transversal
International Journal for the Historiography of Science

Transversal: International Journal for the Historiography of Science, 2024 (16): 1-14
ISSN 2526-2270
Belo Horizonte – MG / Brazil

Article

The Physiology of a Lake as a Whole: Edward A. Birge on "Lake Respiration" and the Lake-to-Organism Analogy

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Abstract:

Analogies between ecological systems and organisms are a common trope in early ecology, but discussions of these analogies tend to focus on the particular version of them found in the works of pioneer plant ecologist Frederic E. Clements (1874-1945). This paper partly fills this gap by analyzing the relatively well-developed version of the analogy between lake ecological systems and organisms found in the works of founding American limnologist Edward Asahel Birge (1851-1950). I argue that although, for Birge, the lake-to-organism parallel did not imply that lakes were literally organisms, it reflected his commitment to a holistic view of lakes, which anticipated the distinctive holological perspective on ecological systems of later ecosystem ecology.

Keywords: Organicism; holism; ecology; limnology; Edward A. Birge.

Received: January 23, 2024. Reviewed: May 20, 2024. Accepted: June 2, 2024.
http://dx.doi.org/10.24117/2526-2270.2024.i16.08

Introduction

Analogies between ecological systems and organisms are a common trope in early ecology. The most widely known and extensively discussed version of this trope is indeed the one found in the works of plant ecologist Frederic E. Clements (1874-1945), who portrayed the plant community – or plant formation, in his own terminology – "[a]s an organism … [that] arises, grows, matures, and dies" (1916, 3). It is also known, however, that other ecologists, some of whom worked in other ecological subfields, also used such organismic analogies.[2] One of these fields is limnology, the science of lakes, a domain in which many important

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[2] For general discussions of organismic analogies in ecology, see Acot (1987), McIntosh (1998), and Bergandi (1999).

ecological ideas have been developed and in which one can find some of the earliest uses of organismic analogies in reference to ecological systems (see references below).[3]

In this paper, I will analyze the organismic analogy as it is found in the works of the Wisconsin-based founding American limnologist Edward Asahel Birge (1851-1950). Although scholars have noticed Birge's lake-to-organism analogy (Frey 1963, 22–23; McIntosh 1985, 224, 253; Beckel 1987, 7; Ghilarov 1992, 24), no detailed analysis of it has yet been offered. Birge's use of this analogy, however, deserves particular attention, in part because of its relatively well-developed character in comparison to uses by other early limnologists such as Stephen A. Forbes (1844–1930) and François-Alphonse Forel (1841-1912), but also because, as we shall see, it is an important source of ideas that have later become central to ecosystem ecology. Moreover, as Frank Egerton (1987, 87) notes, Birge's influence on early American limnology is comparable to that of Clements in early American plant ecology.

I will discuss Birge's use of organismic analogies in relation to lakes and, more specifically, in relation to processes of gas circulation both between lakes and the atmosphere above them, and between living organisms within them. Birge called this overall process "lake respiration," and studying it led him to the depiction of lakes as having a *physiology of their own.* I will analyze the philosophical implications of Birge's use of organismic analogies. In particular, I will argue that for him, these analogies did not imply that lakes *were* organisms in any literal sense. Moreover, I will maintain that his use of these analogies nevertheless reflected a view of lakes as holistic systems, one which prefigured what ecologist G. Evelyn Hutchinson (1943; 1978, 214–15) and historian of ecology Joel Hagen (1989; 1992) characterized as the *holological perspective* on ecological systems.

Birge used the organismic analogy mainly in "The respiration of an inland lake," a paper he read as a presidential address to the American Fisheries Society (Birge 1907). He also used this analogy, more succinctly, in another presidential address, and in the introduction of a book-length report on dissolved gases in Wisconsin inland lakes co-authored with his close associate Chancey Juday (1871–1944) (Birge 1910a; Birge and Juday 1911). These works will be my focus here.

Birge, Juday, and Wisconsin Limnology

Edward A. Birge was born in 1851 and grew up near New Haven in upstate New York. He earned A.B. (1873) and A.M. (1876) degrees from Williams College in Massachusetts. In 1873, he went to the Museum of Comparative Zoology in Cambridge, Massachusetts, to work with zoologist and geologist Louis Agassiz (1807-1873). Agassiz died three months after his arrival, but Birge was offered the opportunity to pursue his education at Harvard. In 1876, he moved to the University of Wisconsin when John Bascom, his former professor at Williams who had become president of the University, offered him an instructor and museum curator position. Birge was then given time off to complete his PhD at Harvard (1878) and became a professor at Wisconsin in 1879. During 1880-81, he went to Leipzig to study with physiologist Carl Ludwig (1816-1895). Upon his return to Wisconsin, the university was still very small, and Birge assumed a leading role in developing biological education and research there. In 1897, the Wisconsin legislature established the Wisconsin Geological and Natural History Survey, and Birge served as its director from then until 1919. Throughout his career, he held several administrative positions at the university, including chairman of the zoology department from 1875 to 1906, and president of the university from 1918 to 1925 (see Frey 1963, 4; Beckel 1987, 1–3; Egerton 1987, 87; 2014, 138).[4]

[3] Another field is animal terrestrial ecology (see McIntosh 1980, 19–20).
[4] For an extensive discussion of Birge's intellectual life and career, see also George C. Sellery (1956).

