

CONTRIBUTIONS

History of Ecological Sciences, Part 50: Formalizing Limnology, 1870s to 1920s

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Limnology is unique among sciences in having one scientist name, define, and write the first monograph, first survey, and first textbook of that science (Egerton 1962). Before Forel formally founded limnology, naturalist–philosopher Henry Thoreau had conducted a limnological study at Walden Pond (Egerton 2011:257–259), and others conducted studies that now could be called "limnological" (Beeton and Chandler 1963:542–544, Carlander et al. 1963:324–325, Eddy 1963:303–304, Fry and Legendre 1963:498–506, Pennak 1963:349, Yount 1963:269–270, Elster 1974:8–10, Steleanu 1989:26–99, 111–123), but isolated studies do not establish an organized science. Limnology is fortunate in having a general history of limnology (Steleanu 1989), and although it is heavily focused upon Europe, there is also a magnificent collaborative history of North American limnology (Frey 1963).

Europe

François Alphonse Forel (1841–1912) was born and died in Morges, west of Lausanne, on Lac Léman (Lake Geneva). His father, a distinguished jurist and historian of Switzerland, encouraged his son's interests in science (Blanc 1912, Egerton 1962, 1978, Bartola 1999, Vincent and Bertola 2012). He graduated in science at the Académie de Geneve, then studied medicine at Montpellier, before completing an M.D. degree at the University of Würzburg. In 1870 he joined the faculty of Académie de Lausanne, where he taught anatomy and physiology for 25 years. From the start, his scientific interests were broad, though tending to focus on Lac Léman (Berg 1951, Steleanu 1989:100–110). His bibliography, which he compiled (in Blanc 1912:133–148), lists 126 titles for limnology, 66 for glaciology, 12 for seismology, 19 for meteorology, 28 for natural history, 12 for archaeology, 10 for history, and 15 for biography. He published his first article on limnology in 1866. He named and defined limnology in the first volume of his *Le Léman* (1892–1904, I:vi [all Forel translations by F. N. Egerton]):

I have not been able to call my study limnography because the word limnograph is already appropriated for some instruments used in lake measurements; therefore I have coined limnology. Limnology, then is the oceanography of lakes.

Limnology began when Forel published "Introduction à l'étude de la faune profonde du Lac Léman" in 1869 (Lampert 1925:13, Allee et al. 1949:41, Steleanu 1989:191–196). That study was initiated by an accidental discovery: he wondered if the lake had bottom waves, and the device he used in attempting to find out emerged with mud adhering to it. He placed some of it under a microscope and found a white nematode. Later, he recalled (Forel 1892–1904, III:232–233)

That poor worm, a Mermis aquatilis, was a revelation for me. If one organism could live in that clay, in depths of 40 m, a perpetually cold region, far from littoral vegetation, others must be able to do so. If the ooze is inhabited down to the greatest depths, the profundal region is not a desert; there is an abyssal society.

That insight led to a new question: What do small fish eat in winter? Answer: "The mire of the lake, at great depths, is inhabited by a special fauna, rather rich in species and very numerous in individuals" (Forel 1869:217). He found animals at 300 meters, under 30 atmospheres of pressure, at a constant low temperature, no light, no waves. There was little flora below 20 m, and only a few diatoms at 75 m. He provided a preliminary list of profundal animals and acknowledged that Sars, Lindström, Carpenter, Huxley, and Pourtalès had found comparable animals at similar depths in oceans. Since Swiss lakes were isolated from oceans, profundal species must be related to species in shallow waters (Forel 1869:222)

...our lakes are isolated from the sea and are connected to each other only by surface drainage and that they have been filled relatively recently by glaciers from the last glacial epoch means the origin of the species of the profundal fauna and their differentiation goes back no further than this period in the history of the earth.

Forel proceeded to answer his own questions. In 1872 he outlined a decade-long research program, with costs. He wanted to determine the bottom topography of the lake, in both deep and shallow waters, profundal fauna and flora, lake temperatures, and study the deltas of the Rhone and Dranse Rivers. His subsequent profundal fauna studies included, besides Lac Léman, lakes Constance, Neuchâtel, and Zurich. His profundal studies lasted longer than a decade, culminating in *La faune profonde des lacs Suisse* (Forel 1884) and extended in "L'origine de la faune des poissons du Léman" (Forel 1901*a*). Forel's great monograph, *Le Léman*, three volumes, devoted two volumes to physical aspects of the lake. Volume 1 (Forel 1892) included geography, hydrography, geology, climate, and hydrology (sources and changes in water); volume 2 (1895) included hydraulics (seiches), temperature, optics, acoustics, and chemistry—an aquatic Humboldtian project. Volume 3 (1904) devoted over 400 pages to fauna, followed by human history, navigation, and fishing. In contrast to that encyclopedic work, Forel also published a concise *Handbuch der Seenkunde: Allgemein Limnologie* (Forel 1901, 1977), which summarized three decades of his research, placed in the larger context of contemporary investigations by others.

