Part 57: Aspects of Limnology in America, 1930s to about 1990, Led by Hutchinson and Hasler

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Part 50 described the founding of limnology and its worldwide development, from 1870s to 1920s (Egerton 2014*a*). E. A. Birge and Chancy Juday in Wisconsin and August Thienemann in Germany remained active after the 1920s (Juday and Hasler 1946:472–480, Thienemann 1959:78–489, Frey 1963*b*, Elster 1974:13–19, Egerton 2008*b*, 2015*a*:37–39), but their stories are not continued here, though their influence is mentioned. I am unable to survey fully the history of all American limnology, 1930–1990, but here are aspects of it. The detailed *Limnology in North America* (Frey 1963*a*) is a valuable resource for part of this period and includes Canada, Mexico, and the Caribbean Islands. It is mostly a survey of American limnological knowledge, not history of limnological science. Three directories of biological stations, compiled by U.S. biologists, are useful, though marine stations outnumber freshwater ones: Homer Jack (1945), *Biological Field Stations of the World* is quite brief and includes a few stations not aquatically focused; Robert Hiatt (1954), *Directory of Hydrobiological Laboratories and Personnel in North America* is the most detailed; Hiatt (1963), *World Directory of Hydrobiological and Fisheries Institutions*. The American Institute of Biological Sciences (2010) has reprinted from *BioScience* a booklet (ii + 72 pages) of articles—one from 2002, six from 2009—of historical relevance, entitled *Topics in Biological Field Stations*. Laura Tydecks et al. (2016) compiled worldwide data on biological field stations and have published a summary of their findings, giving a web site for the details. “Mac” McIntosh (1985:124–127) briefly surveyed history of limnology in The Background of Ecology, four pages of which concern the period of this part 57.

Part 57 uses the careers of G(eorge) Evelyn Hutchinson (1903–1991) and Arthur D(avis) Hasler (1908–2001) to illustrate pathways in American limnology, 1930–1990. Hutchinson’s contributions to population ecology were briefly described in part 55 (Egerton 2015*b*:595). He was a leading ecologist of the 1900s and Hasler was the illustrious head of limnology at the University of Wisconsin-Madison. A survey of Hutchinson’s contributions to limnology is facilitated by his own autobiographical *The Kindly Fruits of the Earth* (1979), Nancy Slack’s excellent biography (2010), and by an anthology of Hutchinson’s most notable publications (Hutchinson 2010). For Hasler, there is his own survey of Wisconsin limnology, 1940–1961 (Hasler 1963*a*), a volume commemorating a century of limnology at the University of Wisconsin-Madison (Beckel 1987:31–56, + illustrations on 63–74, Egerton 1987*a*), a biographical memoir for the National Academy of Sciences (Likens 2002), and two biographical summaries (Carpenter and Kitchell 2001, Egerton 2008*a*). Hutchinson (1947–1948) and Hasler (1949–1950) served as presidents of a newly organized American Society of Limnology and Oceanography, and they were the first limnologists elected to the National Academy of Sciences. Hasler was ESA president in 1961.

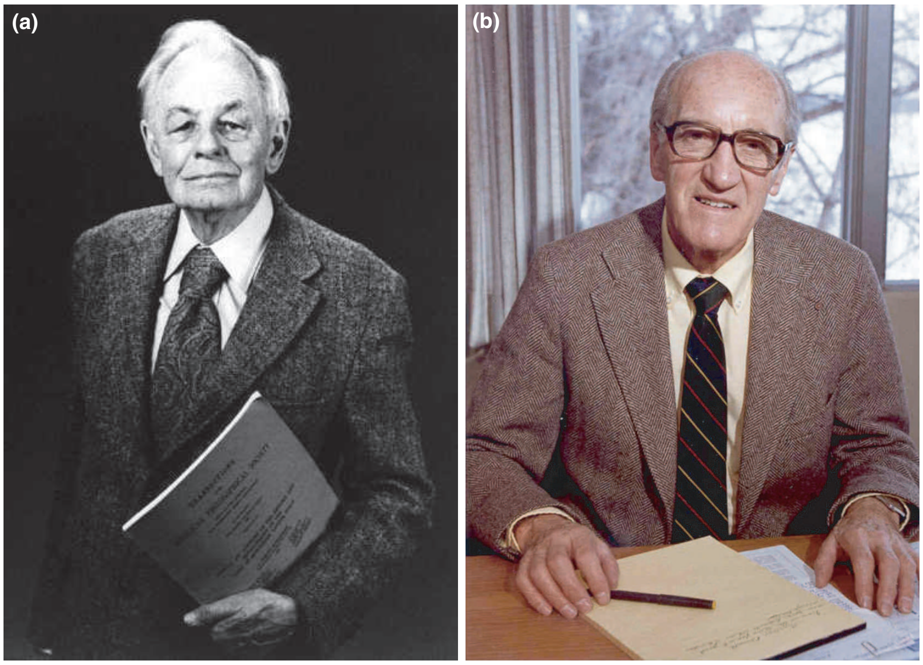


Fig. 1. (a) G. Evelyn Hutchinson in 1935. Wikipedia.
(b) Arthur D. Hasler. Courtesy Center for Limnology, UW-Madison.

Hutchinson and his students at New England

Hutchinson's father was an outstanding mineralogist at the Cambridge University who taught Evelyn about the mineralogy, geology, and flora of Cambridgeshire, and his progressive mother wrote a book, *Creative Sex* (1936; Burgess 1996:56–57, Slobodkin and Slack 1999, Slack 2010:17–22, Egerton 2015*a*:40–42). Evelyn became interested in aquatic animals by age of six, and he won a school prize, a book on insects by Jean Henri Fabre (Slack 2010:22, 138). He also led a Cambridge junior natural history society, and at age 15, he published a note on a swimming grasshopper (1918). His particular interest became aquatic insects (Slack 2010:34). At Cambridge University, he received a prize in zoology, and a B.A. degree, in 1925. He later published his evaluations of the Cambridge zoologists and other scientists he knew there (1979:87–101). He explained that a M.A. degree was awarded after further work in one's field (awarded to him in 1928), and with further publishing, he could have obtained a doctorate by paying a fee, but declined to do so. The zoologist who most influenced Hutchinson was his next-door neighbor, George P. Bidder, whom he had known all his life, and who studied sponges (Slack 2010:50). Bidder's sponge course introduced ecological questions concerning the sponges' environments. Hutchinson also took J. T. Saunders' excellent course on hydrobiology, which covered both limnology and oceanography (Slack 2010:54). When later asked why Hutchinson had stood out as an undergraduate, English limnologist Penelope Jenkin replied it was because of his encyclopedic memory that stored readings since his childhood (Slack 2010:61).

After graduating, a Rockefeller Fellowship enabled him to go to the Stazione Zoologica in Naples to investigate a possible endocrine gland in the octopus. It was not a fruitful investigation—he blamed a scarcity of octopi—but, he managed to publish a tentative article (1928, Slack 2010:70). He applied for and received a two-year lectureship at the University of Witwatersrand in Johannesburg. It was a great chance to study an exotic fauna. However, his research at the University was not on lions or zebras, but on the temperature tolerance and dispersal of South African water bugs, of which there were only 14 species known when he arrived, but 40 known when he left (1929, Slack 2010:74–75). His fiancée, Grace Pickford, after graduating from the Newnham College, Cambridge University, received a Newnham College Traveling Fellowship to travel and study in South Africa, 1925–1927, and they married in Cape Town. Pickford, who kept her maiden name, had also studied under Saunders. After they married, she collaborated with him in his South African research, leading to a half dozen or so scientific articles (with her name only on two as coauthor; Hutchinson 2010:326–327). The substantial article in which they collaborated with J. F. M. Schuurman, on the hydrobiology of pans and other inland waters of South Africa (Hutchinson et al. 1932), was Hutchinson's first important contribution to limnology (W. T. Edmondson, quoted in Slack 2010:117). It was also pioneering work beyond the temperate environments of Europe and North America, simultaneous with Thienemann's first limnological investigations of tropical lakes (Rodhe 1974, Egerton 2008*b*:36–37). In 1928, after reading Thienemann's *Die Binnengewässer Mitteleuropas* (1925), Hutchinson realized that his recent investigations had led him to become a limnologist (Hutchinson 1979:208).

Hutchinson obtained a lectureship at the Yale University in 1928. Pickford had no position when they arrived in September, but she worked on a Ph.D., and eventually they both became professors of zoology at Yale, though their marriage ended in 1933 (Slack 2010:202–205). Ironically, she became an authority on the octopus after he divorced her. Hutchinson became Yale's first ecologist, and he taught limnology, and in 1936 began teaching an ecology course which Russian entomologist-arachnologist Alexander Petrunkevitch previously taught as natural history (Slack 2010:91–92, 99). The chairman of the Department of Zoology, Ross G. Harrison, became an important mentor for Hutchinson (Hutchinson 1979:214–219, Slack 2010:92–97). In 1932, Yale sponsored an expedition to the Himalayan Mountains in the Ladakh region of Kashmir, India, which had never been explored by scientists. Hutchinson became the expedition zoologist, and he collected macroscopic fauna from lakes over 17,000 feet elevation, along with chemical and physical data on the lake waters. He sent specimens to specialists in America, Europe, and India to identify and name, and he published three scientific papers and a book, *The Clear Mirror* (1936), on his discoveries and experiences (Hutchinson 2010:327, Slack 2010:100–114, 434–435). It is an odd book, but odd in a characteristic way. Pages 3–96 are a sort of learned anthropological travelog, describing people, buildings (mostly religious), and ceremonies; pages 104–153, entitled "Lakes in the Desert," are his observations of the barren high elevations, with its few people and its glacial lakes, in northern Kashmir. This latter part emphasizes limnology and geology, but discusses some terrestrial ecology. An end note explains that the natural history material appeared in another form in three articles in the *Memoirs of the Connecticut Academy of Arts and Sciences*. He had a valuable opportunity to compare the limnology of desert lakes in South Africa and India, which he neatly summarized on one page for *Nature* (1933). "Although short, this paper highlights Hutchinson's early capacity to approach lakes from multiple perspectives" (Post and Schindler 2010:84).

Water bugs, a childhood interest of Hutchinson, were the main focus of his research in South Africa. Since Hutchinson was the world's authority on water bugs, the British Museum in 1930 sent to him at Yale 723 specimens to identify. Hutchinson expanded his interests as he progressed through life, but he seldom, if ever, abandoned an earlier interest. As late as 1981, he published a lifetime of "Thoughts on aquatic insects," with new generalizations, showing that he remained the world's authority (Hutchinson 1981).

Hutchinson's greatest influences came from his numerous publications and from mentoring his outstanding graduate students (Edmondson 1971, Kohn 1971). By 1971, when he retired, he had supervised 34 completed doctoral dissertations; five others were in preparation; and he had had a strong influence on nine other dissertations (Anonymous 1971). Not all of his illustrious graduate students studied limnology, and this survey only discusses some who did.

Growing up for Tommy Edmondson (1916–2000) was similar to Hutchinson's in one respect: he also grew up in the city where he would go to college, and he became acquainted with some of its zoologists before entering college; in his case, that was Yale University (Burgess 1996:38, Egerton 2015*a*:49). His high school biology teacher took him to a Yale lecture, and afterwards he met Hutchinson and they discussed Edmondson's interest in rotifers (Slack 2010:115–117). After Hutchinson returned from Ladakh, he turned over to Edmondson his rotifers to describe (while Edmondson was still in high school), which Edmondson did (Edmondson and Hutchinson 1934). Although not limiting his interests to rotifers, Edmondson continued studying them and became the world's authority on them. After earning his B.S. at Yale in 1936, on Hutchinson's recommendation, he went to the University of Wisconsin for the school year 1938–1939, where he took Juday's limnology course and met Yvette Hardman, whom he later married. In Wisconsin, Edmondson collected sessile rotifers and used the extensive data collected by Birge