Birge was a zoologist by training. His early research focused on the systematics of the Cladocera, a crustacean zooplankton. His interest in limnology arose from his reading of a paper by R. H. Francé on the diel migration of zooplankton in Lake Balaton in Hungary (Francé 1894). The paper showed that the Cladocera in the lake comes to the surface at night and returns to the lake bottom around dawn. Birge wanted to know whether the same phenomenon occurred in deeper lakes like Lake Mendota in Madison, and thus started sampling microcrustacea in the lake with the help of students. He found out that no diel migration occurred in Lake Mendota, but his results revealed an unexpected pattern. From summer to fall, a change occurred in the vertical distribution of the crustacea: in the summer, most crustacea are found in the upper layer of water and the lake bottom shows little crustacean life, whereas the crustacea become more evenly distributed in the fall (Birge, Olson, and Harder 1895). This made Birge interested in the physical and chemical factors that might explain this distribution and, in particular, in the thermal structure of the lake and its effect on concentrations of dissolved oxygen and carbon dioxide in its different layers of water. Birge's research on these aspects marks his shift to limnology (see Mortimer 1956, 165–66, 176–77; Frey 1963, 15–18; Beckel 1987, 2–3; McIntosh 1985, 60, 121–22; Egerton 2014, 138–39). It led him to introduce now-standard limnological concepts, such as *thermocline*, the transition zone between the warmer layer of water that forms near the surface of a lake and the colder layer that forms at greater depths, and *epilimnion* and *hypolimnion*, respectively, these warmer and colder layers of water above and below the thermocline (Birge 1898; 1907; 1910b; Birge and Juday 1922).

Birge conducted most of his research and co-authored most of his publications with his research partner, Chancey Juday (1871–1944). Juday had been trained at the University of Indiana in part with German-American ichthyologist Carl Eigenmann (1863-1927), and Birge hired him in 1900 to work on the Wisconsin Geological and Natural History Survey (see Mortimer 1956, 183; Frey 1963, 4–5; Beckel 1987, 4–5; Egerton 1987, 87; 2014, 139). Birge and Juday are renowned for their pioneering works on several topics, such as the relationship between biomass and the stratification of dissolved gases in lakes, the transmission of solar radiation in water, lake productivity, and the "heat budget" of lakes (e.g. Birge and Juday 1911; 1922; 1929).

Birge's early studies on crustacea in Lake Mendota showed a correlation between changes in their vertical distribution and changes in the thermal structure of the lake (Birge, Olson, and Harder 1895; Birge 1898). In the summer, the lake becomes thermally stratified, that is, the upper layer of water becomes warmer than the lower layer, and the warmer and colder layers of water do not mix. The above-described distribution of crustaceans then forms: most crustaceans are found in the upper layer. This stratification lasts until the fall, when the surface water cools down to around the same temperature as the lower layer, and the wind causes the upper and lower layers to mix. The crustacea then become more evenly distributed in the lake until the next summer. Birge reasoned that the low temperature of the lower layer of water cannot be what causes the exclusion of crustacea in the summer, because the same species occur in colder waters in other lakes. Looking for another possible causal link, he turned his attention to lake chemistry, and, with the aid of Juday and others, he studied this aspect in many Wisconsin lakes (see Mortimer 1956, 183–86; Frey 1963, 21–24; Beckel 1987, 4–8).

Birge's works using the lake-to-organism analogy present an explanation for the correlation between changes in the distribution of animal life within lakes and changes in lake temperature. The analogy is employed in most detail in his presidential address, "The Respiration of an Inland Lake," read at the Thirty-Sixth Annual Meeting of the American Fisheries Society (Birge 1907). As Birge and his associates discovered, the mediating link between these changes was the modifications in the concentrations of dissolved oxygen and carbon dioxide in the upper and lower layers of the lake, which are driven by changes in temperature. The next section will give a detailed presentation of Birge's explanations of this link, and of his associated analogy between lakes and organisms.

