mainly, fish and crustaceans) is five times greater than their biomass on land (0.4 Gt C, basically arthropods and annelids) [6].

Thirdly, the biogeochemical cycles of carbon linked to trophic relationships are much more intense in the ocean than those on land. In the ocean, 1Gt C of producers of new organic matter provide an energy base for 5 Gt C of consumers of that production [6] owing to their enormous rate of growth and reproduction. On the land, the situation is opposite: the respective estimates are 450 Gt C and 20 Gt C. Thus, the ratio of producers and consumers in the ocean is two orders of magnitude higher (0.2 vs. 22.5), which again points to the enormously higher intensity of the biogeochemical processes in the ocean.

Therefore, confident estimates of the living matter stock on the planet have recently appeared. There are still ambiguities related to the hydrosphere; however, in recent years, significant progress has been made there as well.

THE QUALITY OF LIVING MATTER: THE DIVERSITY OF HOMOGENEOUS LIVING MATTER

Among morphological varieties, the varieties or subspecies that are related to geographic ranges and ecological conditions of the area are the most important for the geochemist.... Homogeneous living matter (the total of individuals of the same species) is in many ways analogous in its geochemical effects to those chemical natural compounds—minerals—that participate in geochemical processes [1].

According to V. I. Vernadsky, an inventory of the species diversity or “homogeneous living matter” is as important for geochemistry as the inventory of minerals. However, this task, even now, 100 years later, is far from being solved. We can now predict the number of species on the planet with the same accuracy as in the days of Vernadsky: since the 1950s, the estimates of the total number of species have varied (and still vary) in the range of 1 to 100 million [10]. We cannot even estimate the order of magnitude—let us only note that the number of species of multicellular plants and animals may reach many millions. Even the most current concepts based on extensive databases are contradictory. According to some of them, there are only 1.8−2.0 million plant and animal species on the planet, and only 0.3 million of them are marine species. The updated databases give similar estimates (from 2.0 to 2.3 million) (http://www.catalogueoflife.org/annual-checklist/2018/info_totals, https://www.catalogueoflife.org/data/metadata; Table 1). At the same time, other estimates show that 0.8 million species of multicellular plants and animals [11] inhabit coral reefs, i.e., the coral reefs alone contain almost three times as many species as the entire ocean including poorly explored depths. It turns out that the estimates of diversity of homogeneous living matter give extremely inconsistent results even for organisms from accessible habitats, which are relatively well explored. The estimates of the true diversity of living matter of viruses, archaea, bacteria, and protists, as well as the estimates of the diversity of living matter in the deep ocean or in the subsurface biosphere, should be left for better times; they are not even given in databases (Table 1).

The only solution of this issue is making a slow, step-by-step inventory of individual groups of organisms. Certainly, such an inventory requires many years of professional efforts for different groups of experts—zoologists, botanists, microbiologists, and virologists. For multicellular organisms, the combined application of morphological and molecular genetic methods, as has been done for a number of oceanic groups, makes it possible to obtain an evolutionary model describing the phylogenetic relationships of all known species of the group and to judge their true diversity confidently [12]. For unicellular organisms, the key to solving the problem lies in the application of molecu-
lar genetic methods: they allow us to reveal the diversity of microbiota, especially in the deep ocean [13].

The inventory is even more complicated because Vernadsky considered subspecies, rather than species, as a unit of homogeneous living matter. The subspecies are often geographically isolated and occur in different biogeochemical provinces and, therefore, play a different role in the biosphere. When the subspecies are taken into consideration, the total number of taxa multiplies by many times. For example, the recent studies of such a seemingly well-studied group as krill are taken into consideration, the total number of taxa differs by 1–2 orders of magnitude and can currently be estimated by remote sensing methods with certain limitations [15].

In recent decades, two new films of life (according to modern terminology, narrow layers of the biomass concentration) have been identified in the benthopelagic zone (near-bottom layer) and in the mesopelagic zone (depths of 200–1000 m). The first film of life is associated with geochemo processes in the ocean near-bottom layer due to the proximity of the bottom and the water column [16]. This province is continuous in the ocean and takes on a different “face” in the coastal waters, over the continental slopes and undersea mountains, over the ocean floor, and in the vicinity of hydrotherms. The benthopelagic zone exchanges organic matter with both the overlying waters and the sediments owing to vertical migrations of living matter [16]. It is in this film (along with the surface film) that organic carbon mineralization is most active (97% of the C_\text{org} of primary ocean production along with C_\text{org} input from the land) [3].