An even larger-scale survey of limnology than Forel's *Le Léman* was the *Bathymetrical Survey of the Scottish Fresh-water Lochs* (six volumes, 1910). This survey of 562 lochs, which followed a survey



Fig. 1. (a) François Alphonse Forel in his study– laboratory, Morges. By Ernest Biéler. (b) Water mite *Campognatha* (now *Hygrobates*) *foreli* from Lake Geneva benthos. Forel 1879. From Vincent and Bertola 2012:52, 54.



of saltwater lochs (1884–1891), was sponsored by the Royal Societies of London and Edinburgh and the British Association for the Advancement of Science, and supervised by John Murray (1841–1914), who is famous for participating in the voyage of the *Challenger* (1873–1876) and editing the 50-volume *Report on the Scientific Results* (Burstyn 1974, Price 2004), and conducted during 1897–1909. The general results are all in volume one, the other volumes being devoted to descriptions and maps of the lochs. Four of the articles in volume one, 163 pages, emphasized bio-limnology: James Murray, "Biology of the Scottish lochs," John Hewitt, "Some distinctive characters in the fresh-water plankton from various islands of the North and West Coasts of Scotland," William A. Cunnington, "On the nature and origin of fresh-water organisms," and C. Wesenberg-Lund, "Summary of our knowledge regarding various limnological problems," with the last article not being limited to biology. James Murray's survey was limited to invertebrates and microscopic algae, as the Scottish vertebrates were already well studied. John Murray contributed "Characteristics of lakes in general, and their distribution over the surface of the globe" (45 pages). Additionally, James Chumley compiled an impressive 95-page bibliography of limnology.

In Germany in 1891, E. Otto Zacharias (1846–1916) founded a Biologische Station on the Grossen Plöner See, at Plön, which opened 1 April 1892 (Thienemann 1917, Wetzel 2004). Also in 1891, he published a text, *Die Tier–und Pflanzenwelt des Süsswassers* (Leipzig), with contributions from other limnologists, including Forel. He was "an independent scholar and former teacher who supported the station from soft money grants and his earnings as a popular writer" (Nyhart 2009:321). In 1893 he began publishing an annual *Forschungsberichte aus der Biologischen Station zu Plön* (Chumley 1910:750–751), which evolved into *Archive für Hydrobiologie* (Elster 1974:9). Zacharias also published two more books on plankton in 1907 and 1909. Also in 1909, Bruno Eyferth and Alfred Kalberlah published their rather encyclopedic work on European fresh-water plankton.

In 1917, after Zacharias's death, the Biologische Station he had founded became affiliated with the

Kaiser Wilhelm Gesellschaft, under the excellent direction of August Thienemann (1882–1960), who had studied at Heidelberg under Robert Lauterborn (1869–1952), "Germany's leading river biologist" (Nyhart 2009:321). Thienemann joined the faculty of the University of Kiel, and eventually became Europe's leading limnologist (Thienemann 1959, Ohle 1961, Steleanu 1989:300–308, 385–404, Egerton 2008). He remained director at Plön for forty years and edited *Archiv für Hydrobiologie* for more than forty years.

In Sweden, Finnish immigrant fisheries manager Oscar Nordqvist (1858–1925) organized a Södra Sveriges fiskeriförening (South Sweden Fishery Association) in 1907, with laboratory at Aneboda (Söderqvist 1986:80). In summer 1910, Nordqvist hired two assistants at Aneboda, students Gunnar Alm (1891–1962), Uppsala University, who studied Ostracoid Crustacea and received his Ph.D. in 1915, and Einar Naumann (1891–1934), Lund University, who studied lake plankton and bottom fauna and received his Ph.D. in 1917 (Thienemann 1937, Söderqvist 1986:80–81, Steleanu 1989:382–385). Alm pursued a career in fisheries management and studied the biota and environment of lakes in relation to fish populations. Naumann became a leading European limnologist. In 1921 Thienemann traveled to Sweden and met Naumann. They developed a close working relationship (Stelleanu 1989:381–404), and Naumann suggested that they organize an international association. Thienemann agreed, and in January 1922 they sent a prospectus to 100 colleagues and got a very favorable response (Rodhe 1974, 1975, Steleanu 1989:405–411). A foundation meeting was held in August, and the Internationale Vereinigung für Limnologie (later, Societas Internationalis Limnologiae) was formed with 188 members in 23 countries, and at Thienemann's suggestion it published an annual *Verhandlungen*. Naumann was active in this society during the remaining 12 years of his life.

In 1907, C. A. Weber introduced the German terms for eutrophic (nährstoffreichere), mesotrophic (mittelreich) and oligotrophic (zuletzt nährstoffarme) regarding the chemical nature of the soil solution in German bogs (Hutchinson 1969:17, Rodhe 1969:50). Naumann became a leading limnologist who introduced Weber's concept, but with different terminology ("eutrophic" and "oligotrophic") into limnology to indicate poor or rich phytoplankton communities (Naumann 1919, Hutchinson 1969:17–18, Rohde 1969:50–51, Elster 1974:10). In 1921, Thienemann accepted Naumann's terms but applied them to clear lakes rather than phytoplankton and added "dystrophic" for lakes with brown, humic waters with little lime.

