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RESEARCH

Rethinking some roots of ecosystem approach in aquatic ecology: between the food cycle and lake metabolism

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Abstract

The present study provides new insight into the key aspects of the early formative period of the ecosystem concept in aquatic ecology. Raymond Lindeman's trophodynamics is known to be a starting point for the development of the modern concept of ecosystem. The trophodynamic approach in ecology was proposed by Lindeman in his widely cited paper of 1942. Lindeman's views are analyzed in comparison with the contemporary production studies in aquatic ecology. It is shown that a similar theoretical system has been proposed in the USSR at the end of the 1930s by Georgiy G. Vinberg. He introduced the concept of biotic balance based on the wide appraisal of the dark and light bottles method. The study shows that both Lindeman's trophodynamics and Vinberg's concept of biotic balance relied on an energy-based approach in considering the wholeness of a water body. The two scientists, however, differed in several important aspects concerning the interpretation of the role of living organisms. The holistic interpretation of ecosystem by Lindeman and Vinberg can be seen as part of the dilemma between physicalism and organicism. At the same time, the main emphasis in the concepts of both Vinberg and Lindemann was on the primary production component, a feature that was common to the first holistic systems in production hydrobiology (e.g., E. Naumann's regional limnology). It is clear that modern problems of aquatic ecology should be addressed from the perspective of the organismocentric understanding of the ecosystem, but undoubtedly at the new level of development of this view.

Keywords Trophodynamics · Biotic balance · R. Lindeman · G.G. Vinberg · Ecosystem · Organicism

Introduction

Raymond Laurel Lindeman (1915–1942) has undoubtedly left an indelible mark in the history of ecology and its theory. It was his seminal work of 1942 (Lindeman 1942), still widely cited in the literature, that marked the beginning of modern ecosystemic studies (Bocking 2013; Egerton 2017; Golley 1993). Lindeman's primary achievement was that he gave real substance to the term "ecosystem," which was coined in 1935 by A. Tansley while discussing contentious issues in plant ecology (Tansley 1935). Lindeman attempted to find quantitative relationships for the energy flow through the trophic chain (in particular, during succession ("aging") of a water body). During the post-World War II period, this attempt has led to a burgeoning of ecosystemic thinking in ecology, first in the American academic community and then worldwide. The concept of ecosystem has relied significantly on the ideas of the general systems theory and cybernetics, which also rose to prominence in the 1950s (Voigt 2011).

The ecosystem is known to include both living organisms and their abiotic environment, but what makes it a biological object, one of the levels of life? The ecosystem is a biological object, because it is inconceivable without living organisms, whose biological activity is the driving force for circulation of matter and energy. What attitude, however, expressed the ecologists including R. Lindeman toward the role of living organisms in ecosystems in the mid-twentieth century? Another, more general question, also pertinent in this context, is whether someone else has proposed ideas about the ecosystem, similar or alternative to Lindeman's trophodynamics (but perhaps without explicitly using the term "ecosystem"). And if so, then why has Lindeman's

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trophodynamic approach eventually become crucial for developing the modern ecosystem theory?

While answering these questions, we unavoidably enter into an area of the so-called production branch of ecology. Production ecology deals with circulation (making—production and unmaking—destruction) of substances and energy flow in the ecosystem. This approach owed much to practical problems of estimating fish reserves and their food resources in water bodies (Bocking 1990; Elster 1974; Talling 2008). It is thus not a coincidence that the first holistic ideas have emerged in the course of the studies done on lakes, which are, by their nature, relatively closed and isolated objects. It is enough to recall, in this respect, the classical 1887 work by S. Forbes "The lake as a microcosm" (Schneider 2000). The development of holism in production ecology and in aquatic ecology in general has been driven in the first quarter of the twentieth century by the works of several European scientists such as E. Naumann (Naumann 1929), A. Thienemann (Schwarz and Jax 2011), and K. Münster Strom (Strom 1927/1928; Strom 1928), and the tradition of comparing a lake to a living organism, which can breathe, goes back to E.A. Birge, the founder of the Wisconsin limnological school (see, for example, Beckel 1987; Birge 1907; Frey 1963).

Attempts to measure metabolism of water bodies have a long history (Staehr et al. 2012). For instance, in the early twentieth century the German physiologist (take note of his professional specialization), A. Pütter, measured rates of oxygen consumption and release in the water samples taken from the Bay of Naples. This idea and the corresponding measuring technique called the dark and light bottles method (Goldman 1968) have found their most explicit expression in the works of the Soviet limnologist G.G. Vinberg and somewhat later and independently in experiments of G. Riley, a disciple of G.E. Hutchinson (Hutchinson 1973). Hutchinson later recognized that Vinberg, whose works were little known outside the USSR because of the political isolation of the country, had actually been the first to develop this technique (Hutchinson 1973).

Using the dark and light bottles technique, Vinberg developed the concept of biotic balance, whose principles will be discussed in the present paper. The study of biotic balance in the ecosystems of different types of water bodies became one of the elements of the International Biological Program (IBP) (Golley 1993). Vinberg and his co-workers took a leading part in these studies by publishing several methodological guidelines (for instance, Vinberg 1971), although the name of this scientist is even now only rarely mentioned outside Russia. It is noteworthy that a similar set of ideas about a water body as an integrated whole (Lindeman's trophodynamics, Vinberg's biotic balance) has emerged during the same period (at the turn of the 1940s) in different countries.

The aim of this study was to identify the most important aspects of ecosystem ideas in aquatic ecology of the mid-twentieth century worldwide. This was accomplished through a comparative analysis of Lindeman's trophodynamics and Vinberg's biotic balance. The analysis is preceded by a detailed examination of prerequisites for the development of these concepts. In particular, the discussion will touch on the elaboration of the dark and light bottles method. Unlike Lindeman's works, which have been thoroughly examined in a number of studies, Vinberg's works have remained almost unexplored by historians of science, even in Russia. The comparison of ideas of the two scientists may give new insight into ecosystem as a concept (at least, when applied to aquatic ecology) and estimate some modern-day prospects of ecosystem views.

R.L. Lindeman and his trophodynamics

Since R. Lindeman and his trophodynamics have been discussed in a significant number of publications (see his academic biography in Cook 1977; the analysis of the concept of trophodynamics in Golley 1993; and some modern appraisals in Sobczak 2005; Sterner 2012), I will give only a very brief overview of his ideas.

Throughout his very short life, Lindeman published only a few papers. At the beginning of his career, Lindeman was involved in studying Cedar Creek Bog under the supervision of the botanist W.S. Cooper. This lake was regarded as "senescent," that is to say it was close to being obliterated by overgrowth. The collaborative efforts of several scientists who studied different aspects of the lake resulted in a series of papers under the collective title of "Ecological Studies of a Senescent Lake" published in the scientific journals "The American Midland Naturalist" and "Ecology." Lindeman's paper titled "The Developmental History of Cedar Creek Bog, Minnesota" (Lindeman 1941b) was mostly descriptive. In this paper, Lindeman described succession of higher water plants, geological characteristics of the lake and sediment types, which led him to conclude that the lake was indeed "aging," i.e., overgrown to such a degree that water covered only 10% of its former area.

In his next paper (Lindeman 1941a), Lindeman attempted to conduct a quantitative analysis of interactions between ecological groups of organisms in this lake. Lindeman wrote that the problem of food relationships of organisms is of the utmost importance, but only a few efforts have been made to solve it. In this paper, he presented his diagram of food cycle (Fig. 1), which was very similar to the previously published diagram of the German limnologist A. Thienemann, and then described in meticulous detail, almost like a zoologist or botanist, the taxonomic composition of ecological groups of hydrobionts in the lake.

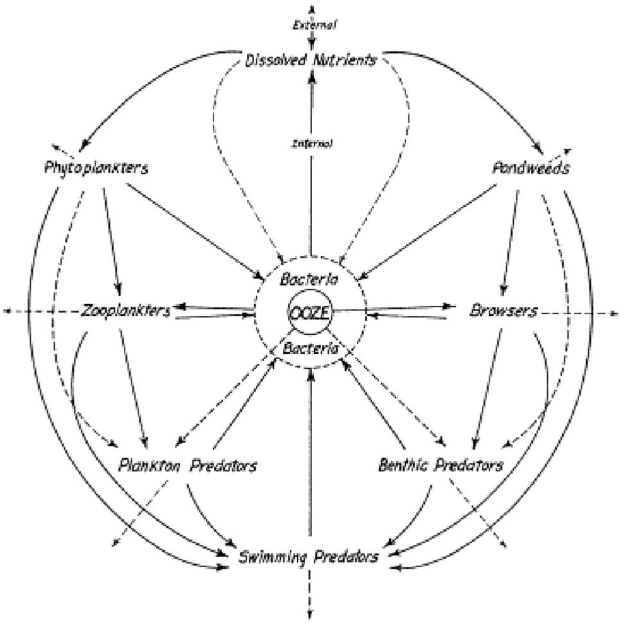
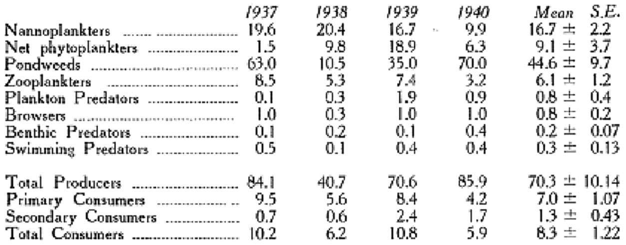


Fig. 1 Diagram showing relationships between groups of organisms in a "senescent" lake (after Lindeman 1941a)



	1937	1938	1939	1940	Mean	S.E.
Nannoplankters	19.6	20.4	16.7	9.9	16.7 ±	2.2
Net phytoplankters	1.5	9.8	18.9	6.3	9.1 ±	3.7
Pondweeds	63.0	10.5	35.0	70.0	44.6 ±	9.7
Zooplankters	8.5	5.3	7.4	3.2	6.1 ±	1.2
Plankton Predators	0.1	0.3	1.9	0.9	0.8 ±	0.4
Browsers	1.0	0.3	1.0	1.0	0.8 ±	0.2
Benthic Predators	0.1	0.2	0.1	0.4	0.2 ±	0.07
Swimming Predators	0.5	0.1	0.4	0.4	0.3 ±	0.13
Total Producers	84.1	40.7	70.6	85.9	70.3 ±	10.14
Primary Consumers	9.5	5.6	8.4	4.2	7.0 ±	1.07
Secondary Consumers	0.7	0.6	2.4	1.7	1.3 ±	0.43
Total Consumers	10.2	6.2	10.8	5.9	8.3 ±	1.22

Fig. 2 Table summarizing annual production of different groups of organisms in Cedar Bog Lake (after Lindeman 1941a)

The quantitative counts of different groups of organisms were used by Lindeman in combination with his calorific values to calculate the annual production of ecological groups expressed in calories per square centimeters for each year (Fig. 2). In conclusion, Lindeman discussed the question of ecological efficiency of food chains. According to Lindeman, the production ratios for food groups can reflect the ratios of physiological efficiency (i.e., efficiency of using food for growth) only if food is the single limiting factor. But in reality this is often not the case and therefore the production ratios for different groups are much lower than might be expected from purely physiological calculations.[1] Lindeman, for the first time in ecology, proposed an energy-based interpretation for circulation of matter in the water bodies. In doing this, Lindeman used nutrition as the basis of circulation and viewed sunlight as the only energy source for the water bodies.