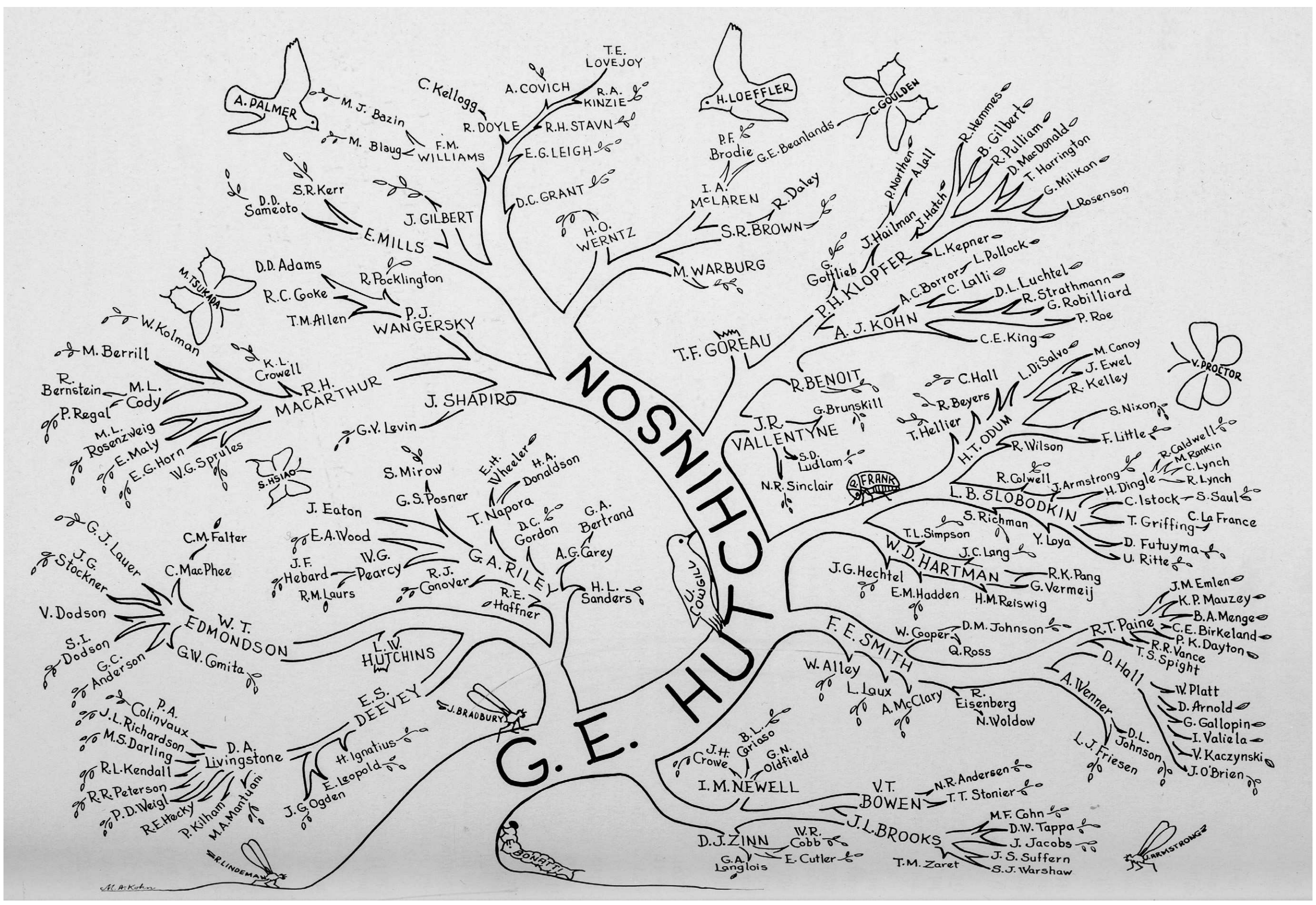


Fig. 2. Hutchinson's family tree of intellectual descendants to 1971. By Marion Kohn. Edmondson (1971:163). Courtesy John Wiley and Sons.

and Juday on Wisconsin lakes "to examine the relative significance of calcium concentration, bicarbonate concentration, and pH as measures of alkalinity" (Hutchinson 1988:1231). He then returned to Yale and wrote a dissertation under Hutchinson, and obtained his Ph.D. in 1942. After teaching at Harvard and at the Woods Hole Oceanographic Institution, Edmondson moved to the University of Washington in 1949, where he and Yvette spent the rest of their productive careers (she became editor of *Limnology and Oceanography*). He became best known for restoration of Lake Washington.

Gordon A. Riley (1911–1985) became Hutchinson's first graduate student, after obtaining his M.S. degree from Washington University in St. Louis in 1934 (Burgess 1996:92, Egerton 2015*a*:42–43). He had come to Yale to study experimental embryology, but after attending Hutchinson's course in limnology, he asked Hutchinson to accept him as a graduate student (Slack 2010:121–124). Since Riley had a solid background in chemistry, Hutchinson asked him to write a dissertation on the copper cycle in the Connecticut lakes. Copper is essential for the blood of crustaceans. Riley and Hutchinson went out on Saturday mornings to collect lake water—using the same rubber boat Hutchinson had used in Ladakh—and in the afternoons, Riley analyzed the water for copper while Hutchinson analyzed for phosphorus and nitrogen. One summer, undergrad Edmondson assisted Riley in his collections because Hutchinson was in England. In March 1937, Riley went on an oceanographic cruise in the Gulf of Mexico as a water chemist—the first time he had ever been to sea. "The limnological methods he had pioneered worked fine for oceanography" (Slack 2010:126). After receiving his Ph.D. degree in 1937, he accepted a post-doc fellowship at Yale and studied photosynthesis and respiration in phytoplankton at Linsley Pond, where he had done much of his previous research. When he wrote up his findings, Juday was editor of *Ecological Monographs*, and he agreed to publish Riley's data, but not his statistical analysis (Riley 1939). Riley published his statistical analysis in a new *Journal of Marine Research*, and he pursued his productive career in oceanography at the Dalhousie University. Later, Riley recalled that Hutchinson "had inspired students with an almost euphoric feeling about science, and we were drawn to him with utter fascination" (Riley 1971:178). Even later, he reflected that (quoted in Slack 2010:127):

> *I am deeply indebted to Evelyn for introducing me to his own scientific philosophy about ecology, which was ahead of its time and has permeated all my plankton work. He maintained that populations needed to be studied in terms of dynamic processes—rates of production and consumption and the way these are affected by ecological factors.*

Riley's career shows how easily an American ecologist might move between limnology and biological oceanography (Slack 2010:142).

Edward S. Deevey, Jr. (1914–1988) was Hutchinson's second graduate student (Burgess 1996:36, Slack 2010:128–132, Egerton 2015*a*:115). He received his B.A. degree in biology from Yale in 1934, with his main interest in botany. However, he wanted to study the history of Linsley Pond by taking cores from the bottom. No one in the Botany Department was interested in that (until he got his cores), but Hutchinson was, and so Deevey worked under him. Linsley Pond, like Walden Pond, qualifies as a lake in current terminology (photo in Hutchinson 1941*b*:24). Deevey studied paleobotany using pollen grains in the cores and paleozoology using fossil fauna in two Connecticut lakes. This was in the 1930s, before radiocarbon dating became available. In 1946, a vacancy became available at Yale, and he remained there for the rest of his career. He and Hutchinson adopted radiocarbon dating when that method became available, and Deevey got a grant to establish a Yale Geochrometric Laboratory in 1951.

Fig. 3. Linsley Pond, near New Haven, Connecticut. Courtesy Connecticut Agricultural Experiment Station.

Limnologists Birge and Juday had studied extensively the stratification of temperature and oxygen in Wisconsin lakes (Egerton 2014*a*). One might expect that studies on lake distribution of other elements would merely show that those elements followed the same or similar patterns. However, that was not what Hutchinson and his associates found at Linsley Pond. They studied the distribution of alkalinity (bicarbonate ion) in the hypolimnion and found that that water interacted chemically with the bottom mud, when its water was stirred by epilimnion movement from wind, but without the waters in the two layers mixing (Hutchinson 1938). Hutchinson then wondered what one might learn by following the paths of other elements in the aquatic environment. He built upon this study in the first two parts of his 40-page article on "mechanisms of intermediary metabolism in stratified lakes" (1941*b*), in which he again emphasized the bottom mud as a source for hypolimnion alkalinity (Hutchinson 1941*b*:39–40). This highly mathematical article may have been an intimidating shock to descriptive ecologists of that time, and a hint to ecology students to take as many mathematics courses as they could manage. The third part is on "The Phosphorus Cycle in Linsley Pond." Hutchinson used the methods Juday and Birge (1931) had used in their own studies on lake phosphates. He also compared his findings at Linsley Pond to theirs from Lake Mendota. On the occasion of the opening of the University of Wisconsin's Laboratory of Limnology, Hutchinson talked on "The lacustrine microcosm reconsidered" (1963, published 1964) and took as his starting point publications by Birge and Juday and by Forbes.

Raymond L. Lindeman (1915–1942) received his Ph.D. from the University of Minnesota in March 1941 and came to work under Hutchinson on a post-doc grant in September 1941 (Cook

1977:22, Reif 1986, Burgess 1996:66). Lindeman had already become familiar with Hutchinson publications while in Minnesota, and so their meeting of minds went smoothly from the start—which was fortunate since Lindeman died about 10 months later, on 29 June 42. Lindeman (1941) published a couple of papers based upon his Ph.D. dissertation, but he is remembered mainly for "The trophic dynamic aspect of ecology" (1942). Its starting point was the last chapter of his dissertation, and it represents Lindeman's broad synthesis of his own, Hutchinson's, Thienemann's, Juday's, Elton's, Tansley's, and others' ideas. An introductory statement to Lindeman's article summarizes the scope of its discussion: "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" (1942:157). He had studied the succession of shallow lakes to marshes and then to land. This article is often seen as the beginning of a "new ecology:" more dynamic, quantitative, ecosystemic, theoretical, and less descriptive than the "old." It was too theoretical for two referees for *Ecology* (Juday and Welch), who turned it down, but Hutchinson prevailed in having *Ecology* publish Lindeman's posthumous article (Cook 1977:23–24, Golley 1993:48–52; Hagen 1992). Lindeman's 1942 article had implications far beyond its limnological context, but that was its context.

On June 21, 1946, Hutchinson had a sample of radiophosphorus (P^{32}) that was introduced into Linsley Pond, in 24 parts, distributed across the lake. He was assisted by graduate student Vaughn Bowen, who was also Hutchinson's research assistant. This is the first known experiment in nature using radioisotope tracers (Slack 2010:159). They returned to Linsley Pond a week later and collected water samples from four depth layers (Hutchinson and Bowen 1947:149). Previous studies indicated, indirectly, that "there is a continual liberation of phosphorus from the mud into the free water." (Hutchinson and Bowen 1947:148). What they now found was that "phosphorus has entered the epilimnion during a period when there can have been practically no vertical mixing," and "Of the 25.8% of the P^{32} put into the lake and not recovered, the greater part had probably entered the aquatic plants and sediments in contact with the 0–3 m. layer" (Hutchinson and Bowen 1947:152). Later, he noted "Rigler's extraordinary discovery (1956, 1964) that the turnover time of ionic phosphorus in the epilimnion of a lake in summer can be of the order of 1 minute." (Hutchinson 1969:19).

H(oward) T(homas) Odum, like Hutchinson, was son of a prominent university professor; he was also the younger brother of ecologist Eugene Odum (Hall 1995, Burgess 1996:82, Brown and Hall 2004, Egerton 2015*a*:99–102). During World War II, H.T. served in the Air Force "as a tropical meteorologist, where undoubtedly he gained his basic interest in large systems and the energetics behind them" (Brown, Hall and Jorgensen 2004:4). After graduating from the University of North Carolina, he went to graduate school at Yale and worked under Hutchinson for his Ph.D. Hutchinson (1943) had published a thorough analysis of the "Biogeochemistry of aluminum and certain related elements" which provided an example of an analysis for comparable studies on other rare elements. It seems likely that Hutchinson suggested to Odum that he do his dissertation research on the strontium cycle (Limburg 2004:31). Odum's dissertation was entitled *The Biogeochemistry of Strontium* (1950), and he published afterwards two articles from it in *Science* (Odum 1951*a*,*b*).

Hutchinson's "Copepodology for the ornithologist" is not about waterbirds transferring copepods from one pond to another on their feet, as I expected. Rather, his misleading title refers to a parallel dynamic of bird and copepod evolution (Hutchinson 1951:573):

> *The role of size differences in permitting the coexistence of closely allied species of birds and mammals has been stressed by Huxley (1942:280–281) and Lack (1944). Brooks (1950a) has employed the same idea in his interpretation of the distribution of Odontogammarus in Lake Baikal. It is obviously possible that in invertebrates with little metamorphosis and prolonged life histories, competition of adults of the smaller species with sub-adults of the larger species may produce complications. In spite of this and perhaps other difficulties, the existence of size differences seems to one way by which sympatric species of restricted groups of planktonic animals can exist under conditions in which, in general, competition might be supposed inevitably to eliminate one form.*

This paragraph is an early example of Hutchinson's theoretical thinking.

Hutchinson proved himself as a talented limnologist in a wide variety of investigations, and his *Treatise on Limnology* (four volumes, 1957–1993) is probably the longest treatise in ecology published by one person (Slack 2010:151–155); it exceeds François Alphonse Forel's achievement in *Le Léman* (three volumes, 1892–1904), the longest treatise written by one person on one lake (Lake Geneva). Hutchinson's *Treatise* has thematic volumes: (1) *Geography, Physics, Chemistry* (xiv + 1015 pages, 1957), (2) *Lake Biology and Limnoplankton* (xi + 1115 pages, 1967), (3) *Limnological Botany* (xi + 660 pages, 1975), and (4) *Zoobenthos* (xi + 944 pages, 1993). He died before finishing volume four, which Yvette Edmondson edited; Hutchinson had enlisted her assistance in 1988. He had plans for additional chapters in volume four on aquatic communities and for a fifth volume on productivity, succession, sediments, and paleolimnology (Edmondson 1993:ix–x). All the volumes have numerous charts, illustrations, and bibliographies.

The theory for which Hutchinson is most remembered is a quantitative niche (Slack 2010: 275–280, 285–288 et passim). A detailed nonmathematical version was a talk he gave in 1964, "The Niche: An Abstractly Inhabited Hypervolume" (Hutchinson 1965:26–78). According to Garret Hardin (1960) and some less prominent predecessors (Hutchinson 1965:27–28), two species cannot occupy the same niche; one will prove to be the better competitor and drive the other species out. However, in both oceans and fresh waters, different species of phytoplankton coexist in a fairly uniform environment. Hutchinson presented his answer to this puzzle at a symposium on 27 December 1960, partly inspired by Hardin's article (Hutchinson 1961), but his response was also an updating of an earlier article (Hutchinson 1941*a*). The longest chapter in Hutchinson's *Introduction to Population Ecology* is on "What Is a Niche?" (1978:152–212). It is a mathematical presentation, though its end-summary of 3.5 pages contains only one equation.