Frenchman Emile Gadeceau (1845–1928) of Nantes at age 16 participated in a field trip of the Société botanique de France at Nantes, which led to his becoming a disciple of English botanist James Lloyd (1810–1896), who had settled in Nantes (Desmond 1977:390, Perrein 1994:181). Lloyd had published *Flore Loire-inférieure* (1844) and *Flore de l'ouest de la France* (1854). In 1893 Gadeceau met Université de Montpellier plant geographer Charles Flahault (who is discussed in Egerton 2013:344–345) at a meeting of the Société botanique de France, held at Montpellier (Perrein 1994:187–188). They began to correspond, and Flahault became an important influence on Gadeceau. Flauhault (Flauhault 1900:444–445) introduced the term "écologiques" into French botanical discussion, and he wrote a preface for Gadeceau's *Le Lac de Grand-Lieu* (1909), which monograph won a prize from the Société Botanique de France.

Le Lac de Grand-Lieu is 13 kilometers south of Nantes, and Nantes is on the lower Loire River in

western France. According to the scale on Gadeceau's foldout map of the lake, it is roughly 6.5 km wide by 8 km long, but has a very irregular shape. Two small rivers, la Boulogne and l'Ognon, flow into the lake from the southwest and northwest respectively, and l'Acheneau River flows out at the northeast, to the Loire (Gadeceau 1909:17). In his introduction, he stated that he had access to James Lloyd's unpublished journal of observations, 1837–1889, and his own observations, 1879–1908, from all seasons, but mostly from summers. He also thanked a number of botanists and others who had assisted his research. His title page indicates that his book is a "monographie phytogeographique," but it does devote 11 pages to an inventory of the lake's birds, fish, and insects. The book's 120 pages of description and discussion are divided into three parts: geography, 30 pages (including 10 pages on animals); aquatic plants, 55 pages (7 pages on ecological influences, 48 pages of annotated plant list); and biological ecology (in three chapters: physiographic classification, ecological groups, and phytogeographic history).

Aside from Flahault (whose physiographic nomenclature, 1901, flora and vegetation of France, 1901 were cited), who influenced Gadeceau's thinking, observations, and organization of his monograph? His general bibliography (as opposed to his local sources) provides clues: Forel's *Le Léman* was obviously important, as also was Schröter and Kirchner's *Die Vegetation des Bodensees*, both parts, and two works by Ant. Magnin: "Les Lacs du Jura et notes additionnelles sur la limnologie juras-sienne" (1893) and *La vegetation des Lacs du Jura* (1904). The only British title he cited was the French translation of Darwin's *Origin of Species* (1887). He cited plant ecology works by Oscar Drude (in French translation, 1897), A. F. W. Schimper (1903, in English), and Eugene Warming (in German translation). He cited two articles by Henry Cowles in the *Botanical Gazette* (1899, 1901) and Conway MacMillan's "Observations on the distribution of plants along shore at Lake of the Woods" (1897). Gadeceau achieved a synthesis of his own and Lloyd's observations with the leading limnological–ecological literature of the day.

Cambridge University zoologist J. T. Saunders apparently taught the first course in hydrobiology in Britain, 1924–1925, and with W. Pearsall and algologist F. E. Finch, organized The Freshwater Biological Association, which established a station at Lake Windermere in 1926 (Jack 1945:43, Hiatt 1963:194, Slack 2010:see index). In 1901, Eustace Gurney had built a station on Sutton Broad, near Stalham (Juday 1910:1260, Kofoid 1910:166–168). Jack (Jack 1945:43–44) did not include either station in his survey of world stations around 1940. Hiatt (Hiatt 1963:194) cited the date of Windermere Laboratory founding as 1931—perhaps the date its current building was erected.

In July 1928, Thienemann, Austrian limnologist Franz Ruttner (1882–1961), director of the Biological Station at Lunz, and German zoologist H. J. Feuerborn embarked on an expedition to the Sunda Islands (Java, Sumatra, and Bali) for 10 months to collect plants, animals, water samples, and environmental data, believing that "only knowledge of the primordial, tropical conditions can give the scientist a deeper understanding of how life proceeds at our latitudes" (Thienemann 1959:129, translated in Rodhe 1974*b*:540). They studied lakes and running waters. Later, collaborating with over 100 European specialists, they described 1100 new species. They published their findings in 11 supplementary volumes to *Archiv für Hydrobiologie*, 1931–1958, entitled *Tropische Binnengewässer*, in 7920 text pages and 348 plates (Thienemann 1959:263). Ruttner provided hydrographic, physical, and chemical data for 15 lakes that could be correlated with their flora and fauna. That breadth of knowledge of temperate and tropical limnology enabled Ruttner to write an introductory textbook (1940) that was worth translating into English from the second and third German editions (Ruttner 1963), the textbook Art Hasler used to



Fig. 2 . (a) August (Friedrich) Thienemann. Web page. (b) Food web in a lake. Thienemann 1925:57. [Egerton 2007:60.]

teach me limnology in spring 1963. Despite detailed investigations, however, Thienemann and Ruttner evaluated productivity in tropical lakes somewhat differently, leaving it to later researchers to resolve the differences (Rodhe 1974*b*:545).