In this paper, Lindeman employed a calculation scheme similar to that previously used by C. Juday (Juday 1940), who was cited in Lindeman's paper. In his 1940 paper, Juday attempted to determine the energy balance of a lake. To accomplish this, he had to consider also purely physical processes (for instance, thawing of snow and evaporation), which has not been done by Lindeman, because his primary focus was on food chains. Juday, like Lindeman after him, computed the energy equivalent for the biomass of different animal groups relying on their calorific values (Lindeman himself used Juday's conversion coefficients). Juday, however, did not calculate any ratios, which is understandable, since he only tried to provide the energy value for lake components.

In his next paper (Lindeman 1942), which is his most widely known work, Lindeman attempted to combine the concepts of productivity, food chains and community successions (Golley 1993). Unlike his previous work, this paper made extensive use of the term "ecosystem," but a more traditional term "community" was also employed.

The story behind the publication of Lindeman's 1942 paper is quite complex and was described in detail in the literature (Cook 1977). It may be worthwhile to repeat it here briefly, because it is quite edifying. When Lindeman, influenced by G.E. Hutchinson, made a significant revision of his initial version of the manuscript, he submitted it to the "Ecology" journal. The manuscript received two negative reviews from renowned ecologists (one of whom was Juday), and T. Park, the chief editor of the journal, rejected the paper. The principal arguments for rejection were that the manuscript was much too theoretical (i.e., speculative) and was based on the material obtained by studying only a single lake, rather than a series of water bodies. The paper was saved by Hutchinson who had interfered and convinced the chief editor to accept the manuscript for print after revision. One of Hutchinson's arguments was that it is impossible to expect that one researcher would be able to study dozens or hundreds of water bodies in a short period of time. For such work to be done, this researcher needs a certain established position in the academic world, which can only be attained if he already has some published works. Park sent a response to Lindeman saying that "time is a great sifter in these

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[1] R. Lindeman is often credited with the statement (see, for instance, the reference in Karpowicz et al. 2020) that every next trophic level accounts only for 10% of energy of the previous level (i.e., the production ratio between adjacent trophic levels is 0.1). In the popular-science sources, this rule is often called "10% law"

Footnote 1 (continued)

or "Lindeman's law." However, there is no reason to attribute this statement to him. It will be shown in the following text that Lindeman only postulated a progressive decrease in energy (because of energy dissipation) in going from one trophic level to the next, higher level.

matters and it alone will judge the question" (Sobczak 2005, p. 54). We now know that he did a great favor to science by accepting the work of the young researcher despite highly negative reviews from distinguished scientists. It is probably so far the only known example of this kind and provides an edifying perspective on existing relationships in the modern system "author – editor – reviewers," which leaves little room for such informal decisions. It is noteworthy that one of the reviewers (Juday) has later accorded high esteem to Lindeman's paper. Unfortunately, Lindeman did not live to see his work published, because in 1942 he died of serious liver illness.

In this paper, Lindeman first discussed trophodynamics ecology, a new approach that he proposed. The term "trophodynamics" was defined by the author as energy transfer from one to another part of the ecosystem in the process of food relationships of organisms. Lindeman wrote: "Quantitative productivity data provide a basis for enunciating certain trophic principles, which, when applied to a series of successional stages, shed new light on the dynamics of ecological succession. <…> The trophic-dynamic viewpoint, as adopted in this paper, emphasizes the relationship of trophic or "energy-availing" relationships within the community unit to the process of succession" (Lindeman 1942, p. 399).

Lindeman emphasized the wholeness of the lake, which "is considered as a primary ecological unit in its own right, since all the lesser "communities" mentioned above (*i.e., commonly distinguished planktonic and benthic communities,* etc.—*A.R.*) are dependent upon other components of the lacustrine food cycle (here he references a diagram (Fig. 1)—A.R.) for their very existence" (ibid.). Influenced by A. Tansley, Lindeman concluded that living and non-living components of a water body are intimately interconnected through matter cycling: "Upon further consideration of the trophic cycle, the discrimination between living organisms as parts of the "biotic community" and dead organisms and inorganic nutritives as parts of the "environment" seems arbitrary and unnatural. The difficulty of drawing clear-cut lines between the living *community* and the non-living *environment* is illustrated by the difficulty of determining the status of a slowly dying pondweed covered with periphytes, some of which are also continually dying. As indicated in Fig. 1 (Fig. 1—A.R.), much of the non-living nascent ooze is rapidly reincorporated through "dissolved nutrients" back into the living "biotic community." This constant organic–inorganic cycle of nutritive substance is so completely integrated that to consider even such a unit as a lake primarily as a biotic community appears to force a "biological" emphasis upon a more basic functional organization" (*italics mine—A.R.*; Lindeman 1942, p. 399–400). In these words, Lindeman specified what he meant exactly by the wholeness of the ecosystem, i.e., reified the concept introduced by Tansley. It is also noteworthy that the author essentially erased the boundaries between the living and non-living components of the ecosystem.

Lindeman stressed that all life in the ecosystem depends on incoming energy of the sun. Based on the ideas about the roles of producers, consumers, and reducers (the terms coined earlier by Thienemann) and Hutchinson's views about trophic levels, Lindeman concluded that different trophic levels have different energy reserves. The estimates of these reserves, however, should be corrected for energy losses due to respiration, predation, and decomposition. While discussing the values of these energy losses, Lindeman asserted that the intensity of energy dissipation through respiration increases progressively at the higher levels of the food cycle. Lindeman presented the results of his calculations as a traditional Eltonian pyramid,[2] but in his paper the pyramid was expressed in energy units, rather than in numbers or biomass, as it was done previously: "the rate of production cannot be less and will almost certainly be greater than the rate of primary consumption, which in turn cannot be less and will almost certainly be greater than the rate of secondary consumption, which in turn…, etc." (Lindeman 1942, p. 408).

Lindeman then discusses ecological efficiency in lakes and reflects on productivity of the lake as a whole. According to Lindeman, the lake, because of the concavity of its substrate, depends on the supply of nutrients that come from outside. The lake is slowly being filled with sediment and eventually becomes overgrown to be integrated into the terrestrial ecosystem. Lindeman considers eutrophication phases from the standpoint of efficiency of consumers. In oligotrophy, the "thrifty" food cycle occurs, which is associated with a relatively high efficiency of consumer populations, because there is no surplus of organic substances and the level of production is limited by the reserve of substances dissolved in water. As the surplus of organic substances accrues and the trophic level of the water body increases, gradual oxygen deficiency ensues. As a result, the efficiency of consumers begins to fall. As the trophic status of the lake increases, phytoplankton productivity grows rapidly during the first phases of this process, but the accumulating silt ("ooze" according to Lindeman) begins to act as a buffer maintaining lake productivity at equilibrium during the eutrophic phase of succession. Succession continues at a rate that corresponds to the rate of sediment accumulation. The duration of this phase depends not only on the intensity of sedimentation,

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[2] The Eltonian pyramid is a graphic representation of the numbers of individuals, biomass or energy across the trophic levels in an ecosystem. Consequently, there are Eltonian pyramids of numbers, biomass and energy.

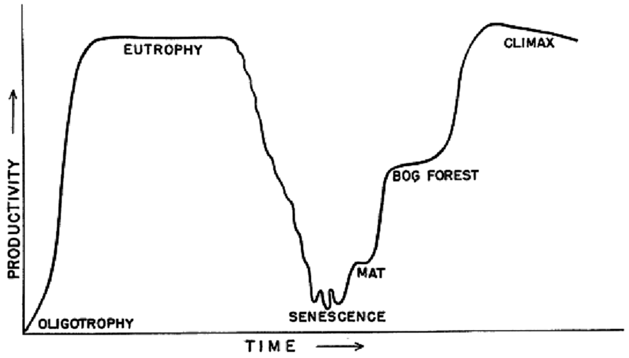

Fig. 3 Diagram showing changes in productivity during succession of lacustrine communities to their climax state. After Lindeman 1942, see text for further explanations

but also on the mean depth of the lake. As the lake ages, its productivity drops rapidly and during the late senescent phase, total productivity begins to increasingly depend on climatic factors, which is especially evident during the terrestrial phase. Lindeman illustrated this line of arguments with a diagram (Fig. 3). In conclusion, Lindeman also touches, albeit briefly, on the need to study the efficiency of producers (percentage of sun energy that they use) and consumers.

Lindeman's concept was far from being fully developed presenting only broad outlines for further research of lacustrine ecosystems in terms of their productivity. But the most important point is certain: Lindeman used quantitative ratios (efficiency) to consider the transfer of sun energy captured by autotrophs through a series of consumers linked by food relationships. The proportionality between autotrophs and heterotrophs, which had been declared earlier by the Soviet ecologist V.V. Stanchinsky (Weiner 1988), acquired in Lindeman's views a real biological basis in the sense of proportion of energy usage. Lindeman also gave a specific meaning to the relationships in the ecosystem as the energy flow through the food chains. Furthermore, the ecosystem as it was imagined by Lindeman is a dynamic system: in the course of succession the efficiency of energy usage by different trophic levels changes according to the general conditions (in particular, the depth of the lake and common morpho-edaphic conditions).