Hutchinson was one of the greatest limnologist of the 1900s (Forel held that honor for the 1800s). Modern science, more than ever, is a collaborative effort, and Hutchinson was also a great collaborator, who was generous in acknowledging contributions from his collaborators. That trait undoubtedly accounts for the number of animals named for him. Although an anthology of his writings devotes less than a quarter of its pages to limnology (Hutchinson 2010:83–157), the following section on theory, also includes limnological subject matter (pages 222–230, 236–241). He retired from teaching at Yale in 1971, and in recognition of his scientific and pedagogic contributions, both *Limnology and Oceanography* and the *Transactions of the Connecticut Academy of Arts and Sciences* had special issues in his honor. The March 1971 issue of *Limnology and Oceanography* had an introductory essay by editor Yvette Edmondson, "Some components of the Hutchinson legend," with eight photographs of him from

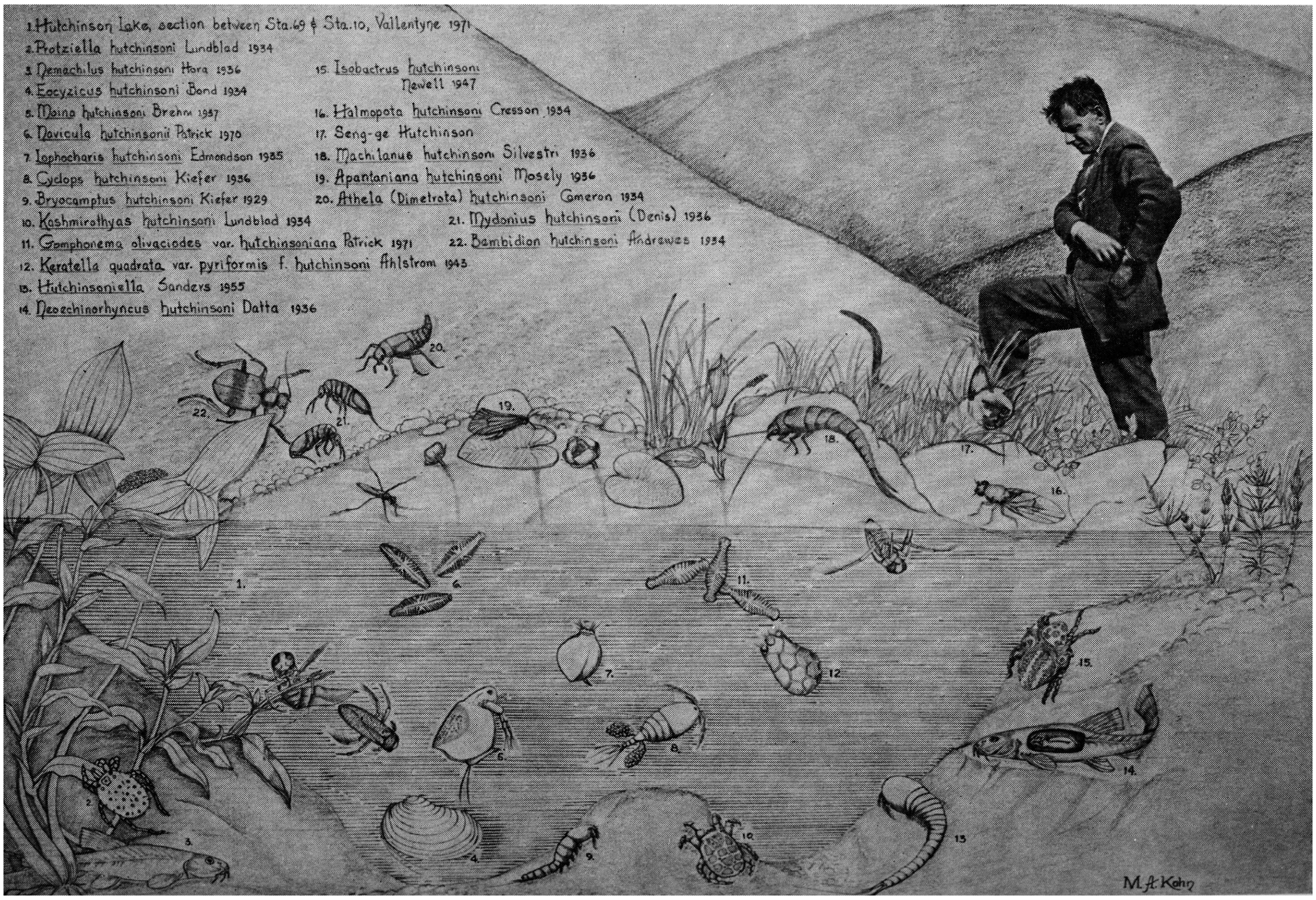


Fig. 4. Aquatic or semi-aquatic animal species named to honor Hutchinson.
By Marion A. Kohn. *Limnology and Oceanography* 16: (1971:477); comments on species, 476.
Courtesy John Wiley and Sons.

boyhood to 1971, followed by his bibliography until 1971, followed by a list of 34 students who had written doctoral dissertations under his supervision, five students who had begun dissertations under him which were not yet finished, and nine students who wrote under supervision by other faculty in which he was on their dissertation committee, with a strong influence. Those lists were followed by Alan J. Kohn's Phylogeny and Biogeography of *Hutchinsonia*: G. E. Hutchinson's Influence Through His Doctoral Students (with Kohn being one of his doctoral students). In addition to that ingenious article, Marion A. Kohn drew two illustrations, of "Hutchinson's Phylogenic tree of intellectual descendants," and of the 22 animal species named in his honor (above, Figs. 2, 3).

Chapter 4, "New England," was by John L. Brooks (b. 1920), and Deevey, two Hutchinson former students still at Yale in 1963. Their long account on Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine has numerous maps, tables, and charts, but no portraits of limnologists. Their "History" section is on environmental history and human use history, not history of the study of New England limnology. The above discussion of Hutchinson and his students concerns limnology in New England. An example of Brooks' own research is Predation, Body Size, and Composition of Plankton (Brooks and Dodson 1965).

F. Herbert Bormann (1922–2012) was a World War II U.S. Navy veteran who used the G. I. Bill to attend Rutgers University, where he studied plant ecology under Murray Buell (Likens and Hedin 2014, Egerton 2015*a*:83–85). After Bormann graduated (B.S. 1948), Buell sent him to the Duke University (M.A. 1950, Ph.D. 1952), where he studied forestry as well as plant ecology. He visited U.S. Forest Service Experiment Station at Coweeta, southwestern North Carolina, while at Duke, and when he later taught at the Emory University (1952–1956), he took students there. He moved to Dartmouth College in New Hampshire in 1956; when he saw the U.S. Forest Service Hubbard Brook Experiment Station, he realized that watershed experiments could be conducted there similar to those at Coweeta. Gene Likens (b. 1935) taught at Dartmouth for the fall semester 1961, and after he received his doctorate at Wisconsin under Hasler, he joined the Dartmouth Zoology

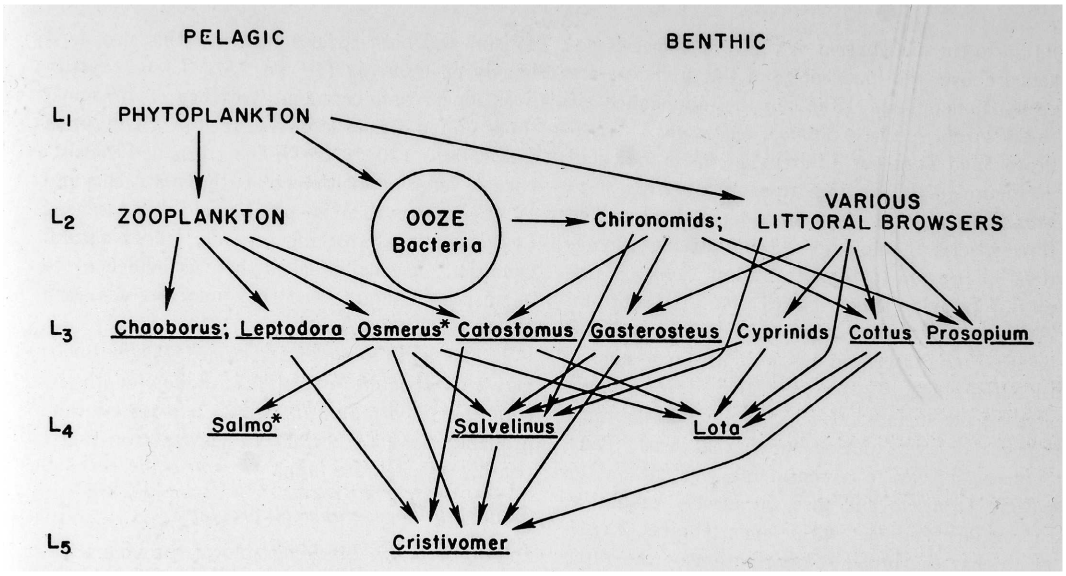


Fig. 5. Food web for Moosehead Lake, Maine. Cooper and Fuller (1945). Courtesy, Maine Department of Inland Fisheries and Wildlife. From Brooks and Deevey (1963:143).

Department (1963). Bormann and he applied for a NSF grant to study the Hubbard Brook ecosystem, which they received, and that research, first explained in Bormann and Likens (1967), has been continued by them and others ever since (Likens et al. 1977, Egerton 2015*a*:85–87). Stream analysis is an important aspect of these studies. Likens and Hubbard Brook collaborators discovered for the first time that atmospheric acids were an important environmental problem in America, affecting even aquatic environments (Likens et al. 1972, Likens and Bormann 1974, Jenkins et al. 2007:41). Acid rain had only recently been discovered in Europe (Mysterud 1971, Rodhe 1972). In a retrospective article, Likens (2010) discussed difficulties going from discovery of acid rain to legislation to control pollution causing it.

The Hubbard Brook Experimental Forest had been established in the White Mountain National Forest, New Hampshire in 1955 as a center for hydrologic research for New England. It is a bowl-shaped valley of 3138 hectares (~32 k^2). Bormann and Likens began their still-ongoing ecosystem study in 1963, and this area became a Long-Term Ecological Research site in 1988. Hydrological data for this site, 1955–2000 is online (Bailey et al. 2003). Bocking (1997*a*:116–147) and Likens (2013) summarized years of research at the Hubbard Brook Ecosystem Study.

Hasler and his students at Wisconsin

David Frey's chapter on early Wisconsin limnology (1963*b*) ends in 1940, and Hasler's following chapter (1963*a*) extends from 1940 to 1961. By 1930, Wisconsin limnological studies covered a broad array of topics, and continued to do so during the 1930s, still under Juday's guidance (Juday and Hasler 1946, Egerton 2015*a*:37–38). The University of Wisconsin maintained limnology laboratories at both Madison and at Trout Lake in northern Wisconsin. Juday was a founder of the Limnological Society of America and was its first president (1935–1937). Juday's The Annual Budget of an Inland Lake (1940) was "exceptionally important…because it gave ecologists a theoretical structure that would show if an energy analysis was complete" (Golley 1993:47; Hagen 1992).

Fig. 6. Hubbard Brook experimental stream weir. U.S. Forest Service.

Art Hasler was born in 1908 into a Mormon family in Lehi, Utah (Burgess 1996:52, Egerton 2008*a*, 2015*a*:70–73). He believed that his Mormon background provided him with ethical and intellectual values that contributed substantially to his successful career. His boyhood interests were in fishing, raising livestock, camping, nature study, and the Boy Scouts. As an undergraduate at the Brigham Young University, he decided to follow his father's example to become a physician. However, when he graduated in 1932, his father was ill, and in the Depression, he was unable to afford medical school. He had majored in zoology and could afford to enter graduate school at the University of Wisconsin in Madison because he could earn expense money while a student (Egerton 1987*a*:94–95, 2015*a*:70–73, Likens 2002:3–4). He was one of the 13 graduate students who obtained a Ph.D. under Juday, and

Juday suggested that he write his dissertation on the digestion physiology of plankton crustacean. He agreed and published his findings (Hasler 1935, 1937). In summer 1935, he began working for the U.S. Fish and Wildlife Service studying the effects of sulfate pulp mill wastes on oysters in the lower York River in Virginia. He transferred sick oysters from the York to the nearby Piankatank River and healthy oysters from the Piankatank to the York. Undisturbed oysters in both rivers served as controls. He found that sick oysters recovered when moved to the Piankatank and that healthy oysters sickened when moved into the York (Galtsoff et al. 1947). This research, a controlled field experiment, was a prelude to Hasler's later introduction of experimental limnology as a hallmark of his guidance in limnology.

After two years with the Fish and Wildlife Service, Hasler returned to the University of Wisconsin, completed his Ph.D. in 1937, was hired as an instructor of zoology, and was promoted to assistant professor in 1941. He had become fluent in German during his teenage Mormon field service in Germany, and in 1945, when he entered Germany with the U.S. Strategic Bombing Survey, he took the opportunity to become friends with Karl von Frisch in Munich—who later won his Nobel Prize for studies on bee behavior (Egerton 2016:66–67), but who had also studied fish behavior (von Frisch 1941*a*,*b*)—and Wilhelm G. Einsele at the Anstalt für Fischerie, Weissenbach an Attersee, near Salzburg, Austria (Egerton 1987*a*:97). Frisch conducted sensory and behavioral studies on bees during the summer and on fish during the winter. In 1949, he went on a lecturing tour in the United States and was Hasler's guest when he lectured at the University of Wisconsin (von Frisch 1967:138–139, 165–166). Hasler obtained a Fulbright Research Scholarship for the school year 1953–1954, which he spent at Frisch's laboratory in Munich, refining his skills in researching fish behavior.