Perhaps Thienemann never saw the Illinois journal containing Stephen Forbes' "The lake as a microcosm" (Forbes 1887, reprinted 1925), yet Thienemann used the same word, "microcosm" to describe life in a lake, and he used the superorganism metaphor to describe interacting species. His lake researches led to three important generalizations, the first two from the 1920s:

- 1. The more variable the biotope (environmental) conditions, the greater the number of species in the biocenosis (biotic community);
- 2. The more biotope conditions deviate from optimal for most species, the smaller the number of species, but the greater the number of individuals of species represented;
- 3. The longer a locality retains the same conditions, the richer and more stable is its biocenosis.

Thienemann in 1926 first used the concepts of producers, consumers, and reducers to organize his biological data, and included a diagram that would influence Raymond L. Lindeman in his epochal "Trophic–Dynamic Aspect of Ecology" (1942) that cited this (1926) and two other Thienemann papers (Egerton 2007:60–61).

The earliest biological research stations were marine (Jack 1945:9–11). In 1910, two American aquatic biologists, Chancey Juday and Charles Kofoid (on both, see below), published—independently

of each other—illustrated surveys of European biological stations, freshwater and saltwater. Juday's was an article, Kofoid's a book. The earliest founding date Juday listed of 11 freshwater stations is 1888 for the Bohemian Portable Laboratory under Dr. Karl Fritsch, first located near several Bohemian lakes and later moved to the Elbe River (Juday 1910:1274). Zacharias' station at Plön may have been the earliest permanent freshwater station. In The Netherlands, several pleas before World War I for government to establish a hydrobiological laboratory (like other countries) were unsuccessful, and the Netherland's first notable advance was Professor H. J. Jordan's 1918 text on animal life in freshwater (Cramer 1987:68–70).

North America

Limnology in America began, like plant and animal ecology, in the upper Midwest. Stephen Forbes' "The Lake as a Microcosm" (1887) provided "the first concept of the limnological ecosystem" (Elster 1974:10; Hagen 1992:7-10, Golley 1993:36-37). In one respect, establishment of field stations, limnology was ahead of plant ecology and animal ecology (Kofoid 1898). In 1893, Jacob Reighard (1861–1942), with support from the Michigan Fish Commission, led a team in a biological survey of Lake St. Clair, located between Lakes Huron and Erie (Chandler 1963:98-99, Bocking 1987:81-91, 1990:478–495, Burgess 1996:91). In 1894 the survey moved to Traverse Bay, Lake Michigan. The two reports from these collaborations were substantial contributions (Reighard 1894, Ward 1896) which dealt with aquatic fauna, biota, and fisheries, but there were no funds for a third year. However, in 1898–1901, the U.S. Fish Commission funded Reighard and his team in a biological survey of Lake Erie, operating from the Fish Commission's Hatchery at Put-in-Bay, Ohio, and using the Hatchery's boats (Stuckey 1988, Bocking 1990:485–497). That survey produced a series of valuable reports. Ohio also had a fish hatchery at Put-in-Bay, to which Ohio State University provided funds to Prof. David S. Kellicott (1842-98) in 1896 to build a second floor for a Lake Erie biological station, which operated for two summers before Kellicott's death (Langlois 1949:1). Kellicott's successor at Ohio State was Herbert Osborn, who operated the station in that location, 1899–2 July 1903, in its own building until 1918, when it returned to the State Fish Hatchery (Langlois 1949:3-6). Now, it has separate facilities and is named Franz Theodore Stone Laboratory (Kofoid 1898:394-395, Gerking 1963:239).

Prof. Stephen Forbes, whom we met in part 45 (Egerton 2013*a*:72–73), established a University of Illinois Biological Research Station on the Illinois River at Havana (originally three rooms and a boat) in 1894 (Kofoid 1898:398–406, Bennett 1958:165–166, Gunning 1963:167–168, Bocking 1987:101–117, 1990:472–478). It was America's first research station on a river. By 1900, the University of Minnesota had a temporary station on a houseboat (Kohler 2002:68). Charles A. Kofoid (1865–1947), an Illinois native with a Harvard Ph.D., became head of the Havana station until 1900, when he joined the Department of Zoology at the University of California, Berkeley (Mullen 1973, Burgess 1996:62), and the Illinois station continues to conduct valuable research. Kofoid's specialty was plankton, and he was one of the very few who studied plankton in rivers. His publications on Illinois river plankton extended from 1897 to 1908, with his most substantial and general results appearing in 1903. By 1900, his studies extended throughout the Illinois River watershed

In 1895, German immigrant Carl Eigenmann (1863–1927), who had studied ichthyology under David Starr Jordan, established an Indiana University field station on Wawasee (earlier called Turkey) Lake, which was moved four years later to Winona Lake (Kofoid 1898:395–398, Frey 1955, Gerking

1963:239, 263, Shor 1971). The U.S. Fish Commission sponsored a physical and biological survey of Lake Maxinkuckee, in northern Indiana, 1899–1908, which was said to be "one of the most complete ecological surveys ever conducted" (Gerking 1963:263), though publication of the two-volume report was delayed (Evermann and Clark 1920).

Botanist Conway Macmillan had a University of Minnesota station at Gull Lake (Kohler 2002:51–52), but before 1900 another one opened at Lake Itasca in a state park (Hiatt 1954:181) and the Gull Lake one probably ended then.