From an organism to photosynthesis

R. Lindeman built his trophodynamic concept on the ideas of several authors. First, as mentioned previously, he used the term "ecosystem" introduced by A. Tansley and further elaborated on this concept. Second, Lindeman adopted the calculation scheme for the lake's energy budget proposed by C. Juday, but, unlike Juday, he considered only the biological component of water bodies and immediately focused his attention on food relationships of organisms. Third, Lindeman had a high regard for A. Thienemann's views about the wholeness of water bodies and used his division of organisms into producers, consumers, and reducers (it is possible that these terms have first been used by J. Johnstone (1908)). Thienemann was a proponent of the idea that water bodies are super-organisms (Schwarz and Jax 2011). According to Thienemann, circulation of substances in the water bodies can be likened to the physiological processes in an organism (Egerton 1973).

It is of interest to note that the organismocentrism and the idea of natural balance were closely associated even during their formative period (see Egerton 1973 for a more detailed discussion): the interactions between organs in an organism and between organisms are based on the general principles of parsimony and consideration of mutual interests, i.e., a certain kind of balance. This idea in limnology was most clearly expressed by S.J. Forbes (Forbes 1925). This also explains why E. Haeckel in 1866 considered the new branch of biology—ecology—as "physiology of interaction between organisms" (Watts et al. 2019).

At the turn of the twentieth century, the organismocentric approach in limnology was actively promoted by E. Birge, the founder of one of the branches of the American limnological school (Frey 1963). Birge wrote: "The lake, like the organism, has its birth and its periods of growth, maturity, old age and death… The lake is morphologically a very simple creature, resembling rather a gigantic amoeba than a more highly organized being. Perhaps it would be better to compare the lake, for the purpose of this subject, not with the organism as a whole, but with the special respiratory substance of the animal—the blood" (Birge 1907, p. 223). This comparison has led the author to a very important conclusion. By comparing the lake to an organism, Birge noted that the absorptive surface of the lake is very small compared to its mass. For this reason, the lakes are much less efficient than the animals in their ability to absorb oxygen. This comparison helped Birge to conclude that oxygen is exceptionally important for the functioning of the lake: "… in many lakes the amount and character of the higher life which the lake will support is conditioned by the amount of oxygen which the lake contains rather than by the amount of food which it can produce" (ibid., p. 230). According to Birge, one of the main sources of oxygen is photosynthesis of planktonic algae. The organismocentric position thus persuaded Birge to accept the special importance of the gas regime in the life of the lake. It is also important that Birge noted the role of living organisms in changing this regime, although he did not elaborate explicitly on this aspect.

At the beginning of the twentieth century, the idea of organismocentrism was in wide circulation also in terrestrial ecology. One has only to think of F. Clements' writings on succession of plant communities (Valk 2014). It should be noted that W. Cooper, who supervised the research works on Cedar Bog, was working for a while under Clements' administrative guidance (Sterner 2012).

Birge has made only the first step toward understanding the wholeness of the lake in the spirit of organismocentrism, especially since he has not provided any quantitative assessment of the gas regime presenting in his works only the oxygen distribution curves for water bodies (see, for instance, Birge and Juday 1911). The organismocentric interpretation, however, created new possibilities for applying physiological methods to studying water bodies. In the Russian Empire, the aquatic chemist A.A. Lebedintsev, who worked at the Nikolsky fish-breeding farm, used the data of his experiments on respiration of fish and plankton and the results of oxygen fluctuation measurements in water of one of the lakes during the period of ice cover to calculate productivity of the water body in terms of fish weight (Lebedintsev 1908). It is important that Lebedintsev was the first to assess the contribution of life activities (respiration) of individual groups of organisms (plankton and fish) to the oxygen balance of the lake.

Lebedintsev was a strong supporter of organismocentrism. He wrote in one of his works: "…the whole process of gas exchange is essentially the respiration process of a water body" (Lebedintsev 1904, p. 113). Lebedintsev compared the water surface to "lungs," which receive "venous blood" (oxygen-poor water) and return "arterial blood" (oxygen-rich water). According to Lebedintsev, as in organism's respiration, "pathological events" can happen in the process of lake's respiration. Accumulation of hydrogen sulfide in the water bodies and the periods of minimum oxygen levels were regarded by Lebedintsev as examples of such events. His previous research experience at the Black Sea, whose near-bottom zone is called hydrosulfuric because of the extremely high concentration of hydrogen sulfide, was probably helpful in formulating these ideas.

A. Thienemann has examined the character of oxygen curves in the water bodies of different trophic types (according to Naumann—Thienemann's lake classification): only in the oligotrophic water bodies the oxygen curve was shown to reflect the temperature curve, while in the eutrophic lakes, which are rich in life, physicochemical relationships are distorted by biochemical processes (Hutchinson 1973). The author noted the phenomenon of the so-called metalimnial oxygen maximum, which he explained by the presence of a large quantity of photosynthetic phytoplankton in the lake metalimnion.

By the beginning of the 1920s, the aquatic ecologists still ignored the habitat-forming activity of organisms in their discussions over the integrity of water bodies. Recognition of the need to study this role of living organisms has become the foundation of the concept of a water body as "a biological entity," which was introduced by the Soviet planktonologist V.M. Rylov. Rylov maintained that not only the environment affects an organism as it was traditionally thought but the organism also influences the chemical composition of water through its life activity (Rylov 1927). In this respect, the aquatic environment is especially favorable, because it accumulates all influences from organisms and then itself acts on organisms through its composition and all its properties. Rylov was thus the first to address the problem of the organism as an environmental factor ("a unit of life with a certain physiological ability") and proposed to measure its effect by monitoring the rates of change in water chemistry parameters (for instance, measuring released or consumed oxygen) per unit surface of an individual (the so-called biodynamic standard).

For limnologists, plankton has always been the most convenient research subject for studying general patterns of intrabasin processes. This is primarily explained by the fact that the quantitative methods of plankton analysis had been known since the late nineteenth century, while the bottom-dwelling communities have attracted attention only at the beginning of the 1910s when the techniques of their quantitative analysis were developed. On the other hand, because of the plankton's size range, it was considered to be most closely associated with the chemical composition of water column. In this respect, one has to take into consideration everyday observations of fishermen and peasants over water blooms. As a result, throughout the first quarter of the twentieth century the plankton and hydrochemical studies have been going hand in hand (Frey 1963). Moreover, the plankton, being a group of minute organisms scattered in water column, was easily perceived as a certain physiological unity. This thought was eloquently expressed by N.V. Voronkov, one of the pioneers of Russian limnology, in his famous monograph "Freshwater plankton": "The study of plankton is especially interesting because the physiological relationships of its organisms and the environment that surrounds them are relatively easy to evaluate. We can always analyze the natural or aquarial water that contains the planktonic organisms under study. In this way, we can identify the substances required by these forms, the substances consumed by them from the environment over a certain period of time, and the substances released into this environment. This research does not require any complex tools of the kind needed for the experiments on physiology of terrestrial organisms. Furthermore, we can deal here with the physiological phenomena not of a single individual but rather of an immense array of individuals, and can determine, on the one hand, the influence of this array on the environment and, on the other hand, its dependence on this environment" (Voronkov 1913, p. IV).

In regional limnology, its founder E. Naumann (Naumann 1929), while developing a classification of water bodies, attached primary importance to the quantitative development of phytoplankton. According to Naumann, this development, in turn, depends on geological conditions in the catchment, which determine water chemistry. The Hungarian aquatic chemist R. Maucha, whose works are now almost completely forgotten, saw a clue to solving the problem of unity between living organisms in the water body ("hydrobios" under his terminology) and inorganic environment in the photosynthesis of planktonic algae (Maucha 1924). For this, he proposed to measure the rate of oxygen release in water samples. Maucha was a student of L. Winkler, the author of the method for measuring oxygen content in natural water (Entz 2008). Maucha also noted that due to physicochemical reasons oxygen is more efficiently delivered through the surface of the algal cell than through the water surface. This led him to the conclusion about a relative independence of aquatic organisms from the air environment above the water body.

V. Rylov and R. Maucha attempted independently and each in his own way to provide a quantitative and experimental basis for two pivotal aspects of hydrobiology in the first quarter of the twentieth century. First, these scientists noted the importance of measuring habitat-forming activity of organisms. Second, they posed a question concerning the physiological unity of the water body or at least of its water column. Unfortunately, their ideas have not been accepted by any of the contemporary aquatic ecologists. This is especially surprising given that Rylov, for instance, gave his presentation on the biodynamic standard at such respectable event as the International Limnological Congress and Maucha published his works in an international journal. Apparently, the ideas of studying the wholeness of water bodies using physiological and physicochemical methods were still only "floating in the air."

In the USSR, during the same period (in the 1920s), a whole new field of experimental research emerged, which viewed water bodies in terms of their functioning as integrated entities. This field was founded by S.N. Skadovsky, who had a very unusual academic background (Rizhinashvili 2019). During his student years at the Moscow University, at the beginning of the 1910s, he was already strongly influenced by N. Voronkov, who, as Skadovsky himself reminisced, introduced him to aquatic ecology and its methods. In 1911 and 1913, Skadovsky studied plankton in the Moscow River. After his graduation from the University in 1914, Skadovsky started working at the Laboratory of Experimental Biology of the Al'fons L. Shanyavsky People's University, which was directed by the eminent biologist N.K. Koltsov. Many Koltsov's students became distinguished geneticists, cytologists, and embryologists who made a significant contribution to the development of the modern evolutionary synthesis.

Skadovsky began his work at Koltsov's laboratory with the study of the influence of pH on phagocytosis in ciliates. At that time, pH was only recently introduced in aquatic chemical measurements. First pH measurements were probably performed only in the early 1920s (Frey 1963). Skadovsky (Skadowsky 1926), however, stated that he measured pH as early as the 1910s at the Zvenigorodskaya station, which he himself founded at the Moscow River. He was probably not the only aquatic ecologist to make pH measurements. For instance, in 1914 K. Buch published an article in the "Fennia" journal written in German, in which he provided pH values for some water bodies of Finland (Juday et al. 1924).

The 1920s were the period when the physicochemical branch of experimental biology experienced a burgeoning growth. Many scientists sought to study the dependence of organisms on colloidal and osmotic properties of cells, which in turn depend on the ionic composition of the environment, including pH. A good illustration of these attempts was the studies by J. Loeb (Loeb 1916), who discovered, among other things, the antagonism of ions in their effect on the organism. Skadovsky, for his part, thought that physiological properties, like morphological characters, can be used in taxonomy, which means that research was needed to determine the possible range of their applicability (Skadovsky 1928).