One of the most remarkable forms of the benthopelagic film are the hydrothermal systems. The chemosynthesis—the formation of new C_\text{org} owing to the energy of chemical compounds of hydrothermal fluids—is the energetic basis of living matter of these systems. Biological fractionation of stable isotopes made it possible to determine pathways of C_\text{org} on the basis of the δ^13C and δ^15N distribution in living matter [17] and to prove the quasi-closeness of the hydrothermal systems. Owing to the quasi-closeness, the concentration of living matter can be up to tens of kg/m^3 (i.e., hundreds of grams of C_\text{org} per cubic meter), possibly the highest concentration of C_\text{org} in the hydrosphere [18]. Even apparently lifeless porous carbonates of the hydrothermal systems contain a significant amount of living matter in the form of various microbiota, an invisible component that has been studied by molecular-genetic methods [19].

The second oceanic film of life, which was not identified by Vernadsky, is not a proper “film” if we consider its thickness (several hundred meters). This is the mesopelagic zone of the ocean at the depths of 200–1000 m. Until recently, the concentration of living matter was believed to be maximal in the surface layer and decreased exponentially with depth. However, recent studies have shown that the stock of living matter in the mesopelagic zone may exceed that in the surface layer [15].

The living matter stock in the mesopelagic zone is significantly underestimated, which is easy to demonstrate. Let us estimate only the total C_\text{org} contained in a large fraction, for which the estimation is reliable: in meso- (0.2–2 cm) and macroplankton (>2 cm) and in fish. If we extrapolate data on the average C_\text{org} of mesopelagian (1.85 t C/km^2 [15]) obtained for the Atlantic to the tropics and subtropics of the whole ocean, we get a total of 0.3 Gt C. Taking into account C_\text{org} of mesopelagian of the Southern Ocean (0.1–0.2 Gt C [20]), mesopelagic fishes (0.6–0.8 Gt C), and shrimps (0.1 Gt C [9]), we get the total living matter of 1.1–1.4 Gt C. The areas to the north of 40° N and the eutrophic zones of the ocean, where integral assessments are premature, are not included in these calculations. The mesopelagic zone contains, therefore, over half of living matter of the hydrosphere (2 Gt, Table 1).

It is important that the main bulk of mesopelagic living matter is represented by migrating organisms (mesopelagian, shrimps, fishes) that feed in the
C$_{org}$–rich upper water layers at night and descend to deeper layers to avoid daytime predators. The scales of such vertical movements are tremendous: mesopelagic shrimps alone vertically redistribute 0.1 Gt C$_{org}$ [9] over a distance of several hundred meters every day. Other groups—planktonic copepods, fishes, krill—also participate in the redistribution of living matter, but the scale of this redistribution remains to be estimated. This assessment merits a special attention because a very active living matter incorporates C$_{org}$ and oxygen in the upper water layers, provides C$_{org}$ transport to the depth of 200–1000 m and, further, pellet transport to greater depths with a daily cycle. Without the mechanism of pellet transport, the dying living matter of plankton would have to be almost completely decomposed in the water column and could not reach the bottom sediments [7]. The vertical migrations of the mesopelagic zone significantly drive the mechanisms of the pellet transport in the redistribution of C$_{org}$ of the hydrosphere. The assessment of their biogeochemical role is one of the most urgent tasks of biogeochemistry of the ocean.

Overall, a greater progress has been made in the study of the distribution of living matter in general (and life films in particular) than in the study of the total amount and composition of living matter. Relatively few white spots remain, and one of them is linked to the distribution of living matter outside the life films. The deepest zone of the ocean, bounded by the mesopelagic zone from above and by the benthopelagic zone from below, represents the greatest part of the hydrosphere, although it has a reduced concentration of living matter. The concentration of living matter of an invisible component (bacteria, archaea) in this zone is unknown, and the ostensible lifelessness of these transparent waters is misleading.

CONFLICT OF INTEREST

The author declares that he has no conflicts of interest.

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