Edward A. Birge (1851–1950), from Troy, New York, earned A.B. (1873) and A.M. (1875) degrees from Williams College in Massachusetts, then entered Harvard to work on a doctorate. Agassiz set him to work on the Museum of Comparative Zoology collection of sea urchins. Three months later, Agassiz died and Birge was saved from becoming a specialist on echinoderms. One of his professors at Williams was John Bascom, who soon became president of the University of Wisconsin. He invited Birge to become instructor in natural history and curator of the university cabinet (museum). Birge accepted and began teaching in January 1876. Later, he received time off to complete his doctorate at Harvard (1878), and he was promoted to professor at Madison in 1879 (Sellery 1956:4–14, Noland 1970, Beckel 1987:1–2, Egerton 1987:86–94, 1999*a*, Burgess 1996:16).

Like Forel, Birge began by studying aquatic invertebrates and later devoted the majority of his studies to lake environments (Juday and Hasler 1946:470–472, Mortimer 1956, Frey 1963:15–34, Steleanu 1989:279–299). His *Notes on Cladocera* (1878) was a standard zoological treatise, representing three years of work in both Cambridge, Massachusetts and in Madison, the published version of his Ph.D. dissertation. During subsequent research on plankton Crustacea he and his coauthors discovered (Birge et al. 1895:481–482)

During July, only the upper 12 m. of Lake Mendota are tenanted by crustacea, and over 90 per cent are in the upper 9 m. Nearly 50 per cent are in the upper 3 m.; 30 per cent between 3 and 6 m. and over 15 per cent between 6 and 9 m. There is, therefore, apparently an "abyssal" region with little crustacean life. This region is only temporarily unoccupied, being peopled by the crustacea later in the year, as the temperature of the lake falls.

This discovery marks Birge's transition from zoologist studying aquatic species to limnologist (Frey 1963*b*:16–18). What caused lake and crustacean stratification? Did it persist year round? To find out, he continued studies on Lake Mendota's Crustacea, July 1894–December 1896. The resulting monograph was the longest one Birge ever published as a single author (Birge 1898, 1977). The thermal stratification found in July lasted until surface waters cooled to nearly the deep water temperature in October, when surface winds caused the bottom and top waters to mix. The Crustacea then became more uniformly distributed. As the lake water cools during winter, the temperature from top to bottom remains about the same. In April, with the melting of ice on the lake, another mixing of the waters occurs, followed by the July–August stratification. In discussing the top-to-bottom temperature gradient formed in July, Birge introduced the term "thermocline" to describe the temperature curve on a graph, but did not offer at this time a formal definition (Birge 1898:287). However, he returned to the subject in 1904. Later he introduced two terms related to thermocline (Birge 1910*b*:1005, note)

I employ two new words in this paper, which seem convenient in writing of the temperature and other phenomena of lakes. These terms are epilimnion, for the warm layer of water which develops in the lake in summer, and hypolimnion, for the lower colder water. These two parts of the lake differ widely in their temperature changes, as well as in their chemical and biological phenomena. It seems advisable, therefore, to assign definite names to them. The word thermocline, first used by me in 1897, is the equivalent of Richter's term Sprungschicht, or the discontinuity layer of Wedderburn. It lies at the top of the hypolimnion.

Birge's bibliography (Birge 1910*b*:1014–15) cited three papers by E. M. Wedderburn, 1907–1908, but one must consult Birge's previous paper in the same volume (1910*a*:1000) for a citation to Eduard Richter's paper of 1897.

Birge's career resembled Stephen Forbes' career, with an accumulation of academic and government positions and responsibilities, but with little or no diminishing of research and publishing. He was Chairman of the Zoology Department (1875–



Fig. 3. Birge and Juday. Beckel 1987:cover.

1906), Dean of the College of Letters and Science (1891–1918), Acting University President (1900– 03), President (1918–25), Director of the Geological and Natural History Survey (1879–1919), and Commissioner of Fisheries (1895–1919). He needed an assistant, and in 1900 hired Chancey Juday (1871–1944), from Indiana, as biologist with the Survey (Frey 1963:4–6, Noland 1973, Beckel 1987:4–5, Burgess 1996:59–60, Egerton 1999). Juday had B.A. and M.A. degrees from Indiana University, where he had studied under Eigenmann. In 1908 Juday also became instructor in zoology at the University of Wisconsin, and in 1931, when he became professor of limnology, he resigned from the survey. Birge and Juday's first substantial collaboration was on dissolved gases in Wisconsin lakes (Birge and Juday 1911, 1977), which "is the single most outstanding single contribution of the Wisconsin school" (Mortimer 1956:188). The central question raised in this bulletin was why lakes differed so substantially in their ability to support plankton? Birge and Juday devoted the rest of their limnological careers to providing answers to such environmental questions. A major part of the answer was in their bulletin on the quantity and chemical composition of plankton (Birge and Juday 1922, 1977), followed by studies on penetration of sunlight into lake waters (listed in Juday and Hasler 1946).

Evelyn Hutchinson later evaluated Birge and Juday's achievement (Hutchinson 1969:109-110).





Birge's mature point of view is expressed in the concept of the heat budget, which, though derived from ideas of Forel and others, represented a highly original and important contribution because it first called attention in the lake as a natural system with an input and output. This point of view has tended to underlie most of what has been done in lake chemistry and in the study of primary productivity during the past three or four decades.