Hasler was interested in Einsele's efforts to increase the productivity of Austrian lakes by adding superphosphate, and later Hasler introduced this as an experimental project in Wisconsin. They collaborated in a report on the subject (Hasler and Einsele 1948). This became a subject of lasting interest for Hasler, and he and his collaborators conducted similar studies on Wisconsin lakes (Hasler 1963*a*:55–57, Egerton 1987*a*:99–100).

Hasler returned to the University of Wisconsin as associate professor in 1945 and became full professor in 1948. The University is along the shore of Lake Mendota, which is now the most limnologically studied lake in the world. In his spare time while in Europe with the Air Force, Hasler visited five biological stations where limnology research was conducted, and he published his findings on their post-war conditions and activities (Hasler 1946).

Birge had run a successful limnology program at the University of Wisconsin since the later 1800s, with Juday's collaboration since 1900 for four decades; over 400 limnology publications came from the University of Wisconsin during that period (Juday and Hasler 1946). That achievement was from a series of collaborations, often between them and other scientists (Frey 1963*b*); it was not the fruit of a planned scientific school. Juday was interested in the growth of fish in Wisconsin lakes, and some of his studies on it were in collaboration with his doctoral student Clarence L. Schloemer. Beyond Schloemer's own dissertation, The Age and Rate of Growth of the Bluegill, *Helioperca macrochira* (1939), they collaborated on three reports (cited by Frey 1963*b*:49). They found that adding fertilizer to lakes increased productivity of plants and of animals other than fish, whose productivity was unaffected (Frey 1963*b*:42).

In contrast, Hasler (1964) deliberately planned a scientific school of limnology, based upon experimentation, which lasted slightly over four decades under him. He was to supervise the M.S. theses for 41 students, the Ph.D. dissertations of 53 students, and partial supervision of 14 other Ph.D. dissertations (he compiled lists of names, dates, and current locations and another list with names and titles of theses and dissertations, of which I have copies). Unlike Birge and Juday, Hasler often collaborated with his graduate students. Findings in these theses and dissertations often led to joint publications between advisor and student. Whether Hasler was listed as senior or junior author in such papers depended upon his relative contribution. However, before he had such graduate students, he collaborated with a colleague, endochrinologist Roland Meyer., on hormonal experiments with fish, which were later useful to fish culturists (Hasler et al. 1939, Hasler and Meyer 1942). Hasler was sole or joint author of 195 publications, 1935–1984 (Hasler 1979, 1984). He also taught a popular limnology course for upper classes and grad student (my memory, from taking it).

His first doctoral student, Jay D. Andrews, wrote his dissertation on *The Macroscopic Invertebrate Populations of the larger Aquatic Plants in Lake Mendota* (1946)—not an experimental topic, they had previously collaborated on a study of "Fluctuations in the animal populations of the littoral zone in Lake Mendota" (Andrews and Hasler 1942). Hasler's second published contribution to Lake Mendota limnology was a study of its winter population of perch (1945*a*). His summary of it (1975*b*:262–263) shows his excellent limnological reasoning. He found that:

> *…by extensive winter netting under ice that this winter population was most abundant in the deepest water of the lake, i.e., nets set at the deepest points (24 meters) caught significantly more fish than those set simultaneously at shallower stations (18, 16, 14 and 7 meters). Moreover, the fish traveled in schools of definite size-classes. Moreover, the fish traveled in schools of definite size-classes. Of the environmental conditions which might influence the concentration of fish in deep water, such as oxygen content of the bottom water, temperature, abundance of plankton crustacean and bottom fauna, correlation with the last was most striking. Not only were bottom-dwelling midges more abundant in the deeper stations, but the perch there consumed more of them than those at the shallower regions. Even though oxygen was zero on the bottom in late winter it did not retard the perch from plying the bottom for food.*

Five of Hasler's students earned doctorates in 1947: Nelson on fish morphology, Ogawa and Yokoyama on development and seasonal variation of perch blood cells, Walker on fish olfactory discrimination of aquatic plants, and Jones on aquatic plant competition. After an algal bloom in Lake Mendota, Hasler had Sara Elizabeth Jones (who would marry limnologist David G. Frey, a Juday student, Ph.D. 1940), conducted experiments to see if rooted aquatic plants would inhibit algal growth. R. N. Pond had conducted experiments—a noteworthy early example of ecological experimentation–that seemed to indicate no impact, and he had argued that since rooted vegetation received its nutrients from soil and phytoplankton from water, they did not compete (Pond 1903). Since the 1920s, several fishery managers had expressed doubts about Pond's findings, but had not conducted experiments to challenge Pond's results. Jones' experiments showed clearly that rooted vegetation inhibited both algae and rotifers. Hasler and she published the results in *Ecology* (Hasler and Jones 1949).

Another vegetation study was by Swindale and Curtis (1957), Phytosociology of the large submerged plants in Wisconsin Lakes. One wonders if authors saw galley proofs, for the Wisconsin map on page 308 was published up-side-down.

After World War II, the Atomic Energy Commission and the new National Science Foundation provided funds which enabled ecology to grow into "big science" in some fields and in some places. (David Coleman's Big Ecology [2010] with the International Biological Program.) Hasler's limnological school at the University of Wisconsin participated in this growth, and he used research funds to hire research managers, since he was unable to advise all students simultaneously. He also obtained funds from the National Science Foundation in 1962 to build a Laboratory of Limnology on the shore of Lake Mendota within the University campus, which opened in 1963 (Hasler 1963*b*). A formal opening ceremony included an address by Hutchinson, "The lacustrine microcosm reconsidered" (1964).

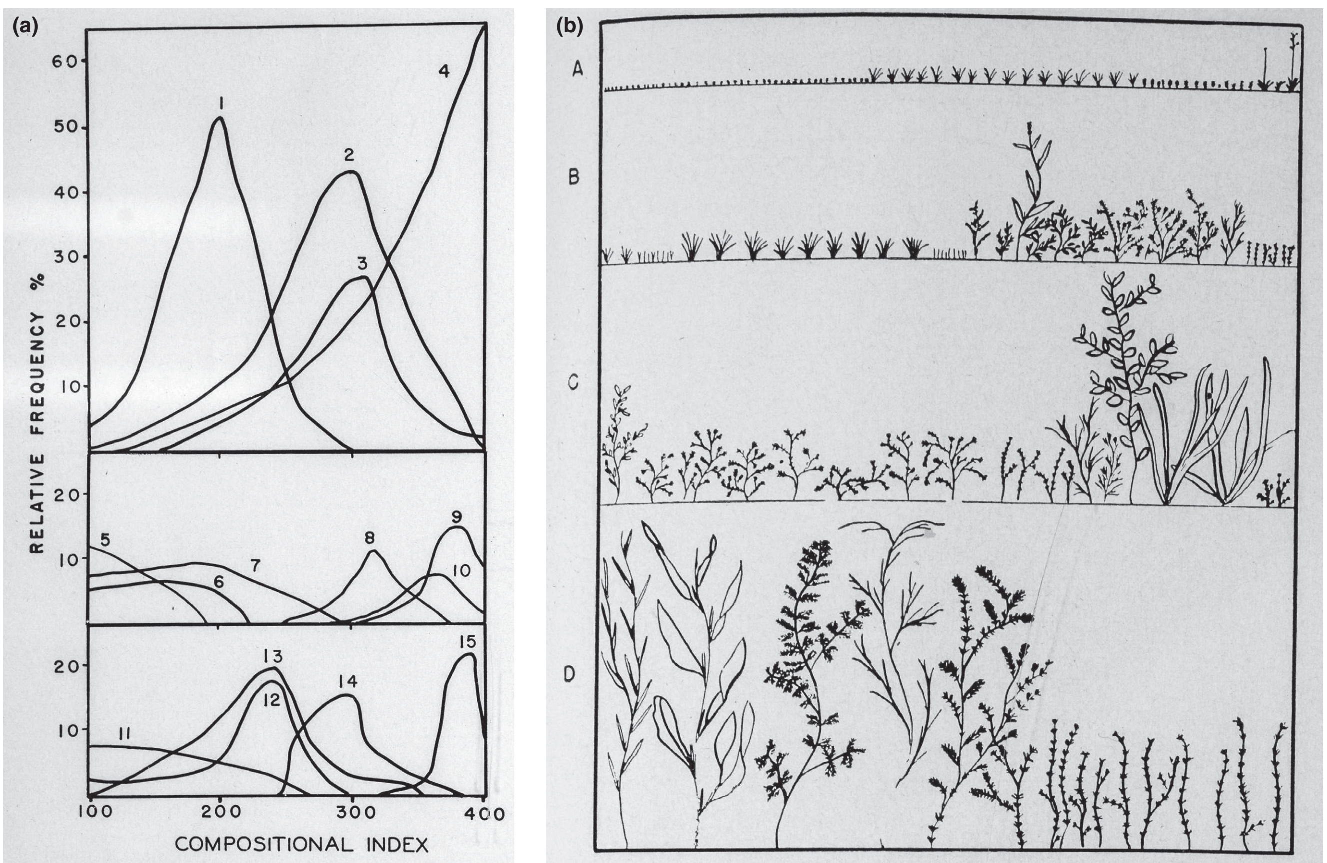


Fig. 7. (a) Relative frequency of important taxa plotted against compositional index. Numbers on curves correspond to species, itemized in Swindale and Curtis 1957:404. (b) Representative stands at indices of 100 (A), 200 (B), 300 (C), and 400 (D). Swindale and Curtis (1957:405).

Another aspect of "big limnology" was Hasler's arrangement for the University of Wisconsin to host the Fifteenth Congress of the International Association for Limnology (IAL) in August 20–25, 1962—IAL's first meeting in America. To assist in preparations for it, Hasler hired Associate Professor John C. Wright, from Montana. It was attended by over 600 limnologists, oceanographers, and other scientists from 34 countries (Hasler 1962). Excursions to American lakes, rivers, and streams were arranged for both before and after the meetings. One important outcome of the meetings was to convince Americans to tell the history of their science in North and Central America and the West Indies. David G. Frey, at the University of Indiana, became editor of a remarkable book, *Limnology in North America* (University of Wisconsin, 1963*a*). Thirty-two authors wrote twenty regional chapters and five thematic chapters, and finally, Evelyn Hutchinson wrote "The prospect before us." As befitted the host university, there are two chapters on limnology in Wisconsin: Frey wrote one on the Birge-Juday Era and Hasler wrote the other on "Wisconsin, 1940–1961." *Limnology in North America* is a treasure unmatched anywhere else in the world. Only the United States and Canada could readily provide resources to support such a venture, and the American Society of Limnology and Oceanography had nurtured a spirit of cooperation that led to this achievement.

Hasler's most important investigations were on homing migrations of salmon (Hasler 1960, 1966, Hasler and Scholz 1983). Salmon are anadromous—breeding in headwaters of streams, migrating to the ocean to mature, and years later returning to their home stream to reproduce and die—the reverse pattern from catadromous eels which Johannes Schmidt had researched (Egerton 2014*b*:402). A personal experience (illustrating Pasteur's comment that chance favors the prepared mind) initiated these studies (Hasler 1975*b*:186):

Fig. 8. Laboratory of Limnology, on Lake Mendota, University of Wisconsin-Madison. Courtesy Center of Limnology, UW-Madison.

My early research, together with what I had read about salmon and homing behavior in other animals, prepared me for an experience I had in 1946 while on vacation in Utah's Wasatch Mountains, where I grew up. As my children and I hiked along a path I had frequented as a boy, the familiar fragrances of columbine and mosses growing just ahead but out of sight triggered

> *a whole flood of memories. The names of boyhood chums and visions of the nearby mountain meadow where we played ball vividly flashed across my mind. I thought, "Well, Art, you're a salmon coning home, and it smells like home."*

If Hasler had been at a western university, he might have investigated salmon immediately, but being in Wisconsin, he wondered if his question about migrating fish being guided by odor could be tested on Wisconsin fish.