While studying water bodies, Skadovsky soon realized that the functioning of a water body as an integrated whole can be understood by examining life activity of individual organisms. In pursuing this goal, Skadovsky focused his attention on planktonic organisms, because he thought that for these organisms the analysis of all factors can be conducted to the fullest extent. In one of his articles published in 1923 in German, Skadovsky coined the term "hydrophysiology" ("Hydrophysiologie" in German) (Skadowsky 1923) to characterize physiology of a water body as an individual. The pH measurement was adopted by Skadovsky as the key parameter, whose fluctuations reflect the entirety of physiological processes in the plankton community. The new approach has attracted considerable interest from the European scientists. This interest was so strong that the organizers of the III International Limnological Congress, which was held in 1925, asked Skadovsky to make a plenary presentation about the goals of hydrophysiology, which he indeed presented (Skadowsky 1926).

In the course of the 1920s, Skadovsky, together with a team of his students and employees, studied the taxonomic composition, quantitative abundance, and morphology of plankton for the water bodies of different types (Skadovsky 1928). Skadovsky selected water bodies such that acidic, neutral, and alkaline pools and lakes were included, i.e., the study covered a wide gradient of hydrogen ion concentrations. Much attention was given to the swamps and swamp waters, because they have a highly acidic reaction.

Skadovsky also attempted to draw correlation between pH-based types of water bodies and Naumann's trophic types (oligotrophic, mesotrophic, and eutrophic).

The results of these studies allowed Skadovsky to draw an important conclusion that pH is an indicator of assimilation/dissimilation ratio in the water bodies. This conclusion was suggested by observations of "alkalization" of water under an intensive growth of phytoplankton (Skadovsky 1928). Consequently, according to Skadovsky, pH can serve as an indicator of the "physiological type" of a water body. One of Skadovsky's students was G.G. Vinberg, who in his first paper noted that changes in water pH are associated with fluctuations in oxygen content (Vinberg 1928). The relationship between oxygen and pH has also been mentioned by other authors (for instance, K. Münster Strom (Strom 1924)).

Consequently, by the turn of the 1930s, an idea about the wholeness of a water body achieved through physiological functions of individual organisms (most notably, photosynthesis and respiration) that affected the chemistry of the environment was gradually being formed in aquatic ecology. Formulation of the concept of the organism as an environmental factor was apparently made possible only as a result of plankton research. An important role in this was played by extremely small sizes of plankton hydrobionts causing their exceptionally high metabolic rates, which during the periods of mass growth is almost immediately reflected in the composition and properties of water. The organismocentrism as a way of thinking popular at the beginning of the twentieth century has begun to take on a new form. An explicit likening of the water body to a super-organism was replaced by an understanding that the relationships between components of this super-organism were created by life activity of hydrobionts. Moreover, attention was increasingly directed toward algal photosynthesis.

Dark and light bottles: G.G. Vinberg and G. Riley

In the 1930s, the limnological station located in the Kosino village, which was part of the Moscow Region (USSR) and is now within Moscow's city limits, was a well-known and internationally recognized center of limnological and hydrobiological research (Talling 2008). The academic journal of the station, titled *Trudy Limnologicheskoy Stantsii v Kosine* ("Proceedings of the Kosino Limnological Station"[3]), was essentially the only limnological periodical published in the USSR in the 1930s. The articles of the station's employees published in this journal, despite being written primarily in Russian, were known far outside the USSR and were often cited by European and American authors.

Since 1924, the station was headed by L.L. Rossolimo, who was a specialist in plankton. Despite his biological education, Rossolimo viewed water bodies as geographic objects and used corresponding research methods to study them. For example, in 1931 he published the annual budget of thermal energy, which was expressed in calories (i.e., energy units), for large Lake Pereyaslavskoe (Rossolimo 1931). To be sure, there was nothing particularly remarkable about this study for that period. Thermal balance in limnology was probably first calculated as early as the end of the nineteenth century by F.A. Forel for Lake Geneva and a similar study was conducted by Birge and Juday in 1912 (Birge and Juday 1912). What set Rossolimo's approach apart was that he also tried to calculate the balance for some substances such as oxygen and he did that in the same way as for thermal balance. As far as I know from the literature, no one has tried to calculate the balance of any substances in a lake in the early 1930s or before (except for the aforementioned study of oxygen balance conducted by Lebedintsev in 1908). This kind of calculations has started to be extensively performed only at the end of the 1930s (see, for example, C. Mortimer's work on nitrogen balance (Mortimer 1939)). It is notable that in the Soviet literature the most commonly used term was "balance," while outside the USSR the term "budget" has become the most widely accepted. These terms were sometimes used as mutually interchangeable. It is possible that the term "budget" was used, for the first time, with respect to chemical compounds in the water bodies by K. Münster Strom in 1928 (Strom 1928).

In 1934, Rossolimo wrote a paper in which he proposed the balance-based principle for studying water bodies (Rossolimo 1934). Rossolimo's balance principle was simultaneously both geographic and holistic. Rossolimo wrote this paper to define the content and boundaries of limnology in as clear a manner as possible. To achieve this he attempted to determine the most fundamental characteristics of lakes as aquatic objects. According to Rossolimo, the principal characteristic of a lake is that it has an extremely slow water turnover. This fact creates the possibility for accumulation of organic substances manifested, among other things, in silting. Rossolimo then proposed to explore the entire range of dynamics of organic substances in the water body, while relying on the association of this dynamics with water balance. As a corollary to this principle, Rossolimo viewed the water body as a single unified object: "Every water object, including the lakes, is an exceedingly complex, yet integrated assemblage of processes and phenomena, none of which, however insignificant, can be taken away and

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[3] This is not an official translation of the journal name.

viewed individually, without any connection to the rest of the assemblage. Water balance and the balance of all those elements that are associated with water apparently constitute a certain integrated whole and if we are to speak about the possibility of studying the balance of matter, energy, etc., we can only speak about it as a way of studying a complex whole" (Rossolimo 1934, p. 16).

The balance principle put forward by Rossolimo played a uniting and organizing role for the research work performed by employees of the Kosino station. Different aspects of water bodies had now to be considered in the context of the overall balance of organic substances. In addition to studying the balance of certain elements (iron, nitrogen, phosphorus), Rossolimo and his employees were also engaged in studying the rates of silt accumulation and interaction between bottom sediments and water mass. The study of oxygen regime has revealed a leading role of microorganisms in physicochemical processes occurring within the water bodies. For instance, the renowned aquatic microbiologist S.I. Kuznetsov wrote: "While studying the balance of a water body as a whole, the first thing we encounter is its micropopulation" (Kuznetsov 1934, p. 49). He believed that microflora can cause rapid changes in physicochemical properties and parameters of water. For instance, disappearance of oxygen in one of the lakes occurred primarily because of bacterial activity in water.

In May 1932, a young aquatic ecologist, Georgiy G. Vinberg (1905–1987), began his experiments in one of the lakes of the Kosino station (Lake Beloe) (Hutchinson 1973). These experiments (later to become classical) were focused on the dynamics of organic substances in the water bodies. Although the circumstances that led to these studies appear to be well known to hydrobiologists (at least in Russia), some aspects remain unclear. It has been traditionally thought that Rossolimo gave Vinberg an assignment to develop a quantitative assessment method for the dynamics of organic substances as part of his balance research program (Ghilarov 2005). To fulfill this assignment, Vinberg went to a library and found there one of A. Pütter's works (Pütter 1924), in which oxygen release rates were measured in the samples of natural water that were placed in a tank and left for several days in the shadow of a large tree. Using this method as a starting point, Vinberg adapted it for measuring phytoplankton production directly in the water body. This chain of events leaves an impression of a certain missing link: transition from a broad goal of studying the balance in a water body to a specific measurement technique appears to me too abrupt. In particular, it is unclear why Vinberg immediately started thinking in the context of oxygen consumption and release in water directing his attention toward Pütter's study. It is certainly true that the oxygen regime was regarded as a crucial element in functioning of water bodies from the very beginning of limnological research (one has only to think of E. Birge's words about lake's breathing). It is possible that the subject of Vinberg's experiments was influenced by his early studies on relationships between pH and oxygen in a study performed under supervision of S. Skadovsky and also by the fact that the latter considered pH to be an indicator of ratio between assimilation and dissimilation in the water bodies.

It is even more surprising that Vinberg immediately made a transition toward an energy-based interpretation of the transformation processes of organic compounds in the water bodies, which was only briefly mentioned by Rossolimo in his balance program, but was never fully realized. In his 1934 paper, Rossolimo wrote about circulation of organic compounds and "associated energy," but that was all he had to say on the matter (although one should not forget about the balance of thermal energy that he had calculated several years previously). Vinberg, in contrast, began with energy, when he wrote his very first paper on the use of the dark and light bottles method as a way to calculate the balance. This seminal work in aquatic ecology opens with the following words: "All numerous and multitudinous transformations that organic substances undergo in the lake can be subdivided *in terms of energy* (*italics mine—A.R.*) into the processes that increase the cumulative reserve of organic compounds in the water body and the processes that decrease it. The processes of the first type are accompanied by energy absorption and can occur only with the participation of living organisms, by photo- or chemosynthesis. By contrast, the destruction of organic compounds is accompanied by energy release and can proceed either with the involvement of living organisms during respiration and fermentation or without them by oxidation. It should be accepted as a first approximation that an increase in overall reserves of potential chemical energy in the form of organic compounds in the water body, apart from the external supply of organic compounds, can only occur by photosynthesis. It should be remembered that an increase in biomass of heterotrophic organisms results in a decrease in the cumulative amount of organic matter in the water body, and, consequently, the energy stored in this matter. The build-up of biomass of heterotrophic organisms is only possible by consumption of a certain portion of energy produced by oxidation of organic compounds in their food" (Vinberg 1934, p. 5). These words summarize the essence of energy relationships within the water bodies: photosynthesis, on the one side, and oxidation during fermentation and respiration, on the other. Unlike A. Thienemann and R. Lindeman, Vinberg did not divide the organisms into groups according to their use of food energy, but only emphasized the existence of two opposite processes (accumulation and dissipation of energy, production and destruction).