Since the University of Wisconsin-Madison is located on the shore of Lake Mendota (largest of five interconnected lakes), Birge and his collaborators first studied the limnology of Lake Mendota without establishing a biological station, making it (eventually) the most studied lake in the world. In 1925, they established a station at Trout Lake, in far northern Wisconsin, to facilitate comparative studies (Frey 1963:5).

Birge never supervised any doctoral students, but Harriet Bell Merrill (1863–1915) received from the University of Wisconsin in 1890 a B.S. degree, summa cum laude, and Birge nominally supervised her M.S. degree in 1893, with a thesis on Cladocera. (Hartridge 1997:ix–2). In reality, "the student was on his [or her] own to sink or swim" (Beckel 1983:18). After receiving her M.S. degree, Merrill then taught at the Milwaukee-Downer College, Cornell, and Chicago Universities, before returning to Madison. On 25 April 1901 she wrote to her cousin Nora Northrup (Hartridge 1997:2)

My work as an assistant professor is increasingly demanding with extra hours of lab for research as a result of "fishing" for Birge. He has developed a fine net, $1/20^{th}$ of millimeter gauge, which is used to gather crustacean from varying depths in the lakes.

She had obviously taken the position in the Zoology Department fairly recently, as her cousin Nora on 28 April 1901 lamented: "we thought you should remain at Downer as head of the science dept" (Hartridge 1997:4).

Why Merrill in 1902 went to South America, and alone, is unclear: "at age 39, Merrill seemed to experience a mid-life self-appraisal that unexpectedly prompted her to demonstrate an independent attitude in a man's world" (Hartridge 1997:xv). Her professional curiosity was possibly an excuse for the trip, 1902–1903, for her collections and notes during that trip were rather modest. However, that trip prepared her for her more serious trip to South America in 1907–1909, when her scientific journals ran to 14 notebooks, compared to one notebook in 1902–1903 (Hartridge 1997:185–190). She collected Cladocera and other invertebrates, and her samples and notebooks are preserved in the Milwaukee Public Museum. It might be more accurate to say her work was zoological than limnological, but it was done within a limnological context. She corresponded with Birge during her trips. One unknown species she collected was named for her. She was working on a Ph.D. at the University of Chicago in 1915, when she died, age 52.

Juday in February 1910 visited lakes in Guatemala and El Salvador, making "one of the first studies in tropical limnology" (Juday 1915; Frey 1963:6). Perhaps Merrill's successful collecting trip to Brazil encouraged Juday to take this trip.

Victor Shelford (1877–1968), whom we met in part 49 (Egerton 2014:69–71), was an animal ecologist whose researches included aquatic as well as terrestrial species. His *Animal Communities in Temperate America, as Illustrated in the Chicago Region* (1913) had more pages devoted to aquatic than to land animals. The chapter titles of his aquatic chapters were: (4) Conditions of Existence of Aquatic Animals, (5) Animal Communities of Large Lakes (Lake Michigan), (6) Animal Communities of Streams, (7) Animal Communities of Small Lakes, and (8) Animal Communities of Ponds. In addition, he also wrote two chapters on transition zones—(10) Animal Communities of the Tension Lines between Land and Water, (11) Animal Communities of Swamp and Flood-Plain Forest, that discussed amphibians and insect species that spend part of their life cycle in water and another part on land, as well as discussing terrestrial feeders that eat aquatic foods.

James G. Needham (1868–1957) participated in a limnological survey of Walnut Lake, Michigan in summer 1907 (Chandler 1963:99, Mallis 1971:174–178, Burgess 1996:80), then returned to Cornell University as Assistant Professor of Limnology, and since he studied freshwater insects, he joined the Department of Entomology (Berg 1963:209, Needham 1946.). In 1908 he began teaching a course in limnology. In 1914 when Professor Comstock retired as chairman of the Department, Needham succeeded him. *The Life of Inland Waters* (Needham and Lloyd 1916) was a well-illustrated, widely used introductory textbook of limnology, with a bibliography of English and German titles. Needham also served as president of the Entomological Society of America in 1919 and vice-president of ESA in 1936. However, it was Birge and Juday (Birge and Juday 1914, 1921) who initiated limnological research on the New York Finger Lakes, as that was beyond the scope of Cornell's limnologists.

Two years after Needham's textbook appeared, he and Birge were among 25 limnologists and zoologists who contributed chapters to *Fresh-Water Biology* (1918), edited by Henry Baldwin Ward





Fig. 5. (a) Victor E. Shelford, 1917. Croker 1991. (b) Food web for ponds in northern Illinois and Indiana. Shelford 1913:70. [Egerton 2007:54]

(1865–1945) and George Chandler Whipple (1866–1924). Ward was Professor of Zoology at the University of Illinois (Burgess 1996:109), and Whipple was retired Professor of Sanitary Engineering at both Harvard and M.I.T. The encyclopedic *Fresh-Water Biology* (1121 pages) is ostensibly limited in scope to the 48 contiguous United States, though it would have been of some use to Canadians and Mexicans. Its coverage includes bacteria, algae, vascular plants, and aquatic invertebrates, and is well illustrated, though not all species are illustrated. It does not cover aquatic vertebrates.