The earliest dissertation study relating to this hypothesis which he had a graduate student conduct was to test bluntnose minnows' discrimination between the odors of plants. The aquarium apparatus developed for these experiments was used in doctoral research of some of Hasler's students. Theodore Walker, first using this apparatus and a controlled experimental regime, showed in 1947 that fish can distinguish odors of different plant species; they turned his findings into a scientific paper. Their final conclusion was (Walker and Hasler 1949:63):

> *6. Results of our studies lend support to the view that aquatic plants may well play an important role in the life of a fish. They may serve as signposts to guide fish into feeding grounds, since many fishes commonly feed in turbid water, at dusk, at dawn, and at night, when visibility is poor. Moreover, the odors of aquatic plants may serve as attractants to immature fishes to prevent them from straying from cover. In addition, other natural odors may direct migratory fishes in locating their homing areas.*

The first graduate student of Hasler who collaborated with homing research was Warren Wisby. They soon published two papers on their research (Hasler and Wisby 1950, 1951), the second of which was similar in content to Wisby's Ph.D. dissertation (1952). Although fish distinguished between odors of different species of plants in a laboratory, do adult salmon actually use such discrimination to relocate their birth stream? The next test was to see if bluntnose minnows could distinguish between odors of two streams, again in laboratory conditions. Waters collected from two Wisconsin streams were used in experimental aquaria. After two months of training, the minnows learned to distinguish between the water that provided food and the water that provided an electrical shock (Hasler and Wisby 1951:237). Wisby and Hasler in 1952 designed a laboratory experimental apparatus to test odor discrimination in salmon fry, and when that succeeded, they tried in 1953 a successful experiment on salmon returning to spawn. They published a separate paper on these experiments (Wisby and Hasler 1954). A comprehensive study which Hasler published on "Odor perception and orientation in fishes" (1954:127) summarized: they had:

> *…captured sexually ripe coho salmon at two branches of the Issaquah River in Washington and returned them downstream below the fork to make the run and selection of stream again. In half of them the nasal sac was plugged with cotton. The great majority of normal fish selected again the stream of first choice, while the plugged-nose fish returned in nearly random fashion. No comparable pressure trauma was applied to the control fish; nevertheless, this experiment is indicative of the important role that the functional olfactory system has in orientation.*

After that success, Hasler collaborated with a science editor on an article, "The homing salmon," which became the cover story in the August 1955 issue of *Scientific American*. That article published an illustration of Wisby and Hasler's laboratory experimental apparatus for testing salmon fingerlings

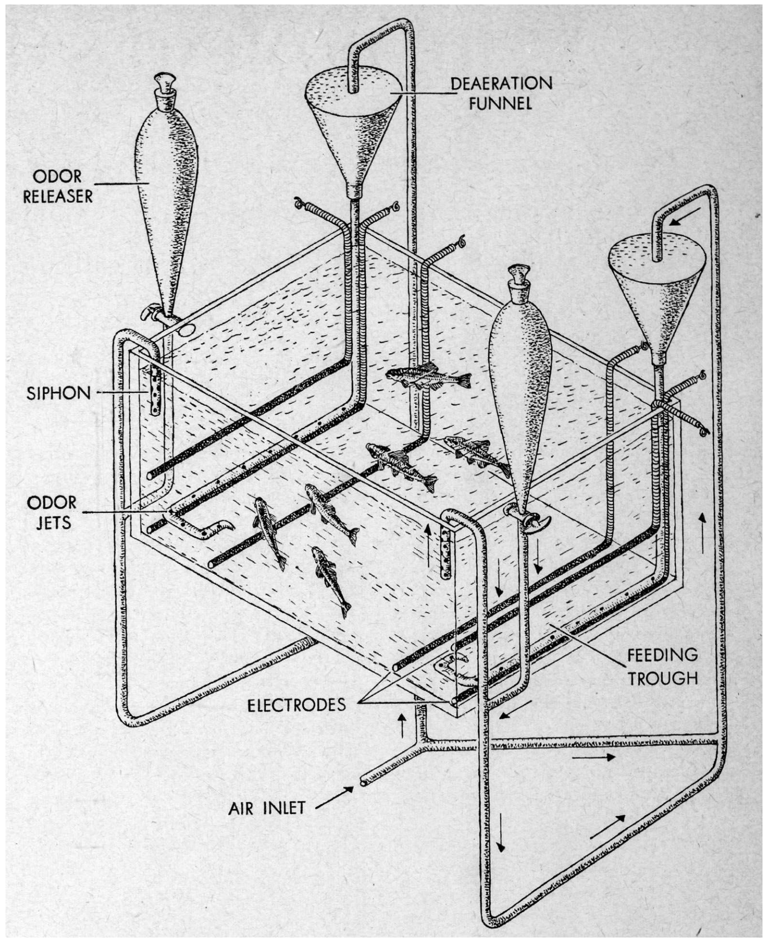


Fig. 9. Experimental aquarium to test fish discrimination of plant odors, developed for Theodore Walker's doctoral dissertation and used subsequently in other researches. This illustration, from *Scientific American*, differs from earlier drawings by adding drawings of fish. Drawn by Eric Mose. Hasler and Larsen (1955:73). Courtesy *Scientific American.*

(Hasler and Larsen 1955:74). An always-active Hasler explored fish odor perception in two more papers (1956*a*,*b*) before collaborating further with Wisby on experiments in actual ponds and lakes (Hasler and Wisby 1958, Hasler et al. 1958). In one experiment, they displaced largemouth bass and green sunfish from their home territory in a half-acre pond to see if they returned home; they did. Then, they ran another set of experiments in which fish were transferred to a different pond and the fish wandered aimlessly.

After determining the role of odor in salmon as the means by which they find their home stream where they reproduce, Hasler tackled the next obvious question: how do salmon find their river after spending years at sea? Perhaps, they depend upon the sun for navigation. This hypothesis was tested on an immature pumpkinseed *Lepomis gibbosus* in an experimental tank sitting on a pier in Lake Mendota, with running lake water. Hasler and collaborators did train the pumpkinseed to enter "the training box in a consistent compass-direction at any time of day" (Hasler et al. 1958:353). However, the fish was unable to find its way under an overcast sky.

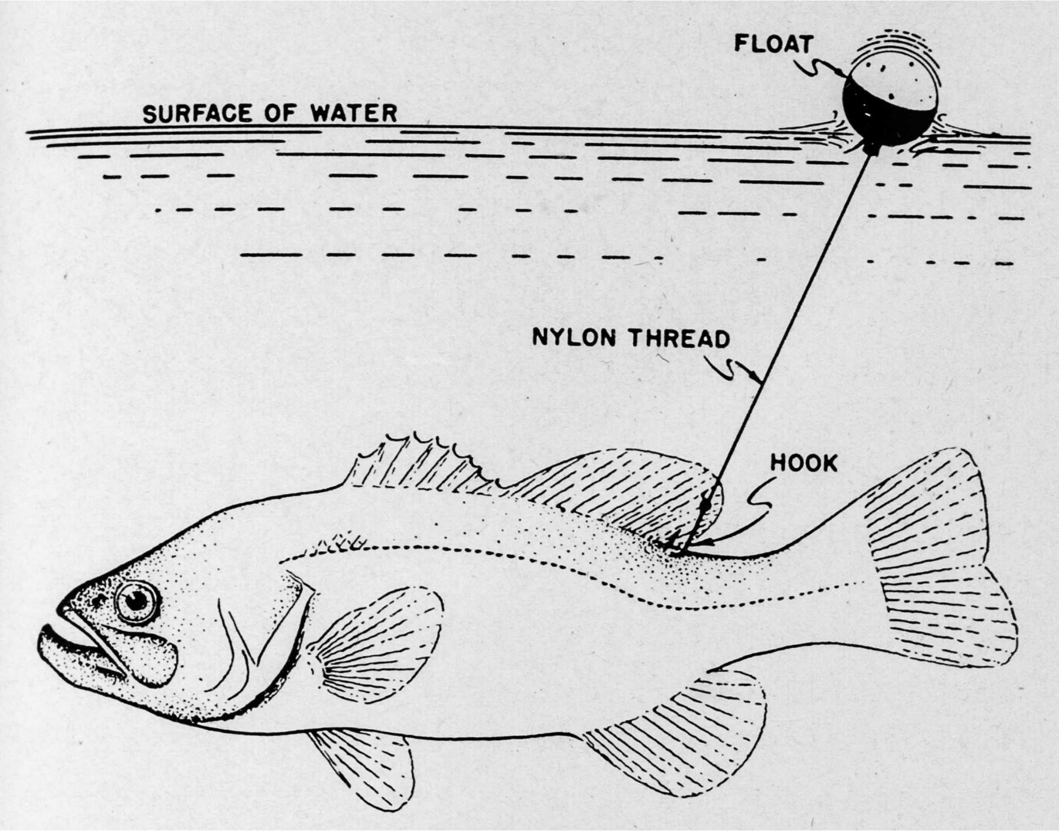


Fig. 10. Movements in displaced fish were followed visually by attaching floats to fish. Hasler and Wisby (1958:291).

Coincidentally, several species of salmon were introduced into the Great Lakes, providing Wisconsin limnologists with a convenient source of salmon for experimentation. In spring 1955, pink salmon were inadvertently introduced into Thunder Bay, Canada, on the north shore of Lake Superior (Kuchenberg 1978:81–83). This spill of fingerlings was not publicized and probably pink salmon were never available to Madison limnologists. Kokanee salmon were deliberately introduced into Canadian waters of Lake Huron in 1964, and in the later 1960s, coho and chinook salmon were deliberately introduced into the Great Lakes. The latter two species were introduced to counter the alewife die-offs that began plaguing Lake Michigan shores, with great masses of them washing ashore, rotting and stinking. The salmon did eat the alewifes and salmon became the basis of a very popular sport fishery.

Most prominent of Hasler's graduate students was Indianian Gene Elden Likens (b. 1935), who earned his B.S. degree in zoology at Manchester College (1957) before moving to Madison for his master's and doctoral degrees (1959, 1962). His dissertation, on movement of radiosodium in a lake led to three articles (Likens and Hasler 1960, 1962, Hasler and Likens 1963). Likens subsequently became one of the leaders in the still-ongoing forested ecosystem study at Hubbard Brook, New Hampshire (discussed above).

Since the University of Wisconsin is on Lake Mendota, that lake has been a convenient location for limnological studies. Such studies by faculty and graduate students, readily published, made Lake

Mendota the most studied lake in the world. Bacteriology Professor Thomas Brock synthesized some results of those studies in *A Eutrophic Lake: Lake Mendota* (1985). Hasler retired in 1978, and his last major publication was *Olfactory Imprinting and Homing in Salmon* (Hasler and Scholz 1983). His successor was Professor John Magnuson (b. 1934), who had joined the faculty in 1974 (Magnuson 2002:858–859, Lange 2013). Magnuson expanded teaching and research by obtaining funds for the Center for Limnology in 1982, enabling the university to increase limnology's faculty from two (Magnuson

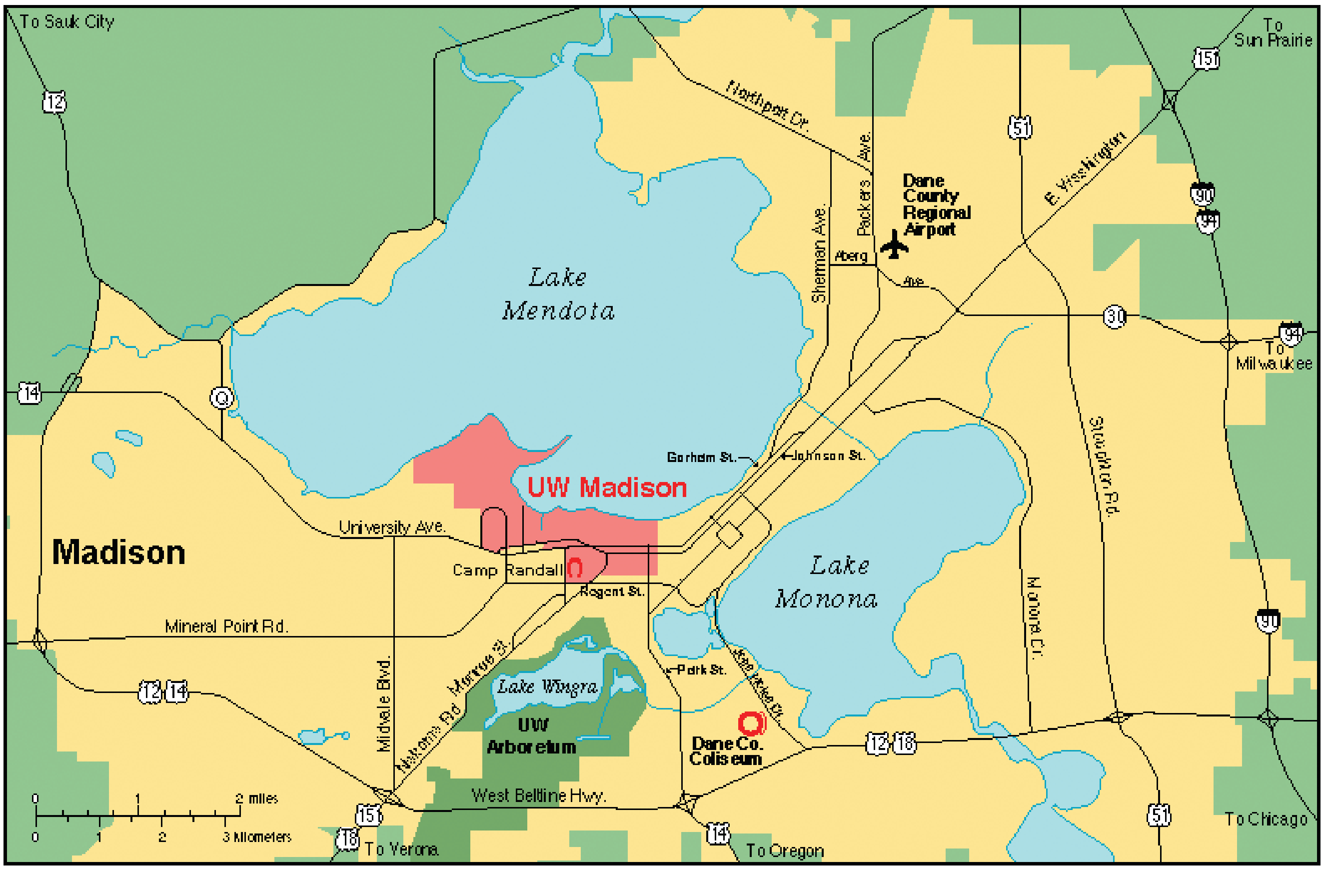


Fig. 11. Lake Mendota, showing University of Wisconsin Campus. Courtesy UW-Madison.

and James Kitchell, b. 1942) to three, adding Stephen Carpenter (b. 1952). Kitchell and Carpenter had already collaborated in research while Carpenter was at the University of Notre Dame, and they developed a major theory to explain the biotic characteristics of lakes, as not due to a bottom-up process that began with phytoplankton, but rather to a top-down trophic cascade that depended upon the kinds and abundance of top predators (Carpenter 1988, Kitchell 1992, Carpenter and Kitchell 1993). Magnuson guided the Wisconsin limnology group toward long-term study of lake dynamics in a landscape context, and toward comparative studies (Magnuson 1990).