The Lake as a Respiring Organism

Birge's lake-to-organism analogy runs throughout "The Respiration of an Inland Lake" (Birge 1907). He starts the paper by calling the comparison between an inland lake and a living being "one of the happiest of the attempts to find resemblances between animate and inanimate objects." Unlike other such comparisons, "which turn on a single point of resemblance …, the appropriateness of this [one] increases rather than diminishes as our knowledge both of lakes and of living beings is enlarged." Just like organisms, lakes, according to Birge, have a life-cycle, seasonal changes in activities, and even fluctuations in the intensity of their vital manifestations. But, in his view, "in no respect does [a lake] resemble an organism more closely than in the topic … [of] its respiration," a topic with respect to which "the resemblance is rather in processes and operations than in form" (Birge 1907, 223).[5]

Birge starts by identifying a broad resemblance between lakes and organisms with respect to respiration: "the lake consists of an unorganized fluid—the plasma of the blood and the water of the lake—and of numerous organized and actively living parts—cells in the case of blood, and the plants and animals in the lake." And "[a]s is the case in the animal, the respiratory gases are absorbed and transmitted to the living structures by means of the unorganized fluid" (Birge 1907, 223–24).

Birge then proceeds by contrasting what he calls the *external* and *internal* respiration of a lake. By the former, he means "the absorption of certain gases from the air and the return of other gases to it, as well as the process by which this exchange is effected," and also "the methods by which the gases are distributed in the lake and conveyed to and from the surface of the water". By the latter, he means "the gaseous exchanges which take place in the lake itself, between its various organisms and the water surrounding them," as well as "the chemical processes by which the character of the gases is altered or new gases manufactured, in the course of the vital activities of the inhabitants of the lake" (Birge 1907, 224).

Birge first discusses the *external* respiration of the lake, centering his discussion on exchanges of oxygen and carbon dioxide between the lake and the atmosphere. He explains that the thermal stratification that forms in the lake in the summer prevents its upper and lower layers of water from mixing. As a result, the oxygen that becomes dissolved in the upper layer of water through contact with the atmosphere is unable to reach the lower layer, and, conversely, the large amount of carbon dioxide that is produced in the lower layer of water through decomposition does not reach the upper layer. The lack of oxygen explains why there is little animal life at the bottom of the lake in the summer. In the fall, when the upper and lower layers of water reach equal temperatures, they become able to mix, and the lake's water is turned over through the effect of the wind blowing on the lake. As a result, the oxygen and carbon dioxide become more evenly distributed between the upper and lower layers of the lake, and the lower layer becomes suitable again for animal life. A similar phenomenon occurs in the spring, but in a less pronounced form, because living processes run more slowly during the winter, such that the oxygen that has reached the lower layer of water in the fall has not become fully depleted. Thus, in the winter and the summer, the animal life and decomposition that occur in the lower layer of the lake depend almost entirely

[5] With respect to form, Birge thought of the lake as "a very simple creature, resembling rather a gigantic amoeba than a more highly organized being," and as perhaps more aptly compared "not with the organism as a whole, but with the special respiratory substance of the animal—the blood." (Birge 1907, 223–24).

upon the oxygen brought there during the fall and spring mixings, and conversely, the plant life that occurs in the upper layer of the lake depends largely upon the carbon dioxide brought there by these events. Birge hence summarizes: "in terms of our [lake-to-organism] comparison, we may say that an inland lake is an organism which takes one full inspiration in the fall, and another, less complete, in the early spring; that during the winter it does not breathe at all and during the summer has only a very shallow and imperfect respiration" (Birge 1907, 224–25). With this overall process of external respiration, Birge emphasizes, the lake solves "one of the fundamental problems of life for any large and active organism" (Birge 1907, 227). It solves it in a way comparable to a cold-blooded animal.

Birge then discusses the *internal* respiration of the lake, again focusing on exchanges of oxygen and carbon dioxide, but now among the organisms that live within the lake. Green plants, he explains, which convert carbon dioxide into oxygen, are an additional source of oxygen in the lake, though one less important than absorption from the atmosphere (Birge 1907, 233–34). This process can nevertheless be important in the upper layers and also in the lower layers when the lake water is sufficiently transparent (Birge 1907, 234–35). In contrast to oxygen, carbon dioxide in the lake comes mostly from internal processes because its concentration in the atmosphere is relatively low, and the lake surface has only a limited ability to absorb it (Birge 1907, 236–37). Most of the available carbon dioxide thus results from decomposition and the activities of animals. In some lakes, another source of carbon dioxide is bicarbonates dissolved in the water, from which algae are able to withdraw carbon dioxide molecules. In these lakes, the bicarbonates act like a "chemical carrier for the carbon dioxide, which may carry this gas somewhat as the hæmoglobin carries oxygen in the blood" (Birge 1907, 239).