Monitoring of oxygen release and consumption in the bottles filled with lake water allows a connection to be established between the organic matter and energy: "It is commonly known that carbon dioxide is decomposed in photosynthesis to release oxygen, the amount of which is strictly proportional to the amount of the resulting product of photosynthesis, and, consequently, to the amount of absorbed energy. When glucose is the primary product of photosynthesis, 1 mg of released oxygen corresponds to absorption of 3.51 cal. The primary products of photosynthesis in many planktonic algae, especially, diatoms and blue-green algae, have not been studied. For energy calculations, however, carbohydrates (glucose) can be accepted as a universal product of photosynthesis, which is likely not far from the truth. This somewhat arbitrary assumption cannot significantly influence the results of energy calculations in those cases, when they rely on the amount of released oxygen, because even if we admit that the product of photosynthesis is fat, the energy absorption per unit of oxygen would still be only 9.4% lower (3.28 cal per mg of oxygen). During the oxidation process, which is opposite to photosynthesis, the corresponding amount of energy is released upon consumption of 1 mg of oxygen, i.e., the complete oxidation of fat releases 3.28 cal per 1 mg of oxygen, and the complete oxidation of carbohydrates produces 3.51 cal per 1 mg of oxygen" (Vinberg 1934, p. 6). Consequently, since oxygen and energy are stoichiometrically correlated, the oxygen-based method for studying the transformation of organic substances appears to be the most convenient and feasible technique for energy calculations. For instance, the calculation of phytoplankton production from oxygen deficit (and also in energy units) was later performed by G.E. Hutchinson (Hutchinson 1938).

It is remarkable that during the same period, sometimes even in the same year (1932), different scientists independently applied similar methods studying lakes in different countries. For example, in 1930 P. Jenkin studied Loch Awe in Scotland (Jenkin 1930) measuring the intensity of photosynthesis of diatoms at different depths (her study has possibly escaped the attention of aquatic ecologists, because I have found no references to this publication, although it had been published in a well-known international journal). It is of interest that Jenkin was one of the few women who began her carrier as an aquatic ecologist in Europe during the first half of the twentieth century (Toogood et al. 2020). The experiments of H.A. Schomer, a member of the research team of the Wisconsin Laboratory headed by E. Birge and C. Juday, started in 1932 (Schomer 1934). Like Jenkin, he studied algal cultures. In the winter of 1934, the German scientist K. Heinrich conducted similar studies (Heinrich 1934), but he was studying water samples. Because of the season, he measured only oxygen consumption. The conclusion that can be drawn from these studies is that in the field of aquatic ecology the idea of the bottles method was perceived in the early 1930s as an urgently felt need.

The principle of the dark and light bottles method, which is widely used by modern hydrobiologists, is quite simple and well known and was described in many textbooks. The bottles filled with lake water are usually left for 24 h either in the same lake (for example, suspended at different depths, as it was done by Vinberg) or in the laboratory under a special illumination regime imitating the natural cycle. Some of these bottles remain transparent, but others are darkened in one way or another for the duration of the experiment to prevent photosynthesis. Vinberg covered the bottles with varnish and wrapped them in dark oilcloth, while in modern studies the bottles are wrapped in foil. After a 24-h period, the rates of photosynthesis and respiration in the water column are determined from the difference in oxygen content between the original water and the water contained in bottles (distinguishing between gross primary production and net primary production). The results are recalculated per unit area and for a certain period of time to yield daily, seasonal, or annual primary production of phytoplankton.

It is notable that marine biologists are usually thought to have been ahead of limnologists in using the bottles method. In the literature on ecosystem metabolism, it is customary to credit T. Gaarder and H.H. Gran with being the first to conduct experiments with bottles (Gaarder and Gran 1927; Staehr et al. 2012). Gran also conducted experiments with bottles submerged in seawater since 1916 (Clarke and Oster 1934). Cultures of phytoplankton in the light and dark bottles were also studied experimentally by G. Clarke and R. Oster, who measured the intensity of photosynthesis and respiration of algae in the sea (Clarke and Oster 1934). One work that has again to be mentioned in respect of freshwater studies are experiments and calculations performed by R. Maucha (Maucha 1924), who should probably be regarded as the now-forgotten founder of such water body studies. It is important to emphasize that Maucha not only determined the amount of organic matter, but also analyzed the results of his experiments in terms of productivity. For instance, Maucha suggested to compare the lakes and ponds for the amount of released oxygen using "winkler," a nominal unit that he proposed in honor of his teacher L. Winkler. He also spoke about expressing productivity in terms of energy (by converting the amount of oxygen into calories and horsepower).

It can be concluded from this overview that the bottles method was well known, especially to marine biologists, even before 1932. As Vinberg (1960) correctly observed, it has no definite author and is in fact a technique that has long been employed in plant physiology to determine the respiratory quotient, which was extended by some specialists to water body studies. Unlike other limnologists, however, Vinberg has not simply made a few attempts, but performed systematic observations of photosynthesis and respiration in water bodies of different types and used his conclusions to address some general problems of aquatic ecology. It is important to note that he was one of the few who worked with water samples from water bodies, rather than with algal cultures. The analysis of the results obtained from bottles experiments led Vinberg to the concept of biotic balance.

A scientist who is commonly recognized as one of the pioneers of the bottles method was G. Riley, a student of G.E. Hutchinson. It is believed that in 1935, independently of Vinberg, he used the same technique on Linsley Pond in Connecticut, USA (Ghilarov 1994), but the results of this study were published only in 1940 (Riley 1940). Hutchinson wrote the following on this matter: "The second major technical advance in the study of eutrophication was the introduction of methods of measuring phytoplankton productivity. The first experiments in lakes were made by Winberg[4] (26) (*reference to* Vinberg 1934—*A.R.*) in the USSR; rather later Riley (27) (*reference to* Riley 1940—*A.R.*) independently started an investigation in Connecticut" (Hutchinson 1973, p. 269). It is often stated that during that period no one among the scientists outside the USSR knew about Vinberg's works in Kosino (Ghilarov 2005). However, the commonly accepted story, which can be encountered in numerous publications, including those written by Russian authors is not entirely accurate.

In Riley's work of 1940, which is cited by many authors including Hutchinson, the bottles method was described only in a rather general passage: "In order to obtain an estimate of the amount of plankton growth, it was necessary to use the well-known technique of measuring the photosynthesis and respiration of plankton in clear and blackened bottles suspended at different depths" (Riley 1940, p. 282). Later in the same paragraph he writes: "To keep conditions as nearly natural as possible, the bottles were filled with ordinary lake water and were suspended at the same depth from which the sample had been taken. They were generally left in the lake for one week and were then analyzed for oxygen by the Alsterberg modification of the Winkler technique" (ibid.). It is clear from these passages that the bottles method was regarded by Riley as a well-known and routine technique. The paper does not mention any new techniques or their modifications. It is of interest that observations in Linsley Pond, according to Riley, date back to 1937–1938, not to 1935, as it was claimed by some authors. Among the references listed in this paper, the bottles method was discussed in only two of Riley's own works (Riley 1938a, 1939). One paper (Riley 1938a) talks about observations at sea (Gulf of Mexico) and discusses possible mistakes associated with placing water in bottles and the statistical analysis of experimental results. Again, this paper contains nothing suggesting Riley's own elaboration or verification of the method or indicating that this method was considered to be new. The reference list of this paper includes a work by Riley devoted to the details of measuring pigments of phytoplankton for determining the quantity of the latter (Riley 1938b). Finally, in the 1939 paper (Riley 1939), Riley discussed the relationship between production and chemical factors and ways of expressing production, and also made an attempt to establish productivity limits for different water bodies (he used for this the results of observations in the Gulf of Mexico and Linsley Pond). This paper again offers no discussion of the bottles method in terms of its novelty or the details of its application. Consequently, there is no reason to credit Riley as the creator of the bottles method for the lakes. It can only be claimed that Riley followed earlier methodology used in marine research and extended it to lacustrine studies. The question that remains unanswered is why did the established opinion arise that the bottles method for measuring phytoplankton production was developed by Riley on Linsley Pond? Why did Hutchinson cite his work, that does not even contain a detailed description of the method, which is rather mentioned only in very general terms? It is clear that this strange confusion has arisen in the literature for some unknown reasons, but, whatever its causes, the same mistake should not be further propagated. Riley should not be acknowledged as the creator of the bottles method for lakes, but he can only be credited as one of the first to apply the technique previously used in oceanology for freshwater research. And he did that in 1937–1938, not in 1935, and his results were published in 1939, not in 1940. It should be emphasized that, unlike Vinberg, Riley did not develop or modify the method, but simply used the already-known experimental design in his research. On the other hand, Riley provided a very detailed discussion of productivity calculation and application of different units for measuring productivity, and also established a correlation between oxygen production and changes in other physicochemical parameters. It should also be emphasized that Riley, like some other researchers of that time, practiced a prolonged 1-week exposition of the bottles, rather than a 1-day exposition, as it was done by Vinberg.

Finally, it should be noted that it would be completely wrong to assume that Vinberg's experiments remained unknown to the specialists outside the USSR. Some of his papers, even though they were written in Russian, were cited by scientists that belonged to the school of E. Birge and C. Juday (Juday et al. 1943; Manning and Juday 1941). In these publications, the authors gave a detailed discussion of the methodology of this technique, discussed the quantitative results that Vinberg obtained and compared them with their own results.

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[4] There are two variants of English spelling of the researcher's surname (Vinberg and Winberg).

The concept of biotic balance

While conducting his experiments using the bottles method, G. Vinberg concluded that the intensity of photosynthesis and respiration in water does not depend on the taxonomic composition and quantitative growth of phytoplankton, but is determined instead by the entire range of characteristics of the lake (in particular, by its depth and transparency). According to Vinberg's observations, the rates of photosynthesis and respiration are not subject to such abrupt fluctuations as the composition and the amount of plankton. For this reason, in Vinberg's opinion, the study of formation and destruction of organic substances requires the use of the methods that would have enabled the scientists to "obtain a quantitative characteristic of the results of plankton's life activity under specific conditions of a given water body" (Vinberg 1934, p. 16), and the use of dark and light bottles can indeed provide a means to evaluate the parameters of life activity of all plankton in the form of production and destruction values and their ratio.