An early collaborative study by that group was Lake Wingra, 1837–1973, a Case History of Human Impact (Baumann et al. 1974). Wingra is smallest of a cluster of lakes, of which Mendota is largest, and it is less than a fifth the size of Mendota. However, being on an edge of Madison, there were records of environmental manipulations going back to 1837. Those manipulations included drainage of adjacent marshes and introduction of carp (1880s), walleye (1900), and white bass (1917). However, that was just the beginning. The Wisconsin Conservation Department introduced 20 to 23 fish species in 1935 to 1945. It is unlikely that the Department sought approval from any University scientist for fish introductions, and after carp became dominant during the 1930s, a carp removal program began. By 1969, Wingra had never been managed as an ecosystem, but in that year, it began being studied as such as part of the Eastern Deciduous Forest Biome US-IBP site. The study by Baumann et al. (1974) was a contribution to that project, as was Orie Loucks, Models Linking Land-water Interactions around Lake Wingra, Wisconsin (Loucks 1975). Plant ecologist Loucks was, at the time, part of the TIE Office of Ecosystem Study, located in Madison. Yet, he neither cited Baumann et al. (1974) nor listed any of the authors of that study among the five whom he acknowledged as assisting him in his study. True, a retrospective article was not relevant to a model-building article, and Loucks' article was only 11 pages. Loucks' study was in an IBP volume edited by Hasler, *Coupling of Land and Water Systems* (Hasler 1975*a*).

Throughout the United States

Chairman Maynard M. Metcalf, Division of Biology and Agriculture of AAAS, in 1925 called a meeting to establish a Committee on Aquiculture, which arranged a program for the AAAS 1926 meeting on encouraging research and training in hydrobiology; that committee subsequently met annually, and in 1932, it established a Subcommittee on Hydrobiology, which organized a program at the AAAS meeting in 1934 on hydrobiology and aquiculture (Lauff 1963:668). Professor Paul Welch published his limnology textbook in 1935, which capably organized existing knowledge, and this symposium represented the "cutting edge" of a growing science. In January 1935, Welch distributed an announcement on formation of an American limnological society, with annual dues of $1. A founding committee met in January 1936 and formed the Limnological Society of America, with 221 founding members. In 1936, it initiated a series of publications; the first entitled *Sources of Limnological Apparatus and Supplies*. In 1938 or 1939, the society sponsored a symposium at an annual AAAS meeting on *Problems on Lake Biology*, and AAAS published the nine presentations as a book (Moulton 1939). It was a comprehensive collection of papers, covering a very broad range of subjects, yet without contributions from Birge, Juday, Hutchinson, or Hasler.

In 1948, the society expanded to become the American Society of Limnology and Oceanography, which began publishing *Limnology and Oceanography* in 1956. In 1962, the society sponsored the XVth International Congress of Limnology, held at the University of Wisconsin, Madison. For that occasion, American limnologists compiled their excellent *Limnology in North America* (Frey 1963*a*), discussed above.

Across Lake Michigan from Wisconsin, Jacob Reighard (1861–1940) continued his fisheries research, though his leadership at the University of Michigan declined after his retirement in 1927 (Chandler 1963:98–100, Bocking 1990*b*, Burgess 1996:91). His successor was Illinoisan Paul S. Welch (1882–1959), who had come to the University of Michigan as an associate professor in 1918 (Chandler 1963:103–106, Burgess 1996:110). Welch had earned his M.A. and Ph.D. at the University of Illinois (1911, 1913), with an initial focus upon aquatic insects. However, Welch (1927) published a substantial paper, "Limnological investigation on northern Michigan Lakes," signaling his new commitment.

He became fascinated by northern bog lakes and published four articles on them before publishing his comprehensive textbook, *Limnology* (1935, expanded edition 2, 1952). As limnology progressed, he concluded that his textbook needed a supplementary text on *Limnological Methods* (Welch 1948). Like Hutchinson and Hasler, Welch was advisor for graduate master's theses and doctoral dissertations on aspects of limnology. David C. Chandler (b. 1911), who earned his own M.A. and Ph.D. degrees (1930, 1934) under Welch's guidance, listed (1963:105–106) 34 authors and their dissertations completed under Welch. The University of Michigan Zoology Department subsequently named its library the Paul S. Welch Library.

An important resource for limnological teaching and research at the University of Michigan was its Douglas Lake Biological Station, established in 1909 under Reighard, directed later by Frank E(gebert) Eggleton (1893–1970), who had earned his M.A. and Ph.D. degrees (1923, 1930) at the University of Michigan, with a dissertation on "A limnological study of the profundal bottom fauna of certain freshwater lakes" (Chandler 1963:105–107). Eggleton was an active organizer and member of the Limnological Society of America, though he never held office in it. Sixteen graduate students earned their Ph.D. under him, 1945–1960. The Michigan partnership between Welch and Eggleton in limnology, 1926–1952, began and ended a little later than the Wisconsin partnership between Birge and Juday, but had a similar impact on advancing limnology at the university. Also, at the university are a Department of Fisheries and an Institute for Fisheries Research, both of which conducted research relevant to limnology (Chandler 1963:110–111). In 1953, Chandler, mentioned above, became professor of zoology, and George H. Lauff (1927–), with a recent Ph.D. from Cornell University, joined the faculty as his assistant. Lauff had a bachelor's degree from Michigan State and would ultimately return there to teach.

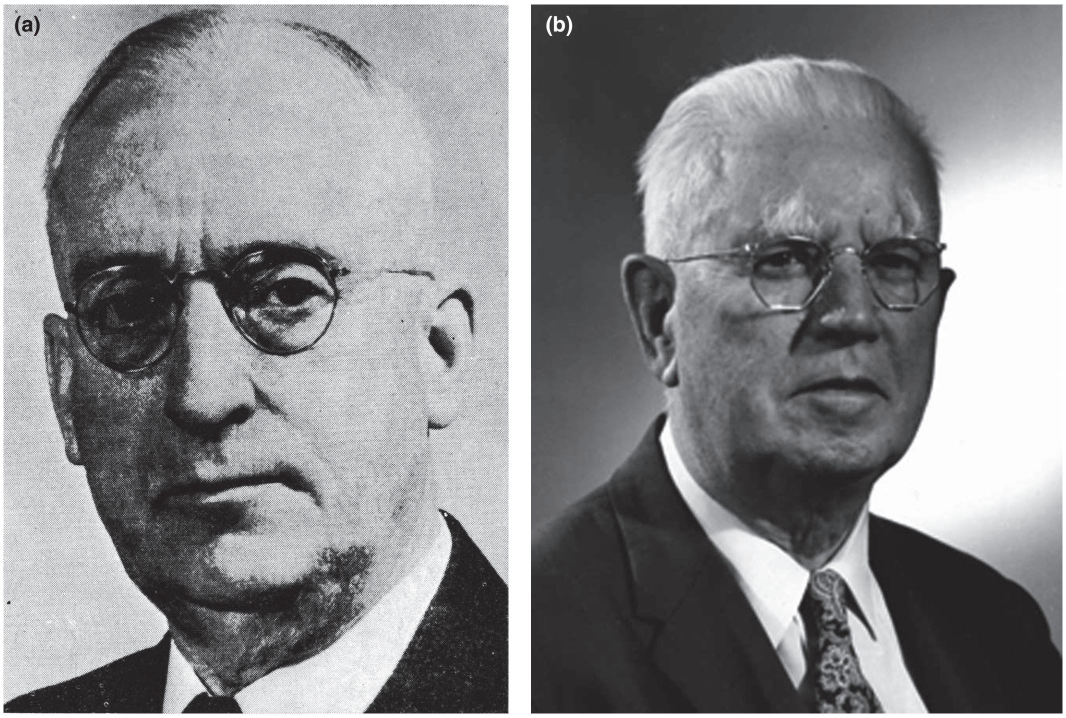


Fig. 12. (a) Paul S. Welch. (b) Frank E. Eggleton. Frey (1963*a*:103, 107).
Courtesy University of Wisconsin Press.

Unlike Wisconsin, Michigan has two large state universities, rather close together (in Ann Arbor and East Lansing). Michigan State University, East Lansing, began as an agricultural and technical land-grant college, but grew beyond those objectives. In 1940, Peter I. Tack introduced a course on fisheries into the zoology curriculum, and he added a course on limnology in 1941, in support of fisheries (Chandler 1963:111–113). In 1946, Ohioan Robert C(ragin) Ball (b. 1912), who had earned his B.A. and M.S. degrees (1936, 1937) at Ohio State University and his Ph.D. (1943) at the University of Michigan under Welch, began teaching a limnology course at Michigan State. In 1950, Ball moved into a new Department of Fisheries and Wildlife and worked closely with Tack. Ball was dissertation advisor for eight Ph.D. dissertations, 1952–1961 (authors and titles listed by Chandler 1963:112).

The breakfast cereal magnate, W(ill) K(eith) Kellogg (1860–1951), born in Battle Creek, Michigan, built a home at Gull Lake in 1926. He had a farm and bird sanctuary nearby, both of which he gave to Michigan State College in 1928. In 1929, a Summer School in Biology began at the farm and sanctuary that continued (excepting in 1933) until 1939. After Kellogg died, his foundation gave the house and surrounding property to Michigan State College, and summer field courses resumed at Gull Lake Laboratories, 1954–1963, under Professor Walter F. Morofsky, Department of Entomology. In 1959, the W. K. Kellogg Foundation provided funds to expand facilities at the Gull Lake Biological Station. In 1964, George Lauff went to the station as its first year-round director, and in 1965, he hired three other faculty members. Subsequently, both the National Science Foundation (1971) and the W. K. Kellogg Foundation (1985) provided funds for expansion of facilities. Robert G(eorge) Wetzel (1936–2005), from Ann Arbor, earned his B.S. and M.S. degrees (1958, 1959) at the University of Michigan, and his Ph.D. in limnology from the University of California, Davis (1962). He was on the faculty of Michigan State, 1965–1985; he was very popular with students at Gull Lake Laboratories (Patricia Werner, *personal communication*), after which he moved over to the University of Michigan, 1985–1990, then on to other universities (Kalte et al. 2005:VII, 592). He published the most detailed limnology textbook in America (Wetzel 1975, edition 3, 2001).

South of Wisconsin and close to Michigan, Illinois limnologists conducted research with a rather different focus. The Illinois River is a prominent feature in the state's geography, practically connecting Chicago and St. Louis, and the neglected study of river limnology was addressed on that river (Gunning 1963). Professor of Zoology and Entomology Stephen A. Forbes (1844–1930), University of Illinois, and a founder of the Illinois Natural History Survey (Howard 1931, Mills 1958:94–98, Bocking 1990*b*, Burgess 1996:42–43) in 1894 established the university's Biological Research Station at Havana, on the Illinois River south of Peoria. Its first director was Illinoisan Charles A. Kofoid (1865–1947), who had a Harvard Ph.D. and produced a monumental sequence of studies, 1897–1908, on Illinois River plankton (Gunning 1963:169–171, Egerton 2014*a*:137). Although he had joined the faculty of the University of California, Berkeley, in 1900, others continued river limnology studies at Havana, including Forbes on fish and insects, leading to *The Fishes of Illinois* (Forbes and Richardson 1908). Kofoid's influence is perhaps seen in the later researches of fellow Illinoisan Samuel Eddy (1897–1972), who earned his M.A. and Ph.D. at the University of Illinois (1925, 1929), then joined the University of Minnesota faculty in 1929, yet continued publishing on Illinois plankton until 1935 (Gunning 1963:171–173). Victor Shelford, discussed in part 50 (2014*a*:141–142), responded to his state's emphasis upon river limnology with instructions on Methods for the Study of Stream Communities (Shelford and Eddy 1929). The Illinois Natural His-