Thus, in his "The Respiration of an Inland Lake," Birge uses the organismic analogy to present a picture of transfers of oxygen and carbon dioxide between lakes and the atmosphere, and among organisms that live within lakes, an overall process he calls "lake respiration."

Birge uses the lake-to-organism analogy also, though more succinctly, in another presidential address, which he read the next year to the Fourth International Fishery Congress (Birge 1910a). After giving a detailed exposition of oxygen and carbon dioxide transfers within lakes similar to the one he gives in his 1907 address, he states:

> [F]rom the few diagrams which I have given one may see that lakes present to the student a *vital story, as definite, as variable, and as complex as is that of a living organism*; a story to be followed by means like those needed to work out biological life histories, and one whose interest is such as to claim far more attention from science than it has received. (Birge 1910a, 1290, emphasis added)

Birge uses the organismic analogy again in the introduction of his and Juday's 259-page report on the inland lakes of Wisconsin, which gives a more detailed account of their research on lake chemistry and its influence on life within lakes (Birge and Juday 1911). Birge presents his and Juday's work on dissolved gases in lakes and their effects on plant and animal life as a study of the *physiology of lakes*. Using wording similar to that used in the passage just quoted, he states:

> Perhaps the chief interest which our work has had for us has been the fact that its progress has revealed to us the existence of *physiological processes in lakes as complex, as distinct, and as varied as those of one of the higher animals* (Birge and Juday 1911, xvii, emphasis added).

Later in this text, describing the complex array of intertwined factors involved in the production of phenomena like the significant existing differences in productivity among lakes, he insists that explanations of such phenomena must be based on "the study of the several lakes *as physiological individuals of a higher order*" (Birge and Juday 1911, xix, emphasis added)

Hence, we find in Birge's works a relatively developed version of the organismic analogy in relation to lakes. Lakes, in his view, achieve an overall process of respiration broadly comparable to that which occurs in individual organisms.

Discussion

Literal or Analogical Organicism?

A question that naturally arises when one considers early ecologists' parallels between ecological systems and organisms is whether they intended these parallels as more than analogies, that is, as implying that ecological systems *are*, in some literal sense, higher-order organisms. This question has been abundantly discussed with respect to Clements's parallel between plant formations and organisms, the common reading being that, for Clements, formations *were* organisms ("complex organisms," in his terminology) and not just *like* organisms (see e.g. Hagen 1992, chap. 2; van der Valk 2014).[6] What about Birge?

Birge's relatively expansive use of the lake-to-organism analogy contrasts with previous uses by other limnologists. Writing 20 years before Birge, founding American limnologist Stephen A. Forbes (1844–1930) is perhaps the first ecologist to have paralleled lakes with organisms (though somewhat implicitly), describing a small lake as "a little world within itself,—a microcosm," and also as "an organic complex" (Forbes 1887, 77).[7] He was followed in the next decade by Swiss limnologist François-Alphonse Forel (1841-1912), who stated that "a lake is an isolated, bounded, organism, better separated than most other geographical individuals" (Forel 1895, 593).[8] Forbes and Forel's lake-to-organism analogies, however, were only made in passing and remained brief in comparison to Birge's. Moreover, we have seen above that Birge showed a certain enthusiasm for this analogy, referring to it as "the happiest of the attempts to find resemblances between animate and inanimate objects" (Birge 1907, 223).

Although these observations may suggest that Birge construed the lake-to-organism parallel more than analogically, the analogical reading is, I think, more plausible overall. One reason is that Birge used this parallel in publications which, by their nature, lend themselves to informal use of language: presidential addresses read before fisheries associations, in which Birge was in part speaking to audiences not exclusively composed of specialists, and the introductory part of a report.[9] I found no instances of the lake-to-organism parallel in more technical sections of his and Juday's works. The contexts in which Birge used this parallel are hence ones in which he may have expected his audience to interpret his prose informally.

Moreover, a rather clear indication that Birge considered the lake-to-organism parallel as no more than analogical is that he, in fact, used it as much to highlight resemblances

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[6] For a challenge to this reading, see Christopher Eliot (2007; 2011).

[7] In an earlier paper, he had used the organismic analogy more explicitly, though not in reference to lakes and also rather briefly (Forbes 1880, 3). Though Forbes's works on lakes antedate the introduction of the term "limnology," he is commonly recognized as a founder of that discipline (see McIntosh 1985, 58–60; Egerton 2014, 137).