Based on his observations, Vinberg focused much of his attention on the introduction of physiological methods to limnology: "In general, with respect to the effect on the environment, the physiological characteristics of organisms come to the forefront. It is easy to see that in different water bodies under different environmental conditions the same place in the overall system of the processes occurring in the water body can be occupied by entirely different organisms. And, conversely, the organisms of different taxonomic position can occupy the same place with respect to the general processes of matter transformation in the water body" (Vinberg 1936, p. 596). Vinberg then draws a more general conclusion: "Methods based on physiological phenomena allow a direct study of the functional significance of certain phenomena in the general system of processes" (ibid., p. 600–601). The advantage of physiological methods is that one can compare life activity of the organisms that have different taxonomic composition. Vinberg stressed that among all physiological functions respiration is the most important to study, because the mechanisms of this process are universal for all living organisms, while the modes and mechanisms of feeding vary across different taxonomic groups of hydrobionts.

Vinberg emphasized a functional similarity of organisms that is independent of their taxonomic position. These ideas were apparently prompted by Vinberg's experience in studying metabolic rates of different organisms and were later significantly strengthened by the results of the experiments performed on different hydrobionts. While studying the respiration of rotifers, chironomid larvae, protozoans, and crustaceans, Vinberg concluded that the respiration rates of animals depend on their body size, rather than on their taxonomic position. As a result, taxonomically distant organisms can show similar metabolic rates and therefore make the same contribution to mineralization of organic matter. This statement sounded unusual for many biologists of that time.

One work that should also be mentioned in this respect is a large paper on establishing an energy equivalent of organic substances, in which Vinberg participated, and judging from the order of authorship, was probably even a leading researcher (Vinberg et al. 1934). The authors of this paper emphasized that the study of dynamics of organic matter eventually seeks to provide the energy balance of a water body. A transition from the amount of organic matter to the energy reserves contained in this matter allows a unified expression to be given for all stages of the balance of organic matter. The authors chose calorie out of all other energy units, because, as they wrote, calorie is typically used to express the nutritional value of substances in physiology of nutrition (a well-known calorific value of food products). According to the authors, the goal of a limnologist is to provide an estimate for the food resources of water bodies in terms of their nutritional value for fish. In its fullest form, the calorific assessment of aquatic organisms was made by V.S. Ivlev, one of the participants in this study (Ivlev 1939). The results of these studies showed the possibility of applying an oxy-calorific coefficient of 3.4 cal/mg O, which is still used by hydrobiologists. In this respect, modern attempts to express energy reserves of organisms or primary production in joules as SI units seem ill-conceived, because calorie, as can be seen from the previous discussion, is a more logically justified energy unit in ecosystemic calculations, which is intuitively easier for an ecologist to understand. Furthermore, estimates made in calories allow researchers to easily use factual material from works published during the first half of the twentieth century.

By the end of the 1930s, Vinberg has developed an entirely complete concept of balance of organic substances in the water body. In his system of views, the general ideas of L. Rossolimo's balance principle assumed a more concrete form. Vinberg reduced the entire multitude of processes responsible for the transformation of organic matter to only two processes, which he interpreted in energy-based terms: production, i.e., the formation of organic compounds during photosynthesis, and destruction, i.e., the breakdown of organic compounds in metabolic processes. On Vinberg's own admission, his notion of biotic balance was narrower than that proposed by Rossolimo.

Vinberg considered plankton as the primary source of organic substances in the water body and as a single production system. He explained: "Primary production is often regarded as a function of plankton in general.

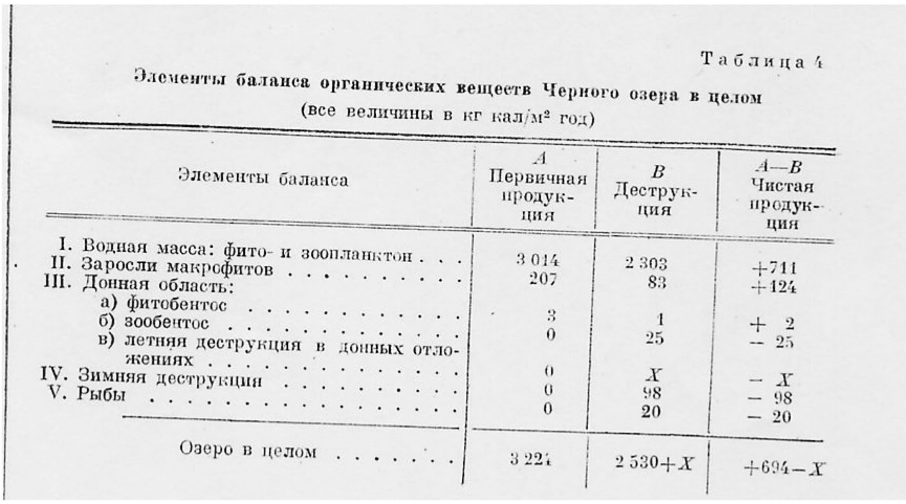

Таблица 4

Элементы баланса органических веществ Черного озера в целом
(все величины в кг кал/м² год)

Элементы баланса	*A* Первичная продукция	*B* Деструкция	*A—B* Чистая продукция
I. Водная масса: фито- и зоопланктон	3 014	2 303	+711
II. Заросли макрофитов	207	83	+124
III. Донная область:			
а) фитобентос	3	1	+ 2
б) зообентос	0	25	− 25
в) летняя деструкция в донных отложениях	0	*X*	− *X*
IV. Зимняя деструкция	0	98	− 98
V. Рыбы	0	20	− 20
Озеро в целом	3 224	2 530+*X*	+694−*X*

Fig. 4 The first table of biotic balance published in hydrobiological literature (after Vinberg 1948a). The left column shows elements of the balance indicated by Roman numerals: I. Water mass—phyto- and zooplankton. II. Macrophytes thickets. III. Bottom zone: **а**) phytobenthos; б) zoobenthos; **в**) summer destruction in bottom sediments. IV. Winter destruction. V. Fishes. The "A" and "B" columns show primary production and total destruction, respectively; the "A–B" column indicates net production. The values are expressed in calories per square km per year

There are reasonable grounds for this belief, as zoo- and phytoplankton are organically interconnected in nature and form a single system of processes. < … > By participating in mineralization of organic substances, zooplankton and bacteria change the surrounding conditions and open new possibilities for the growth of autotrophic organisms, for primary production. This gives reason to regard the primary production as a function of the whole system of planktonic organisms in their unity with the environment, and not of the phytoplankton alone. For this reason, it is entirely justifiable to speak of the intensity of plankton, rather than phytoplankton, photosynthesis" (Vinberg 1956, p. 371).

It follows that the primary organic matter is broken down directly in the water mass and, according to Vinberg, the main role in its mineralization is played by bacteria, rather than by zooplankton, which prevents the possibility of using trophic levels concept. Vinberg also noted that natural water contains a significant amount of dissolved organic substances: "In natural water, bacteria and plankton, together with dissolved organic matter, constitute a single system, whose characteristics determine the rate with which oxygen is consumed by water" (Vinberg and Yarovitsina 1946, p. 507).

At the end of the 1930s, Vinberg was working on the manuscript of his doctoral dissertation. Judging from the references to this dissertation in his papers, the original title of the dissertation was "The balance of organic substances in lakes." Unfortunately, in 1940 Vinberg was arrested (like many other biologists and scientists of that period) and sent to a work camp in the Komi Autonomous Soviet Socialist Republic (Komi ASSR) (Ghilarov 2005). The reason for his arrest was that he participated in writing a handbook on general biology edited by Erwin S. Bauer, who was repressed and executed by firing in 1937. For this handbook, Vinberg wrote chapters "Inheritance" and "Metabolism." From the work camp, he was conscripted to the field army. In 1944, the scientist was demobilized from the army following the petition of the Academy of Sciences and received a position in "Borok," a recently founded biological station of the USSR Academy of Sciences.[5] Here in 1946, Vinberg completed his doctoral dissertation, which was now titled "Biotic balance of matter and energy in the lakes" and successfully defended it at the Moscow Institute of Fishery Industry.[6] It can therefore be concluded that it was in 1946 that the term "biotic balance" was first introduced. In 1948, this term appeared in a published work, in Vinberg's paper "Biotic balance of the Black Lake"; hence, the term "biotic balance" did not exist before 1946 and the term "balance of organic substances" was used instead. Introduction by Vinberg of the adjective "biotic" was apparently to signify the recognition of the leading role of living organisms in cycling of organic substances. The biotic balance was understood by the author as "a resulting quantitative expression of the entirety of processes involved in creation and destruction of organic compounds" (Vinberg 1948a,

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[5] This is now the Ivan D. Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences (the Borok settlement of the Yaroslavl Region).

[6] The Institute is now located in Kaliningrad and is called the Kaliningrad State Technical University.

p. 11). According to Vinberg, the elements of the biotic balance are represented by individual ecological groups of organisms, parts of the water body (water mass, benthic zone), and individual processes (winter destruction) (Fig. 4). For each element, he obtained the values of destruction and for plankton, macrophytes, and phytobenthos, both production and destruction. The net value of production was calculated from the difference between production and destruction. Vinberg obtained the values of production and destruction from the results of his bottles experiments and the other elements of the balance borrowed from the results of other authors or derived from some approximate recalculations. Vinberg also compared different types of destruction with primary production. According to his calculations, for example, in the process of destruction, benthos breaks down from 1/27 to 1/36 of net plankton production, and 1/8 of net plankton production is broken down under ice cover as a result of oxygen consumption. Vinberg came to the conclusion that the lake being studied shows an exceptionally intensive metabolism of water mass; plankton production exceeds several-fold that of macrophytes; and the lake in general is characterized by a pronounced positive biotic balance.

Vinberg’s biotic balance is essentially a table (Fig. 4), in which energy-based comparison is made between oxygen release and consumption by different groups of organisms and in the course of various physicochemical and biochemical processes. This presentation of the results allows an estimation of the quantitative ratios for the participation of specific groups of organisms in the general processes of dynamics of matter and energy.

The concept of biotic balance led Vinberg to two sets of problems. First, he considered the efficiency of utilization of sun energy by phytoplankton. Second, he developed the idea of the wholeness of the water body. In developing these questions, Vinberg was under a significant influence of V.I. Vernadsky’s global biosphere concept. These problems need to be discussed in greater detail.