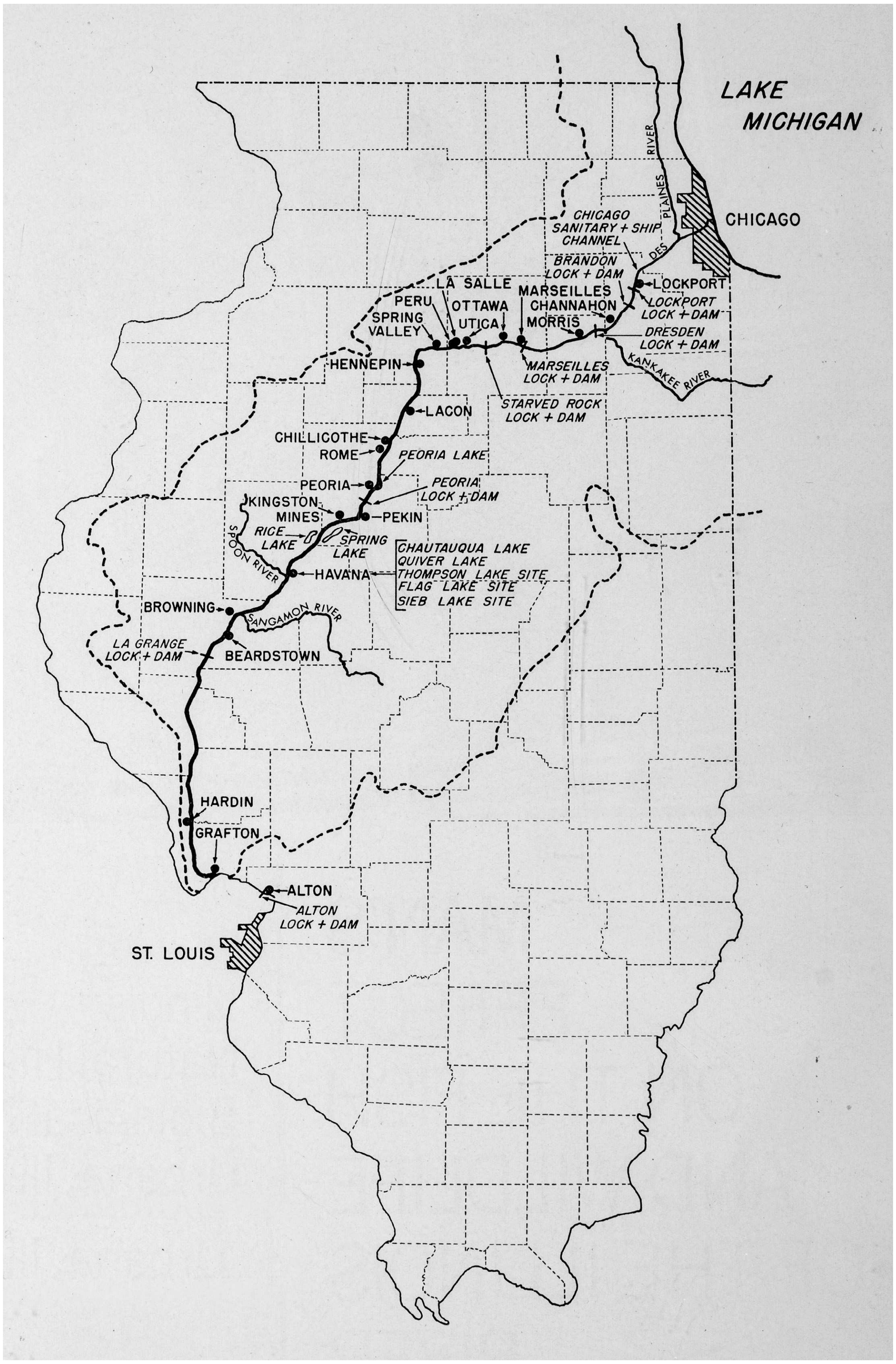


Fig. 13. Illinois River and tributaries, towns, locks and dams, and nearby lakes. Mills et al. (1966:2). Courtesy Illinois Natural History Survey.

tory Survey continued to support limnological studies by its staff and by grants to graduate students at the state universities (Bennett 1958:170–178). The Survey's paper on "Man's effect on the fish and wildlife of the Illinois River" contained two maps of the Illinois River at Havana, 1912 and 1960 (Mills et al. 1966:6).

The northeastern corner of Illinois is on Lake Michigan, but until 1963, it had apparently attracted little attention from Illinois biologists, since Gunning (1963:171–172) only discussed plankton studies conducted there. (It would have been relevant to cite Littleford et al. [1940], an experimental study of certain quantitative plankton methods, though their study had not been conducted at Lake Michigan). The most consequential action taken concerning Lake Michigan was Chicago's reversal of flow in the Chicago River from Lake Michigan into the Illinois River, completed in 1900. The potential peril of this reversal as a route for invasive species was not fully appreciated until about a century later. The Illinois-Indiana Sea Grant Institute was founded in 1982.

Fig. 14. Emmaline Moore. Courtesy American Fisheries Society.

Wisconsinite Clifford Berg (1912–1987) earned his M.S. and Ph.D. degrees (1939, 1949) at the University of Michigan and was Professor of Entomology and Limnology at Cornell University when he wrote chapter 6, "Middle Atlantic States" (1963) on New York, New Jersey, Maryland, and Delaware. His survey combined limnology and geography, with maps and landscape photographs. He discussed findings from several limnological surveys. The New York State Conservation Department conducted biological surveys of lakes and rivers during 14 summers, 1927–1940 "to determine the most practical methods of increasing fish production" (Berg 1963:197). The initial survey was by 14 scientists under Dr. Emmeline Moore (1872–1963), studying the Genesse River System. A survey of the Erie-Niagara System in 1928 involved 41 scientists; Berg did not specifically cite a supervisor's name, but the context indicates it also was Moore. Moore, from Batavia, New York, had B.A. and Ph.D. from Cornell University (1905, 1914). She became (Rossiter 1982:243):

> *…a leader in a brand new field. She left her job as an assistant professor of biology at Vassar College in 1919 to join the New York State Conservation Department, where she pioneered in the field of fish culture, especially fish diseases and pollution studies. She rose rapidly to the position of chief aquatic biologist and became director of the State Biological Survey before her retirement in 1944. She was also in 1928 the first woman president of the American Fisheries Society…*

By 1970, she was still the only woman president of AFS (Benson 1970:14; Burgess 1996:78–79).

A helpful reference for limnology students was Elsie Broughton Klots, *The New Field Book of Freshwater Life* (1966), with over 700 illustrations, most of which were drawings by Su Zan Swain. In 1927, Elsie Broughton had married entomologist Alexander B. Klots, who earned his degrees (B.S. 1928, M.S. 1929, Ph.D. 1931) working under James Needham at the Cornell University. Elsie Klots also earned her Ph.D. (1932) under Needham. Her 1966 bibliography cites many other helpful works published between 1930 and 1965, including Robert Pennak (1953), *Freshwater Invertebrates of the United States*, but not Libbie Hyman (1940–1967), *The Invertebrates* (six volumes), five volumes of which Klots must have known. Hyman's work was worldwide in scope and included marine as well as freshwater species, but not insects. As limnology expanded, so did methodology, and so there was a receptive audience for a translation of Jüdrgen Schwoerbel's (1970) *Methoden der Hydrobiologie* into English. Despite the virtues of Schwoerbel's *Methods*, Owen Lind (b. 1934, Ph.D. 1966) decided there was a market for a brief paperback, *Handbook of Common Methods in Limnology* (Lind 1974, edition 2, 1979). Brusca and Brusca's (1990) *Invertebrates* is a one-volume encyclopedia worldwide in scope and including marine as well as freshwater species, including insects. Thorp and Covich (1991) edited *Ecology and classification of North American freshwater invertebrates*, the scope of which is intermediate between Klots' field guide and Hyman's encyclopedia.

Indianan Shelby Gerking (1918–1998) earned his Ph.D. at the Indiana University (1944) and joined its faculty until 1967, when he moved to the Arizona State University. His chapter 7, Central States (1963) discussed Indiana, Ohio, Kentucky, and Tennessee. He noted that Carl Eigenmann of the Indiana University established a lake biological station in 1895 and David Kellicot of the Ohio State University established a comparable station in 1896, both stations for research, but teaching soon became important at both. "Students from both establishments [universities] were largely responsible for the early progress of limnology in the Central States" (Gerking 1963:239). For geographical reasons, "research on streams and reservoirs characterizes the limnology of the region better than does the lake work," since the former were more common than lakes (1963:239). Nevertheless, Gerking's

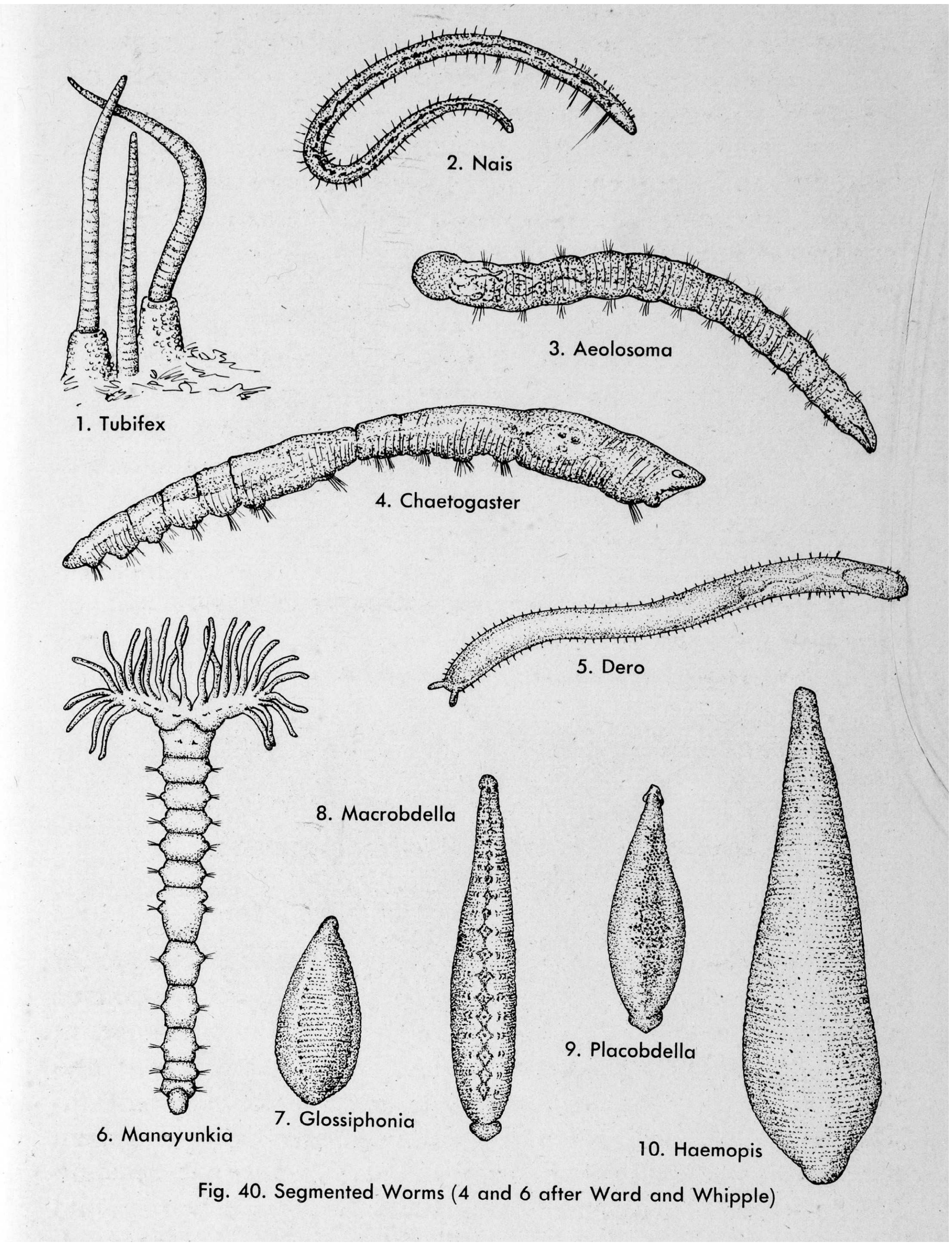


Fig. 15. Segmented worms (4 and 6 after Ward and Whipple). Klots (1966:127).

discussion of "Streams" only occupied 1.5 pages (1963:249–250), which may indicate that limnology of rivers and streams was more difficult and less popular for research than on lakes and ponds. This chapter did not include Ohio's Stone Laboratory, which was included in chapter 19 on the Great Lakes (Beeton and Chandler 1963, see below). Reservoirs that Gerking discussed included those behind dams in the extensive Tennessee Valley Authority, constructed during the 1930s and 1940s

(McDonald and Muldowny 1982). Milton B. Trautman's *The Fishes of Ohio* (1957) was "the finest documentation of the fish fauna of any state" (Gerking 1963:264). Gerking did not cite Edward H. Brown (1960), Jr., *Little Miami River Headwater Stream Investigations: The Fisheries in Relation to Land-use Improvement and to Hydrological Conditions*. David G. Frey (1915–1992), editor of Limnology of North America, was also on the faculty of Indiana University and conducted research on Indiana limnology.

James Yount included a brief historical summary of previous limnological investigations in his chapter 8, "South Atlantic States," covering Virginia, North Carolina, South Carolina, Georgia, and Florida (Yount 1963:269–271). A notable zoologist, South Carolinian Robert E. Coker (1876–1967), earned his B.S. and M.S. degrees at the University of North Carolina (1896, 1897) and Ph.D. at the Johns Hopkins University (1906). He then held several government positions before returning