Fig. 6. *Conochilus unicornis* Rousselet. A. colony. x40. B. Single animal. x150. (After Weber.) Ward and Whipple 1918:616.



Fig. 7. University of Michigan Biological Station, Douglas Lake. Chandler 1963:101.

Another equally remarkable limnological collaboration was *Limnology in North America* (Frey 1963), with 26 chapters by 32 authors. This volume encompasses Canada, Alaska, Mexico, and the Caribbean Islands, as well as the contiguous 48 U.S. states. All chapters have ample bibliographies. Some chapters were used to write the above account on North America, but chapters not already used deserve notice here if they discussed the period 1870s–1920s. These chapters are discussed in their sequence in the volume. David Chandler's chapter, "Michigan," discussed more than Reighard's group surveys (see above). Reighard's own researches continued beyond those turn-of-the-century surveys, and he also helped plan a survey in 1908 that Thomas Hankinson performed at Walnut Lake to learn about whitefish reproduction, as guidance to a fish-stocking program. Reighard was chairman of the University of Michigan's Department of Zoology, and he also encouraged courses in ecology and limnology and establishment of a Biological Station at Douglas Lake, established in 1909, which encouraged limnological research and teaching (Chandler 1963:99–100).

John Brooks and Edward Deevey (1963) focused their 47-page chapter on the limnological features of New England that limnologists had discovered, but with only a bare mention of the limnologists as authors of the studies.

Gerald Gunning thoroughly explained, in 26 pages, the history of limnology in "Illinois" (1963), with brief mention of discoveries. He surveyed the limnological characteristics of Illinois in almost four pages, institutions that studied limnology in 2.5 pages, plankton studies, especially those by Kofoid (discussed above), in the Illinois River, in four pages, benthic studies in 5.5 pages, fish studies in 4.5 pages, miscellaneous studies in 1.5 pages, summary and bibliography in five pages.

Clifford Berg, at Cornell University, surveyed both limnological characteristics and limnologists who studied them in his 46-page "Middle Atlantic States" (1963), devoting six pages to the collective limnological characteristics of the states of New York, New Jersey, Pennsylvania, Maryland, and



Fig. 8. Manville: male student housing at Douglas Lake Biological Station. Photo by Gary Williams. Other student housing buildings were named Womanville and Blissville.

Delaware, almost 17 pages to institutions and limnological studies of New York, 6.75 pages to those of Pennsylvania, 5 pages to those of New Jersey, 1.3 pages to those of Delaware, and 5.4 pages to those of Maryland.

James Yount's 17-page chapter was "South Atlantic States" (1963), but unlike Berg, he did not provide a state-by-state account. Rather, he included a map of Virginia, North and South Carolina, Georgia, and Florida on which was imposed the boundaries of three zones: Mountains, Piedmont, and Coastal Plains, though he subdivided the last into Dismal Swamp, Carolina Bays, Florida Springs Region, and South Florida. His map also identified ecological field stations (mostly in Florida), yet he identified none in the Piedmont (Duke University Forest could have been identified). Yount focused upon limnology, but also discussed briefly those investigators whose works he used. However, very few of his references were published during 1870–1929.

Walter Moore's 14-page chapter on "Central Gulf States and the Mississippi Embayment" (1963) was divided into two parts: "Limnological Resources" and "Major areas of limnological activity." The latter part briefly discusses both investigators and their findings. I only found five of his references that were published before 1930.

Samuel Eddy's 29-page "Minnesota and the Dakotas: (1963), was mostly about Minnesota, because he only found four publications specifically on limnology in North or South Dakota. However, since North Dakota and Minnesota are both bordered by the Red River, any Minnesota study on that river would also be relevant to North Dakota. Eddy traced the history of limnological investigations from the founding of the Minnesota Geological and Natural History Survey in 1872. Very few early studies focused on water physics and chemistry; they were almost entirely faunal surveys, but these ended in 1910. A few limnological studies were made at the University of Minnesota during the 1920s.



Fig. 9. (a) Thomas Macbride.[Iowa Lakeside Laboratory history website] (b) Map of West Okoboji Lake, showing Iowa Lakeside Laboratory (on west shore). Lannoo 2012:17.

Kenneth Carlander, Iowa State University, Robert Campbell, University of Missouri, and William Irwin, Oklahoma State University, collaborated on a 32-page "Mid-Continent States" (1963), which encompassed their states plus Kansas and Nebraska. Their physiographic map of those five states also indicated the locations of 14 aquatic biology research centers. Only one laboratory, that of the U.S. Fisheries, was located on the Mississippi River. These authors divided their chapter into sections on bodies of water: river systems (6.5 pages), reservoirs (3.5 pages), prairie lakes (0.55 pages), glacial lakes (3.5 pages), and miscellaneous (2.3 pages). Under glacial lakes, Carlander described the Iowa Lakeside Laboratory, on West Okoboji Lake, which Botany Professor Thomas Macbride (1848–1934), University of Iowa, established in 1909; Michael Lannoo has since told the story of this laboratory in more detail (1996, 2012). The laboratory's attractive stone buildings were erected in the 1930s.