The calculations made by Vinberg for the portion of energy captured by phytoplankton, out of all energy of sunlight in a certain region, showed that phytoplankton can utilize only about one-tenth of sun energy, which is much lower than the efficiency of even marine phytoplankton, let alone the higher plants (Vinberg 1948b). Vinberg wrote: “There is no doubt that in the course of a long historical process a certain level of sun energy usage has been established for all types of natural communities, which reflects their most important properties” (Vinberg 1948b, p. 29). Consequently, the level of utilization of sun energy in photosynthesis “can serve as a substantive measure for the functional significance of the population (biome) in a certain part of the biosphere” (ibid.). As can be seen from this passage, Vinberg raised the analysis of processes in a water body to the level of the entire biosphere. Once again, the idea was already floating in the air. During the same years, the calculations of biosphere productivity were made by Riley (1944). One cannot help but marvel at the parallel, independent development of nearly identical ideas in production ecology, but it only provides further evidence that this was an objective, logical trend in the development of this branch of ecology.[7]

In addressing the question of the integrity of water bodies, Vinberg relied entirely on the concept of the leading role of living matter in the flows of matter and energy, which was advocated by Vernadsky. According to Vinberg: “While considering a lake as a sufficiently autonomous system with a certain integration level of phenomena, and its population as one of its interdependent components, one should take into account the special place occupied by this component, due to the inherent ability of living organisms to lengthen the dissipation path of sun radiation, to disturb equilibrial physicochemical systems in the surrounding environment and as a result to serve as a powerful factor of matter transformation. This is the "activity" of living organisms, which distinguishes them from non-living matter (Vernadsky), and their property, which allows us to assert that "life is an independent variable in the system of the water body" (Selivanov 1936[8]). <…> By determining the quantitative functional role of the population in the system of the water body, we essentially also measure the force with which it transforms the environment and find an expression for a certain differential moment of the biogeochemical function of life. This formulation of the problem highlights not only an inextricable link between biotic and abiotic phenomena in the water body, but also emphasizes a special role of living organisms” (Vinberg 1946, p. 25). Vinberg stressed that in light of a special role of living organisms he disagrees with the presentation of the ecosystem concept by the British-American ecological school (A. Tansley, C. Juday, R. Lindeman), because these scientists do not place enough emphasis on the active role of living matter. Vinberg

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[7] This “parallelism” presents an opportunity for historians of science to take one particular country as a case study and explore the development of general principles in a certain scientific approach or subdiscipline in this country, without the risk of being accused of parochialism.

[8] This is Vinberg’s own reference to one of the papers of Lev S. Selivanov (1908–1945), a little-known Soviet biogeochemist, who in the 1930s explored the application of V. Vernadsky’s ideas in aquatic ecology. Selivanov considered the water body as a system of equilibria that is disturbed by living organisms. The fate of Selivanov was quite tragic. In 1941, during the Great Patriotic War he joined the army as a volunteer and was believed to be missing in action. Recent archival studies have shown that he was imprisoned by the Nazi and participated in a revolt in the concentration camp, during which he was killed (http://catalog.lib.tpu.ru/files/names/document/RU/TPU/pers/8946).

also noted that it is production ecology that provides an opportunity to understand the functional significance of organisms.

It is evident that Vinberg's ideas were firmly rooted in the deep traditions of the Russian and Soviet planktological schools. The ideas of N. Voronkov, S. Skadovsky, and G. Vinberg can easily be placed in a single line of succession. Voronkov was the first to pay attention to the plankton as a physiological unity. Skadovsky, who was a disciple of Voronkov in hydrobiology, attempted to develop a detailed concept of this unity based on the notion of pH as an indicator of the ratio between formation and destruction of organic compounds. Vinberg, who was a student of Skadovsky, developed an energy-based concept of production and destruction as two leading processes in the circulation of organic matter. In doing this, he linked together life activity of organisms, the general characteristics of the water body (depth, transparency), and its gas (especially, oxygen) regime. This allowed Vinberg to create a concept of plankton (including bacteria) as a single production system, which is the primary source of organic substances in the water body. The biotic balance (i.e., the balance of production and destruction in the water body as a whole) was understood by the author as a cumulative characteristic of life activity of organisms in the water body. Vinberg switched from considering the effects of factors on the organism to the organism as an environmental factor, which opened the way for holistic interpretation of the water body. In this respect, Vinberg tacitly adopted a position of organismocentrism, which was quite popular among aquatic biologists across the world at the beginning of the twentieth century.

R.L. Lindeman's trophodynamics and G.G. Vinberg's biotic balance: from an organism to a machine

This section provides a comparison between two concepts of ecosystem proposed in the middle of the twentieth century: those of R. Lindeman's trophodynamics and G. Vinberg's biotic balance (in the following text, the latter will be called "balance" for the sake of brevity). The most interesting point in this discussion is the manner in which these authors imagined the wholeness of the water body and the role of living organisms in it.

It is clear that a common element in the views held by Vinberg and Lindeman is that both used the energy-based approach to matter cycling in the ecosystem. However, this is only a superficial similarity. A more detailed analysis reveals some fundamental differences between trophodynamics and balance. While Lindeman used the energy equivalent of the biomass for different groups of organisms, Vinberg relied on metabolic rates and converted the concentration of released/consumed oxygen into energy. This aspect also reflects the differences in physiological processes, on which the ideas of these two authors were based. Lindeman rested his views on nutrition, while Vinberg focused on metabolism, especially on respiration of hydrobionts. In both concepts, sunlight and photosynthesis were considered as the primary source of organic substances in the water body. Lindeman, however, envisioned energy flow as the transfer of energy across a successive series of trophic levels, while Vinberg regarded destruction as a general process that uses the energy derived from primary production and involves planktonic organisms that belong to several levels. The leading role in the destruction is often played by reducers (bacteria). Vinberg stressed the role of plankton as the original source of organic substances, while Lindeman did not place emphasis on any specific group of organisms and considered all of them together. Lindeman thus presented the interactions between organisms as a successive transfer of energy in the course of food consumption of organic material, while Vinberg viewed it as a ratio between production and destruction due to metabolism.

It can therefore be argued that the most prominent difference between Lindeman's trophodynamics and Vinberg's balance is that the first author used the ideas of trophic chains and levels and the second those of metabolic processes. Lindeman considered the static index (biomass) and Vinberg based his concept on dynamic parameters (production and destruction). In other words, Lindeman focused on groups of organisms, while Vinberg on life-activity processes.

This also explains different attitudes of these two authors toward the idea of the water body as an integrated unity and the relationships between living organisms and non-living components. Lindeman gave an explicitly physicalistic interpretation of the ecosystem in keeping with the original definition of this term by A. Tansley,[9] while Vinberg used the organismocentric interpretation. Lindeman, of course, made feeding interactions of organisms a focal point of ecosystem relationships, but at the same time asserted the indivisibility of living and non-living components, their very intimate interconnection. Under Vinberg's approach, living organisms play an active physiological role and set in motion the circulation of matter, hence the adjective "biotic." Vinberg himself was well aware of this dilemma

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[9] It should be remembered that A. Tansley was against the organismocentric interpretation of superorganismal levels and introduced the term "ecosystem" as part of criticism of F. Clements' writings (Valk 2014). Tansley understood the ecosystem as a physical object and a certain unit in nature, in which living and non-living components are equally represented and play the same role.

between "physicalism" and "organicism," as noted in the previous section.

It is clear that the differences in views between Vinberg and Lindeman were engendered by the different experiences of these researchers. Vinberg was trained both as an experimenter (a physiologist who used methods of physical chemistry) and as an aquatic ecologist, while Lindeman relied primarily on naturalistic, faunistic approach. Lindeman's goal was probably to collect as much material from one lake as possible and to analyze all groups of organisms in this material, which he indeed accomplished. In doing this, he was guided by the calculation scheme proposed by C. Juday, who also included purely physical processes in his calculations. Vinberg's way of thinking involved seeking generalized parameters of life activity of the water body as a whole (a clear influence of S. Skadovsky's school of hydrophysiology with its emphasis on pH as an indicator of the physiological type of a water body), an approach that was elicited by his interest in plankton at the early stage of his career.

Finally, it should be emphasized that Vinberg considered the water body almost without accounting for its evolution. Lindeman, in contrast, while studying an aging lake, was focused from the outset on the analysis of community succession in this lake. Different attitude of these scientists toward the role of living organisms and non-living components is explained, in fact, by this distinction. Since Lindeman was dealing with the aging process of a water body, the role of physicochemical factors, which were external with respect to the water body, was regarded by him to be the most important. Lindeman incessantly emphasized lake's "concavity" relative to the terrestrial landscapes: as the lake ages, it is filled by sediments, becomes shallower and eventually becomes overgrown. By contrast, Vinberg always treated organisms as an "independent variable" in the system of the lake. He emphasized a special and active role of living matter.

It should also be noted that Lindeman's trophodynamics is mostly a general view, while Vinberg's balance is a more concrete system of views, in which the water body is treated as a system of interconnected components. Of course, certain incompleteness of Lindeman's trophodynamics and speculative ideas that occasionally appear in his 1942 work are quite understandable, as he simply had no time to bring his concept to completion.

Can we speak about differences in cultural settings that accounted for cognitive differences between concepts proposed by Vinberg and Lindeman? I believe that both Vinberg and Lindeman were exposed to a similar set of ideas shaped by the logic of progression of ecosystem concepts across the world. For instance, as shown above, by the early 1930s similar ideas about water body metabolism were "floating in the air." Sharp social and even political differences between the countries, in which these scientists worked, hardly played a significant role in developing their systems of view. One has to agree with the opinion of the Sovietologist L. Graham (Graham 1987), who emphasized a phenomenal productivity of the Soviet science despite severe repressions against scientists. In the USSR, holistic views were repudiated by science ideologists, but they have endured there nonetheless. In addition to Vinberg's biotic balance, at about the same time (in 1940), V.I. Zhadin formulated a theory of biological productivity of water bodies; this theory rested on principles even more similar to those of Lindeman (see Rizhinashvili 2020 for a more detailed discussion of Zhadin's theory). Zhadin considered the succession of benthic communities in rivers under the effect of silting caused by influx of organic substances from the catchment. Like Lindeman, Zhadin regarded water objects (in this case, rivers) as collectors of organic substances. Zhadin, however, never dealt with the terrestrial portion of succession. Unfortunately, isolationism, which for several decades dominated biological sciences in the USSR, prevented an adequate perception of all their achievements outside Russia (Zhadin's forgotten theory is a perfect example).