[8] My translation of "un lac est un organisme isolé, limité, mieux séparé que la plupart des autres individus géographiques." Forel is known as a founder of limnology, and as the one who gave its name to the discipline by coining the French term "limnologie," which he construed as "the oceanography of lakes" (Forel 1892, vi; see Mortimer 1956, 166, 203; McIntosh 1985, 57–58; Egerton 2014, 131–32).

[9] "The respiration of an inland lake," initially published in 1907 in the *Transactions of the American Fisheries Society,* was republished in the *Popular Science Monthly* in April 1908 (Birge 1908).

between lakes and organisms as differences. A recurring theme in "The respiration of an inland lake" is how inefficient the respiratory mechanisms at work in lakes are as compared to those at work in individual organisms. Birge demonstrates this, for instance, with regard to oxygen absorption and transmission. With regard to absorption, the first limitation of lakes, according to Birge, is their relatively small contact surface compared to animals. As he notes, "in any large animal enormous surfaces must be provided for the absorption of oxygen" and, in general, "the necessity for arrangements for a large absorbing surface increases with the size of the animal." Lakes, however, although their size is "enormous as compared with that of any living being," have an "absorbing surface [that] is very small as compared with [their] mass; being only the upper surface of the water" (Birge 1907, 228). A second limitation is the absence within lakes of a chemical substance like hæmoglobin, which binds with oxygen and facilitates its absorption (though we have seen above that he considered bicarbonates to act like a carrier of carbon dioxide in some lakes). Lakes, thus, have a poor capacity for oxygen absorption as compared to organisms.

With regard to oxygen transmission, the main limitation of lakes is their lack of the kind of transport mechanism that organisms typically have. As Birge explains, "[t]he animal shows a complex and very efficient mechanism for the circulation of the blood; an apparatus whose complexity and efficiency are in large measure determined by the necessity for a rapid distribution of the oxygen and a rapid disposal of the gaseous wastes of the body" (Birge 1907, 229). Lakes, in contrast, have only very ineffective modes of transport: diffusion, convection currents, and currents produced by winds. Diffusion, since it is efficient only over short distances whereas lakes have considerable size, is "practically worthless" and "has little or nothing to do with the general circulation of gases within the lake" (Birge 1907, 229). Convection, likewise, has only a limited effect, because it can occur only when a lake's upper layer of water cools down, such that, in the summer, "when vital processes are most active and the need for oxygen is greatest, convection currents afford a minimum of assistance in distributing it" (Birge 1907, 230). Finally, wind-generated currents, as we have seen above, are effective transport mechanisms only in the fall and spring, while, in the summer, "the lower, cooler water is wholly shut off from the direct influence of the wind currents" (Birge 1907, 230).

Birge thus concludes: "an inland lake has an extremely inefficient apparatus for absorbing and distributing oxygen" (Birge 1907, 230). He describes similar inefficiencies of lakes with regard to absorption, transmission and use of carbon dioxide (Birge 1907, 232–33, 237–38).

Birge's emphasis on the dissimilarities between "respiratory processes" as they occur in lakes and in individual organisms makes fairly clear, I contend, that he did not consider the similarities between the two types of objects as substantial enough for lakes to *be* organisms. In fact, he seems to have used the lake-to-organism analogy mainly for communicative purposes. His aim was to make his topic easier to grasp for audiences not familiar with it, and he furthered this aim by paralleling the then unfamiliar phenomenon of transfers of gases within lakes as well as between them and the atmosphere to the more familiar phenomenon of respiration in organisms.

A Holism of Some Sort?

Although Birge did not construe lakes literally as organisms, his lake-to-organism analogy nevertheless conveys a view of lakes as *unified wholes* that his investigations seemed to substantiate (Mortimer 1956, 203; Frey 1963, 21–22; Beckel 1987, 7; Ghilarov 1992, 24). Besides the analogy, some statements he makes in his works also imply such a view. In one of his early papers on zooplankton crustacean, he states: "In carrying out this work it has been my endeavor to make a contribution to the natural history of an inland lake *as 'a unit of* *environment*'" (Birge 1898, 277, emphasis added).[10] Likewise, in the introduction of his 1911 report co-authored with Juday, he asserts:

> The inhabitants of an inland lake form a closed community in a stricter sense, perhaps, than the term can be applied to any other non-parasitic assemblage. … The lake is dependent on its own stock of green plants for the stock of organic matter available for food of other organisms; and the possible amount of green plants is limited by the raw material supplied for photosynthesis from the lake itself. (Birge and Juday 1911, xv).

Birge reasserts this idea in a later work, linking it to Forbes's (1887) notion of the "Lake as a microcosm": "The lake is the one true microcosm, for nowhere else is the life of the great world, in all of its intricacies, so clearly disclosed to us as in the tiny model offered by the inland lake" (Birge 1936; quoted in Beckel 1987, 7).