Robert Pennak wrote 21 pages on five "Rocky Mountain States" (1963). He could cite three limnological studies from 1889, 1891, and 1901, but nevertheless acknowledged that this vast region, extending across Colorado, Utah, Wyoming, Idaho, and Montana (517,000 square miles, 1,341,000 km²), was limnologically poorly known. There were biological field stations in these states, which he described briefly, though none were exclusively limnological. There is now more known about those stations than in 1963 (Vetter 2011, 2012), but later studies do not indicate whether limnological studies were significant at any stations.

W. T. Edmondson wrote 22 pages on the three westernmost states and Nevada (1963), which spanned North America's greatest desert, its highest mountains, major rivers, and the Pacific Coast. The earliest limnological studies he found were two in the 1880s, one 1907–1913, and another in 1910–1913, and only four more in the 1920s.

Gerald Cole (1963) surveyed the limnology of Arizona, New Mexico, Texas, and Middle America (Mexico + Central America) in 42 pages—the second longest chapter after the first of two lengthy chapters on Wisconsin (Frey 1963). One map showed all of the important rivers in the three U.S. states, and another map showed all the important lakes in Mexico and Central America. Cole subdivided 9 pages of his chapter by political territories: Texas, New Mexico, Arizona, Mexico, and all the Central American countries. For Costa Rica, Cole wrote only one brief paragraph, with two citations, 1952, 1960, admitting that very little was known about its limnology. Surprisingly, his two paragraphs on Panama were only slightly longer than the one on Costa Rica, and he only had one limnological citation for Panama (1951), despite the fact that America had occupied Panama since 1903, and there was an American field station on Barro Colorado Island in the Canal Zone. Next, Cole devoted 28 pages to different kinds of freshwaters within his geographical survey: extinct lake basins, volcanic lakes, high altitude lakes, cenotes, irrigation ditches, ponds, and more.

The chapter on Ontario and Quebec was written by F. E. J. Fry (on Ontario, 8.25 pages), and by Vianney Legendre, (on Quebec, 25 pages). Fry cited publications from 1892, 1911, 1922, and 1928, and he conveyed concisely the development of limnology during those years. Legendre was rather encyclopedic in his survey, beginning with Jean Cabot in 1497, but devoted only 4.5 pages to the period 1870–1920s, briefly discussing investigators, organizations, and literature.

Alfred Beeton and David Chandler discussed "The St. Lawrence Great Lakes" in 24 pages, beginning with limnological features, but then a chronological survey of the activities, institutions, and literature, with 3.5 pages for our period. Both authors were at the University of Michigan, and they knew the American literature better than the Canadian literature. However, they did state (Beeton and Chandler 1963:545):

The Biological Board [of Canada] maintained the Georgian Bay Biological Station from 1901 to 1914. Results of most of the work at the station were published in a single volume and included, among others, papers by B. A. Benslely on fishes, G. O. Sars on Entomostraca, E. M. Walker on Odonata, and Wilbert A. Clemens on Ephemeridae (Prince 1915).

Kenneth Johnstone (1977:46–51) provided a brief chapter on this Georgian Bay Station, at Go Home Bay. The Madawaska Club at the University of Toronto petitioned the Canadian Ministry of Fisheries in fall 1900 to support such a station, and since bass propagation was listed as one of its proposed projects, the Ministry provided \$1500 a year for it, beginning in 1901. Since there was little equipment available that first year, very few of the projects planned by Professor E(dward) E(rnest) Prince (1858–1936) were completed that summer. In 1902, a reference collection of fishes, birds, mammals, and plants was developed, meteorological data collection began, a hydrographic survey of the vicinity was achieved. The station never attracted more than a few investigators, and its best season was in 1912, when it obtained a motorboat. The station closed in 1913 because Ontario and the University of Toronto took

over responsibilities begun by the Canadian Ministry of Fisheries, which transferred its resources to its Atlantic facilities.

Conclusions

For those who live near bodies of water, aquatic environments can become objects of fascination. François Forel lived his whole life on the shores of beautiful Lac Léman (Lake Geneva), and his love of nature focused on its aquatic world. There, he developed the vision and initiative to organize a science that he called "limnologie." Yet there were also others who shared his enthusiasm, both in Europe and in America. The limnologically inclined sometimes obtained biological stations like those marine biologists and oceanographers had already built. A conspicuous European example was Otto Zacharias' Hydrobiologische Anstalt at Grossen Plöner See in 1891, which became the headquarters for August Thienemann in 1917, Europe's leading limnologist in the time after Forel. Naumann and Thienemann organized the Internationale Vereinigung für Limnologie (1922).

In America, Forbes limnological publications included a memorable essay, "The Lake as a Microcosm" (1887). He built a University of Illinois station on the Illinois River (1894), where Charles Kofoid began his impressive career. At the University of Wisconsin, Edward Birge, a decade younger than Forel, followed his example of living and working on a lake without a biological station, since the university served as one. Also like Forel, he began his studies with aquatic invertebrates, then spent much of his career documenting properties of the aquatic environment. Unlike Forel, however, Birge acquired a faithful partner, Chancey Juday, who coauthored most of Birge's publications. *Limnology in North America* (1963) included much collective evidence about the flourishing of American limnology during the 1870s–1920s.

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