The opposite opinion was expressed by F.B. Golley (Golley 1993), a distinguished American historian of ecology, who argued in his well-known monograph that after the World War II the ecosystem theory could have flourished only in the USA, because of the nature of its political system. According to Golley, it was in the USA that all necessary and rather favorable conditions were present. First, there were large investments intended specifically to support ecosystemic studies, which soon developed into so-called "big ecology." These investments were driven by a gradually deepening understanding of the practical importance of studying biogeochemical flows (for instance, because of the testing of nuclear weapons). The second favorable factor was a relative personal freedom of scientists (unlike war-torn Europe, the USA did not have to recover from the consequences of war). Third, the holistic ideas in the USA did not have any negative philosophical or political connotations, as, for instance, in Germany, where holism during the post-war period was linked in the minds of many scientists with ideology of the defeated National-Socialism (Jax 2020). These arguments are probably true in the sense that the circumstances mentioned by Golley did encourage an intensive development of ecosystemic studies in the American scientific community. But, whatever is the case, at the turn of the 1940s these studies emerged simultaneously and independently in many countries. It is clear that Lindeman's trophodynamic ideas, rather than Vinberg's balance, have gained widespread popularity because of the prevalence of English as an international language of science. It appears, however, that the concept of ecosystem has acquired its modern form due to amalgamation of different aspects of views held by Vinberg and Lindeman, even if Vinberg's ideas have been used only implicitly.

It would also be worthwhile to discuss in greater detail the frequently mentioned influence of the ideas of V.I. Vernadsky on ecologists. It has traditionally been assumed that Vernadsky's biosphere concept had a great worldwide impact on their ways of thinking (Levit 2011), but a careful examination of literature shows that this view cannot be accepted even with respect to the USSR. The examination of Vinberg's papers gives the impression that Vernadsky's biosphere ideas had a certain impact on his views only during a later period, since he started to cite Vernadsky's works and write about the biosphere only in 1946. It should be noted, however, that in 1940 the journal *Doklady Akademii Nauk SSSR* ("Proceedings of the Academy of Sciences of the USSR"[10]) published Vinberg's paper on gas exchange between the water body and atmosphere, which had been presented for publication by Vernadsky[11] on January 1, 1940 (Vinberg 1940). It can be concluded therefore that the influence of Vernadsky's ideas on Vinberg and perhaps his acquaintance with Vernadsky date back at least to 1939. The leading role of living organisms in biotic circulation postulated by Vernadsky was actually in good agreement with physiological and "planktonic" ways of thinking championed by Vinberg. At the beginning of the 1930s, however, Vinberg relied solely on the experimental approach. It was only later, as he further elaborated his ideas, that he started to think in the context of biosphere. The origin of L. Rossolimo's balance-based approach in studying water bodies, which was the guiding principle for Vinberg's views, also remains unknown. I could not find any evidence that Rossolimo was influenced by Vernadsky's ideas. Rather, it can be stated that the idea of balance is closely related, for example, to that of natural complex first developed by V.V. Dokuchaev (Golley 1993). Vernadsky is only mentioned in this respect as one of several big names. It can be assumed, however, that the concept of biotic balance probably reached its final form under a significant influence of the biosphere theory. This influence, however, should not be overestimated. Zhadin, for instance, did not cite any Vernadsky's works when he was developing his own theory. While working on Zhadin's personal fond at the scientific archive of the Zoological Institute, I could not find any documents indicating his interest toward the works and ideas of Vernadsky.

Surprising as it is, but Vernadsky's biosphere thinking was more readily received by American, rather than Soviet biologists, because both Hutchinson and Lindeman mention him in their works.[12] This reception of Vernadsky's ideas was, however, somewhat superficial, which led Golley (1993) to write that Vernadsky's views, like those of Dokuchaev and many other Russian and Soviet scientists, had a rather insignificant influence on the development of the ecosystem theory, which to a large extent was a consequence of the political isolation of the USSR. In any case, it is still unclear to what extent the concept of biosphere was included in the ecosystem studies of the mid-twentieth century.

In conclusion, it should be stressed once again that holism in hydrobiology has deep historical roots. Explicit or implicit likening of a lake to an organism, whatever was its specific expression, is rooted in archaic, mythological thinking as a way of perceiving a complex object (Ghilarov 1992). It seems paradoxical but organicism, which was rejected by the party ideology in the USSR, has been fully and explicitly incorporated into Vinberg's concept of biotic balance, while in the American scientific community the organicism championed by the school of Birge and Juday has been quickly transformed into technocratism and physicalism (Taylor 1988). It should be emphasized that Lindeman was probably far from radical technocratism. As is evident from the few works that he published, the young scientist was a good naturalist, who conducted a thorough quantitative and qualitative evaluation of flora and fauna in the water body that he chose to study. It is also possible that, like other limnologists, he implicitly endorsed some aspects of organicism, because he considered water bodies from the perspective of aging (i.e., developmental stages, as in a living organism).

Some possible prospects of the aquatic ecosystem theory

A comparative analysis of a widely known trophodynamics of R. Lindeman and the biotic balance concept of G.G. Vinberg, which is relatively little known internationally,

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[10] This is not an official translation of the journal name.

[11] Since its founding in 1933 to the present day, the journal "*Doklady Akademii Nauk SSSR*" accepts articles, whose authors are academicians or corresponding members of the Russian Academy of Sciences (formerly the USSR Academy of Sciences). The articles of other authors are accepted only on condition that they have been presented (i.e., recommended for publication) by an academician of the respective discipline.

[12] It is known that G.E. Hutchinson was closely acquainted with Georgiy V. Vernadsky, a son of V.I. Vernadsky, when the latter was teaching in Yale University as a professor (Golley 1993). Georgiy introduced Hutchinson to his father's works and materials. Lindeman learned about Vernadsky's ideas from Hutchinson and was greatly influenced by them while editing his manuscript on trophodynamics. Although Lindeman mentioned Vernadsky in his 1942 paper, it remains unclear, however, as to how exactly he employed Vernadsky's ideas in developing his own concept.

allows us to identify certain traits common to the ecosystem ideas of the mid-twentieth century (at least in aquatic ecology). Although Lindeman's views can be regarded as being close to physicalism, while those of Vinberg as approaching organismocentrism, both scientists accorded crucial importance to the physiological activity of organisms (feeding and respiration). Both authors proposed an application of the corresponding techniques that permitted monitoring the metabolism of hydrobionts.

It should also be noted that both Vinberg and Lindeman viewed sun energy and consequently the activity of autotrophs as a principal and chief source for the build-up of organic substances in the water body, but attached almost no importance to the allochthonous organic matter. The crucial focus on the primary production component, which was the hallmark of both Vinberg and Lindeman's concepts, brings us back to the roots of production hydrobiology (for instance, to E. Naumann's ideas of regional limnology).

All of this suggests that in the middle of the twentieth century ecosystem concepts have been built along similar lines and more or less independently by scientists who had a different academic experience and were living in different social settings. It appears that the concept of ecosystem has acquired its modern form due to amalgamation of different aspects of views held by Vinberg and Lindeman, even if Vinberg's ideas have been used only implicitly.

In the USSR, G. Vinberg's biotic balance gave rise to the whole school of production hydrobiology, whose center still exists within the walls of the Zoological Institute of the Russian Academy of Sciences (RAS). This center is the Laboratory of Freshwater and Experimental Hydrobiology of the Zoological Institute RAS. Russian hydrobiologists have been engaged in internationally recognized research in production hydrobiology and have successfully carried Vinberg's legacy. Over the last decades, this school was led by academician Alexander (Aleksandr) F. Alimov, a follower of Vinberg and Zhadin's disciple, who, unfortunately, passed away in 2019 (Alimov was also the director of the Zoological Institute RAS from 1994 to 2005). By 2000, Alimov has developed the basic premises for the theory of functioning of aquatic ecosystems in general, based on the results of numerous studies of his research team (Alimov 2003). The works of Vinberg and his school were well known internationally. In particular, Vinberg supervised one of the work groups on productivity of aquatic ecosystems and took an active part in editing methodological guidelines as part of the implementation of the IBP (Vinberg 1971).

In the USA, thanks to the book "Fundamentals of Ecology" by E.P. Odum, trophodynamics has quickly won the minds of scientists (Golley 1993). For instance, in 1953 Dineen published a paper, which almost completely emulated the technique used by Lindeman in 1941 (Dineen 1953). In this country, the ecosystem studies quickly grew in number and resulted in the implementation of a large-scale program, the IBP.

At the same time, in the second half of the twentieth century ecosystem studies have evolved along the path of an increasing focus on metabolic processes and on measuring and comparing production and destruction in the water column of rivers and lakes. This opened the possibility of studying consumption and release not only of oxygen, but also of carbon dioxide. Estimating the extent of carbon dioxide emission by water bodies is undoubtedly a key aspect in resolving the carbon problem of the biosphere. This attests to the exceptional prolificacy of the organismocentric understanding of the ecosystem, at least when applied to aquatic ecosystems.

Further development of the theory of ecosystem functioning should be focused not only on generalized parameters (general ecosystem production, net ecosystem production, ecosystem respiration, etc.), but also on factors involved in the integration of various parts of a water body (or, at least, of its water mass) into a unified whole. As early as the beginning of the twentieth century, many hydrobiologists pointed to a similarity between lake water and blood or cellular protoplasm. The results of studying the reserves of dissolved organic matter add a new dimension to this seemingly speculative analogy. The questions of determining chemical individuality (group composition) of compounds participating in the circulation of organic substances in water bodies and evaluating the magnitude of extracellular phytoplankton production are still being given insufficient attention.

The second important aspect in addressing the question of ecosystem functioning is the problem of producer limitation. In this respect, attention should be given not only to the notorious dilemma of "nitrogen vs. phosphorus," which has been abundantly discussed in the literature for more than 50 years, but also, for example, to the question of provision of carbon dioxide for the photosynthetic organisms. R. Maucha (1924), for instance, wrote about a peculiar symbiosis between algae and bacteria in the planktonic community. This tight interaction arises because the bacteria break down organic substances and release carbon dioxide (together with nutrients), which is then used in photosynthesis. Vinberg (1956) proposed a system of "algae—bacteria—dissolved organic matter," whose properties were supposed to determine the extent of oxygen consumption by water.

It is clear that the problems of aquatic ecology should be addressed from the perspective of the organismocentric understanding of the ecosystem, but undoubtedly at the new level of development of this concept. This was clearly understood both by the scientists who stood at the origin of holistic principles (E. Birge, E. Naumann, A. Thienemann, V.M. Rylov, S.N. Skadovsky, R. Maucha, and many others) and by those who proposed the first explicit concepts for the aquatic ecosystem (R. Lindeman and G.G. Vinberg).

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