A philosophical trend that was influential at the beginning of the twentieth century is *emergent evolutionism*, a trend epitomized in the works of Samuel Alexander (1869-1938), Conway Lloyd Morgan (1852-1936), among others, and, to some extent, in those of South-African Statesman Jan Christian Smuts (1870-1950) (Alexander 1920; Morgan 1923; Smuts 1926). Given emergent evolutionism's focus on wholes and how they form through the synthesis of their constituent parts, it has been tempting for scholars discussing the history of ecology to draw connections between ecologists' holistic views, their use of organismic analogies, and emergent evolutionist philosophies (e.g. Worster 1977, chap. 15; Bergandi 1999). In a nutshell, emergent evolutionism argues that, although everything is made of matter, such that no mysterious forces like Drieschian entelechies or Bergsonian *élan vital* exist, the material world is constituted by a hierarchy of organizational levels (e.g. the physical, chemical, and biological levels). At each level, genuinely novel properties arise, which, in line with the summary maxim "the whole is more than the sum of its parts," are not reducible to, or derivative from, the properties exhibited by matter at lower levels.[11] Applied to ecological systems, emergent evolutionism thus implies that those systems have properties that are not reducible to those of their constituent organisms, populations and/or physico-chemical elements. The reading that connects early ecologists' analogies between ecological systems and organisms to emergent evolutionism finds some support in the fact that Clements and other early ecologists who paralleled ecological systems to organisms often drew explicit connections between their views and emergent evolutionist ideas (see e.g. Clements and Shelford 1939, 22–24; Allee et al. 1949, 693–94).[12]

One does not, however, find in Birge's works any kind of allusion or commitment to emergent evolutionist ideas.[13] In fact, his general approach seems to have leaned precisely in the opposite direction. What he did was to explain lake-wide processes in terms of the physical and chemical properties of water and the chemical elements dissolved in it (and to some extent those of their constituent organisms). One of Birge's main conclusions in "The respiration of an inland lake" is that the purely physical process by which lakes acquire oxygen from the atmosphere are more determinant of their ability to support animal life than the rate at which they produce plants that animals can feed upon (see Birge 1907, 232, 241). Moreover, in his 1908 address, he describes his research as aimed towards "a knowledge of lacustrine physics and chemistry" similar to the "knowledge of soil physics and chemistry"

[10] Birge borrows the phrase "unit of environment" from Eigenmann (1895).
[11] For an overview on philosophical emergentism, see Brian McLaughlin (1992).
[12] Though it is unclear whether Clements's views were truly consonant with emergent evolutionist philosophies (see Hagen 1992, 84).
[13] Emergent evolutionism, of course, reached its peak after Birge's publications on lake respiration, but its hallmark ideas had already been explored in the Nineteenth century, notably by J. S. Mill in his *System of Logic* (see McLaughlin 1992).

that informs agriculture (Birge 1910a, 1291–92). This physico-chemical reductionism characterizing Birge's approach aligned with the scientific orientation promoted by German physiologist Carl Ludwig, with whom, as I noted, Birge studied in 1880-1881 (see sect. 2). Ludwig had applied such an approach to the study of oxygen and carbon dioxide exchanges within individual organisms (see Schubert 1996); Birge extended it to the study of similar exchanges in lakes. Given this orientation, the kind of holism that he endorsed cannot have been of the same strain as that of emergent evolutionists.

Birge's Holological Perspective

Some clue to an understanding of Birge's holistic take on lakes can be found, I think, in Joel Hagen's (1989; 1992) analysis of early ecologists' holistic ideas in terms of what G. Evelyn Hutchinson (1943; 1978, 214–15) called the *holological* perspective in ecology. The *holological* perspective, as characterized by Hutchinson and revisited by Hagen, is holistic in that it focuses attention on the functional interdependence of ecological phenomena and construes ecological systems mainly in terms of flows of materials that occur among their constituent organisms and populations. Its counterpart is what Hutchinson called the *merological* perspective, which construes ecological systems as assemblages of organisms and populations. For both Hagen and Hutchinson, these two perspectives should be regarded as complementary rather than in opposition.

According to Hagen, a key feature of the holological perspective is its "basically physiological" take on ecological systems (Hagen 1989, 435; see also 1992, 58–59). It sees these systems as achieving *physiological processes* similar to those accomplished by individual organisms. The physiological processes could be *development*, as in Clements's well-known theory of ecological succession (e.g. Clements 1916), *metabolism*, as in Hutchinson and others' works on biogeochemical cycles and energy circulation within ecosystems (e.g. Hutchinson 1941; E. P. Odum 1959), or even *homeostasis*, as in the works of other ecologists (e.g. Allee et al. 1949; E. P. Odum 1959). Importantly, the holological perspective, although holistic, involves no emergent evolutionist-like idea of ecological systems as organizational levels at which matter exhibits properties that are qualitatively different from those it expresses at lower levels. What it implies is that the processes carried out by these systems are the product of complex interactions among their components, just as the activities achieved by individual organisms result from the complex interactions of their parts. The complexity of the interactions suffices to make a study of the whole system necessary for understanding the processes it carries out. Furthermore, the interactive nature of the system implies that the activities of its components are in part determined by their interactions with other components of the system, such that these activities can only be understood in relation to their context of occurrence within the system.

Birge's shift from the study of crustacean zooplankton to that of gas circulation in lakes (see sect. 2 above) aligns with this picture. His goal of understanding the correlation between changes in lake temperature and changes in the distribution of zooplankton brought him to the study of the lake-wide gas circulation processes because explaining this correlation required an understanding of processes taking place at the lake level. And, as we have seen above (see section 3), this shift led him and Juday to assert "the existence of physiological processes in lakes" and to describe lakes as "physiological individuals of a higher order" (Birge and Juday 1911, xvii, xix).[14] Just as other ecologists of the time did for other ecological

[14] Scholars discussing Birge's works have typically emphasized their physiological orientation (e.g. Mortimer 1956, 203–4; Beckel 1987, 7; Ghilarov 1992, 24). Mortimer (1956, 203–4) situates Birge's holistic take on lakes with respect to two research outlooks influential in earlier limnology which his own approach synthesized: a *physical-geographical* approach epitomized by Forel's monograph on lac

processes, Birge came to link the lake-wide process of gas circulation he studied to a physiological concept, that of *respiration,* which may be regarded as falling under the broader concept of *metabolism*. The living organisms inhabiting lakes rely on this lake-wide process just as cells within an organism rely on the organism's acquisition of life-supporting gases from its environment, its transport of these gases to the cells, and its discharge of waste products to the environment.

Another key feature of the hological perspective is its focus on flows of materials and energy within ecological systems and its relegation to the background of those systems' constituent organisms and populations (see Hutchinson 1978, 215; Hagen 1989, 437). It aggregates these organisms and populations into more abstract units (e.g. trophic levels) and treats these units as black boxes into and out of which materials and energy circulate. What we saw above of Birge's approach concurs with this aspect of the hological perspective (as Hutchinson (1964, 334) himself notes). The particular types of organisms involved in lakes are not at the forefront in his account of lake respiration. He analytically breaks lakes down into more abstract components: the *epilimnion* and *hypolimnion*, dissolved oxygen and carbon dioxide, animal life, green plants, etc. As Clifford Mortimer (1956, 204) highlights, Birge's investigative strategy involved the identification of "integrating properties" which "record the end-result or the sum of the combined influences of an unmanageably large number of factors," and explanations of these properties in terms of "key processes which permit the investigator to by-pass the complexity and arrive at generalizations." Birge's papers on lake respiration concentrate on processes of circulation of *materials,* which explain properties such as concentrations of dissolved gases and distributions of animals. Processes of transfers of *energy* become a central topic in his and Juday's later works on the "heat" and "energy budget" of lakes (e.g. Birge 1915; Birge and Juday 1929; Juday 1940; 1942).[15]

Later in the twentieth century, the hological perspective became characteristic of ecosystem ecology as it took shape in the pioneering works of Hutchinson, his protégé Raymond Lindeman, and the brothers Eugene and Howard Odum (e.g. Hutchinson 1941; Lindeman 1942; H. T. Odum and Odum 1955; E. P. Odum 1959). As Frank Golley (1993, chap. 3) remarks, Hutchinson and Raymond Lindeman's foundational works in ecosystem ecology were in many respects extensions of Birge and Juday's (see also Pireddu 2023, 342–43). Like Birge and Juday's works, these works took lakes as their object, but, more importantly, they made the physiological outlook and the focus on flows of materials and energy initiated by Birge and Juday, among others, core features of ecosystem ecology. In so doing, they gave the discipline what was to become its distinctive orientations.[16] Later ecosystem ecologists' discussions of ecosystem metabolism can, in this respect, be regarded as further developments of Birge's ideas on lake respiration. And like Birge's, publications by ecosystem ecologists were peppered with parallels between ecological systems and organisms, which were meant to convey deeply-held views about the holistic character of these systems, but

Léman, which studied lakes primarily as geographical objects (Forel 1892), and a *biological* approach epitomized by Danish zoologist and limnologist Carl Wesenberg-Lund (1867-1955), which focused on studying individual organisms in their lacustrine ecological contexts (e.g. Wesenberg-Lund 1910). Birge showed support for the latter outlook, but he insisted that it had to be supplemented with a physiological one (see Birge and Juday 1911, xviii)

[15] On these latter works focused on energy circulation, see e.g. Frey (1963, 25–26, 39–42), McIntosh (1985, 96–97, 125, 156), and Golley (1993, 47–48).

[16] The concept of ecosystem was introduced by Arthur Tansley (1935), but Lindeman is generally credited for having actually put it into operation and, in so doing, laid the foundations for ecosystem ecology (see e.g. Hagen 1992, 90; Golley 1993, 50).

which were nevertheless usually intended as no more than analogies (e.g. E. P. Odum 1959, 257; Patten and Odum 1981, 888; see also Tansley 1935, 289–90).[17]

Discussing the holological perspective as it took form in ecosystem ecology, Donato Bergandi (1995, 167; 2011, 39–40) claims that its inborn physico-chemical reductionism makes it unsuited to being regarded as truly holistic. I would argue however that in the case of Birge at least, it is precisely the treatment of the physico-chemically-driven and biotically-controlled components of lake-wide processes as continuous with each other, in line with the holological perspective, that was the gateway to the view of lakes as unified wholes. Lakes were unified wholes, and not simply aggregates of organisms inhabiting a body of water, because they carry out processes that are the complex result of a multiplicity of interacting factors, some of which have a biotic basis and others an abiotic one.

Conclusion

Above, I discussed founding American limnologist Edward A. Birge's analogies between lakes and individual organisms. I showed how he used these analogies in analyzing an overall process he called "lake respiration," which consisted in transfers of life-sustaining gases between lakes and the atmosphere above them, as well as between the living organisms within them. I argued that Birge's use of these analogies involved no claim that lakes are *literally* organisms, but that it nevertheless reflected a view of lakes as holistic systems along the lines of what Hutchinson (1943; 1978, 214–15) and Hagen (1989; 1992) characterized as the holological perspective in ecology.

I noted above the continuity between Birge's holological take on lakes and that which later became characteristic of ecosystem ecology, as well as the similarity between Birge's and later ecosystem ecologists' analogical parallels between ecological systems and organisms. Discussants of the history of ecology often highlight a continuity between early ecologists' use of organismic analogies and the theoretical orientations of ecosystem ecology (see e.g. Richardson 1980, 468; Simberloff 1980, 27; McIntosh 1980, 21; 1985, 204; Hagen 1992, 48). This continuity, however, is usually interpreted as a historical connection with Clements's approaches and ideas in particular, while what I showed above suggests a less Clements-centered reading. My reading suggests that the continuity between ecosystem ecology's holistic orientations and earlier organismic analogies is a historical connection with sources that are more diverse in terms of their theoretical orientations and the ecological subfields to which they belonged. One of these sources is indeed Clements's views on succession as analogous to the development of an organism, but complementary sources may be found in other subfields where ecologists also made use of organismic analogies. What I presented above suggests, at least, that Birge's works on lake respiration, which prefigured the idea of a metabolism of ecological systems subsequently developed in ecosystem ecology, is one of them.

[17] Given this continuity between Lindeman's, and Birge and Juday's, works, it is one of the greatest irony of the history of ecology that Juday, acting as a referee for the manuscript that became Lindeman's foundational paper, recommended rejection of its publication (the other referee, who also recommended rejection, was Paul Welch of the University of Michigan). Importantly, however, Juday's dissatisfaction with Lindeman's manuscript did not pertain to its holological orientation. As historians have recollected, it stemmed from Juday's skepticism about the highly theoretical content of the manuscript and what appeared to him as sweeping generalizations based on insufficient data (Cook 1977; Hagen 1992, 94–97; Golley 1993, 53–54). These methodological disagreements do not diminish the important convergence between Birge, Juday, Lindeman, and subsequent ecosystem ecologists on an understanding of ecological systems that is in keeping with the holological perspective. For a more general picture of the methodological discrepancies between the Yale and Wisconsin schools of limnology respectively led by Hutchinson and Birge, see Beckel (1987, 23–25). .

Acknowledgements

The work for this paper was supported by research grants from the Fonds de recherche du Québec – Société et culture (FRQSC, 2024-PEC-335614), and the Ministère de l'Enseignement Supérieur du Québec, Programme d'aide à la diffusion des résultats de recherche au collégial (PADRRC, 13370). The author is thankful to Ghyslain Bolduc, Gene Cittadino, and Pier Luigi Pireddu for stimulating discussions and helpful comments. He also thanks Fabio Leite and Alice Everly for editing the manuscript. The content of this article remains the sole responsibility of the author.

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