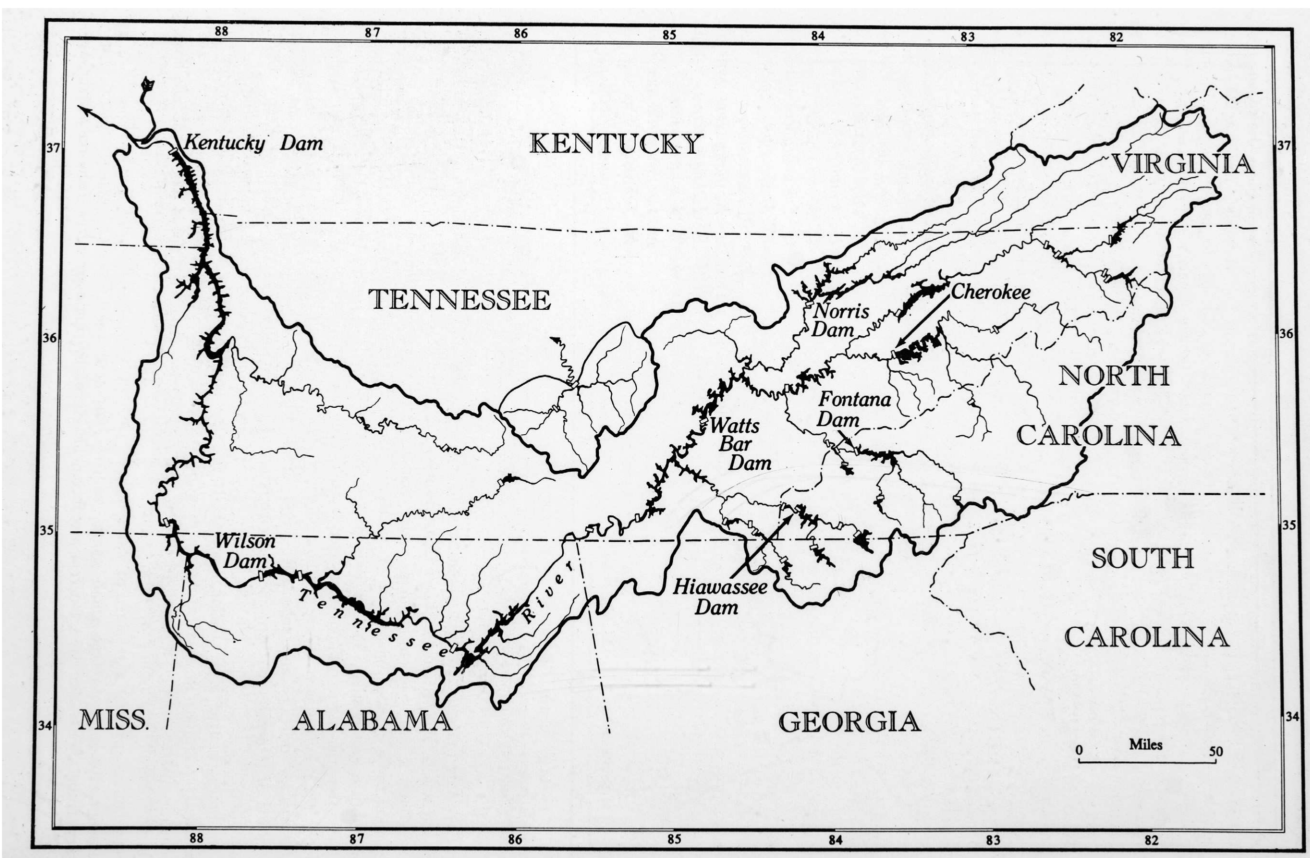


Fig. 7.2.—Map of Tennessee Valley Authority. Only reservoirs referred to in the text are identified. Prepared by the University of Wisconsin Cartographic Laboratory.

Fig. 16. Map of the Tennessee Valley Authority. By Amalia Avramidou. Gerking (1963:242). Courtesy University of Wisconsin Press.

to the University of North Carolina as professor of zoology, 1922–1947 (Lehman 1969, Burgess 1996:27). His researches included both limnology and marine ecology. An example of the former was his *Streams, Lakes, Ponds* (1954), which was a semipopular work, with 15 landscape photographs and seven fish species. However, it also had numerous drawings of aquatic plankton, aquatic plants, and invertebrates. The book went into some detail, but with few technical terms; it was published by the University of North Carolina Press. A virtue of this book was its treatment of the limnology of flowing water. For example (1954:140),

> *The potential effect of current on drifting life becomes impressive if we imagine a copepod in a stream flowing at the rate of two miles per hour, or 48 miles per day. The rate of development from egg to mature breeder varies with temperature and food; but, if we take a reasonable developmental period of 15 days, it is evident that the copepod hatched at one place in the stream might arrive at maturity more than 700 miles farther down the river, where all physical, chemical, and biological conditions are greatly different. In actuality the travel downstream might be interrupted some by temporary sojourns in the eddies and pools that break the uniform flow of the river.*

A much later south-eastern ecologist was Howard T. Odum (1924–2002), whose early years are summarized above, among Hutchinson's doctoral students. Odum subsequently held several positions (including two years in the Duke University Zoology Department, 1954–1956, where he taught me) before settling at the University of Florida in 1970 (Hall 1995, Brown and Hall 2004, Egerton 2015*a*: 99–102). Odum's most important contribution to limnology was his "Trophic structure and productivity of Silver Springs, Florida," with its often-reproduced energy-flow diagram (Odum 1957:61). Here is an early evaluation (Kormondy 1965:188):

The significance of this paper lies in its extensive application of Lindeman's trophic-dynamics concept. It has been a model for subsequent studies on different ecosystems. It also introduced an energy flow model which has had successful instructional value in incorporating the various energy relations of an ecosystem into a readily comprehensible pattern.

Two later evaluations are by Golley (1993:68–70, 78) and Kemp and Boynton (2004). As with Lindeman (1942), this study's significance went beyond limnology, which diverts attention from its significance for limnology. It was an early study of the ecology of flowing water, though a special case in which both flow and climate were constant.

In a year earlier, more general paper, Primary Production in Flowing Waters, Odum (1956:102) commented:

> *A large literature exists on the limnology of streams and the biology of flowing sea waters, but apparently studies on community function have rarely been oriented to obtain information on primary production…. This is very peculiar because the continual mixing makes in situ measurements of production very simple in flowing water.*

At first reading, the first sentence seems surprising, since studies on limnology of American streams by 1956 do not seem abundant, but then one notices that his generalization included sea waters, and his bibliography shows he cited marine studies, European papers (beyond the scope of part 57 of this history; see Elster 1974:14–15), and studies on stream pollution published in sewage studies journals. He did cite three papers by Americans on stream limnology: Denham (1938), Pennak (1943), and Shelford and Eddy (1929). He overlooked Sullivan (1929), "Notes on the aquatic life of the Niangua River, Missouri, with special reference to insects" and Edwin B.

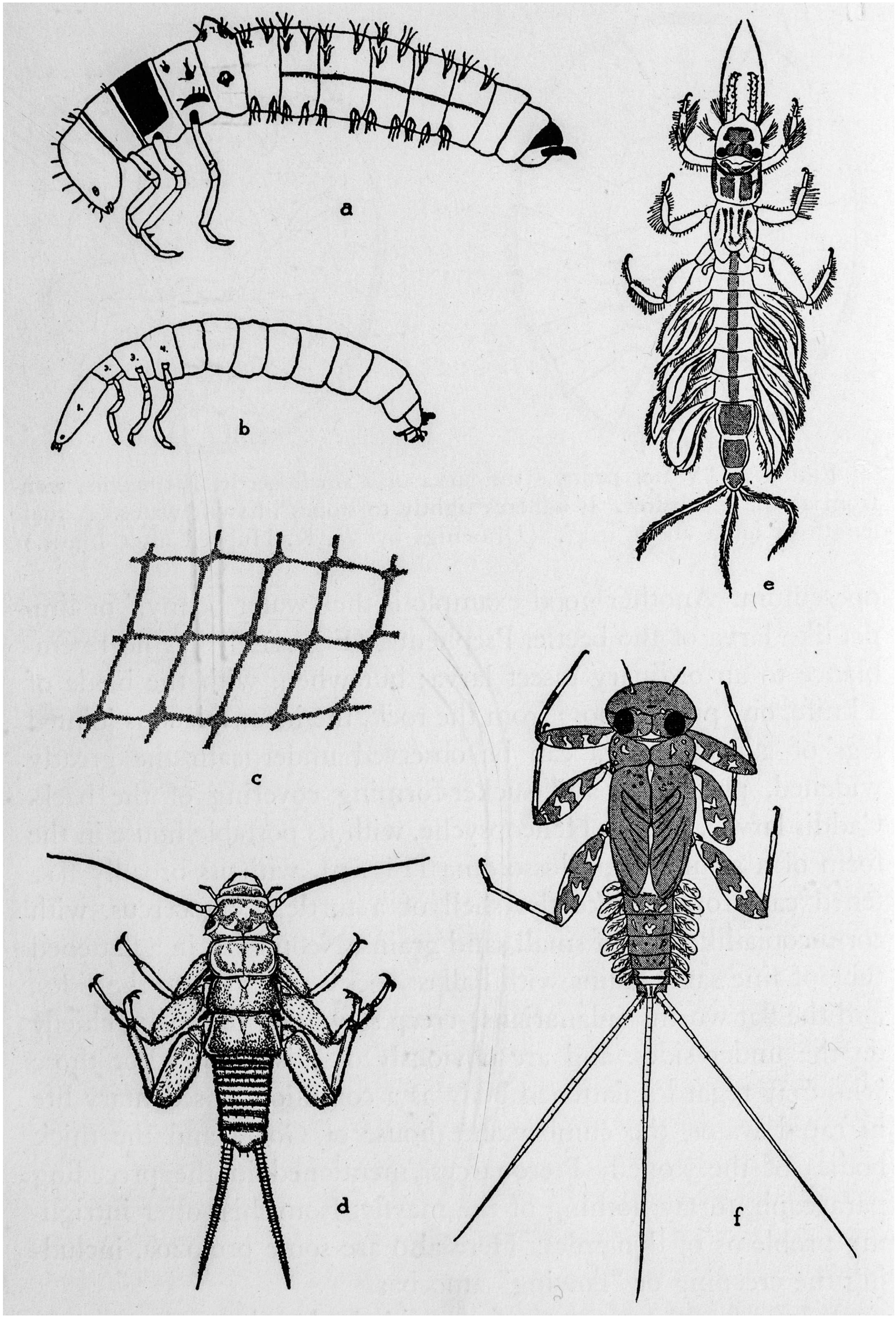


Fig. 17. Insects of streams. Coker (1954:108). Courtesy University of North Carolina Press.

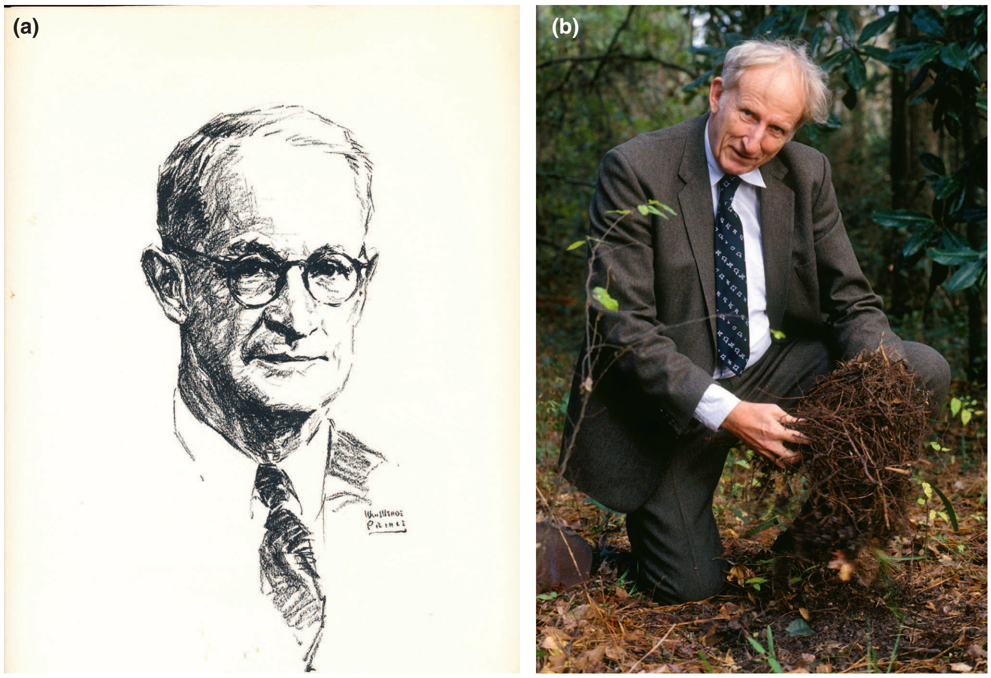


Fig. 18. (a) Robert E. Coker. (b) Howard T. Odum. a—Courtesy Coker family and UNC Institute of Marine Services; b—Wikipedia.

Powers, Fresh Water Studies. I. The Relative Temperature, Oxygen Content, Alkali Reserve, the Carbon Dioxide Tension and pH of the Waters of Certain Mountain Streams at Different Altitudes in the Smoky Mountain National Park (Powers 1939), which, incidentally, deserves an award for length of title.

In both HT Odum's 1956 and 1957 papers, a contrast is obvious between Coker's and his approaches to stream limnology. Coker studied ecological roles of individual species; Odum studied the functioning of ecosystems, with no mention of individual species.

The U.S. Forest Service's Coweeta Hydrologic Laboratory is in western North Carolina, a two-hour drive north of Athens, Georgia. Illinoisan ecologist Charles R. Hurst (1895–1988), who had a B.S. degree from the University of Missouri (1917) and Ph.D. from the University of Minnesota (1923), joined the Forest Service in 1926, and by 1931, he focused upon the Coweeta basin as a research site (Hursh and Barret 1931, Douglass and Hoover 1988, Swank et al. 2001). In 1934, he founded this laboratory for the Forest Service, and it has continued to sponsor research ever since. It may have been the earliest location for a comparison of a logged hillside with a comparable forested hillside, beginning in 1939. During the 1930s, the Civilian Conservation Corps built facilities for the Forest Service at Coweeta. By mid 1950s, numerous visitors had visited Coweeta to learn watershed management. In 1967, Eugene Odum asked the Forest Service if a University of Georgia graduate student could pursue a dissertation study at the Coweeta watersheds. That was acceptable, and so other dissertation studies followed, often funded by NSF. Later, such studies fit into the IBP Eastern Deciduous Forest Biome Project. There is now a wonderful volume on *Forest Hydrology and Ecology at Coweeta* (Swank and Crossley 1988), with 49 authors writing 30 chapters.

Detroit native Walter Guy Moore (1913–) earned his B.A. degree at the Wayne State University (1934) and his M.A. and Ph.D. at the University of Minnesota (1938, 1940), then settled at the Loyola University, New Orleans. His chapter 9, "Central Gulf states and the Mississippi Embayment" (Moore 1963) discussed Alabama, Mississippi, Louisiana, and Arkansas. The Mississippi River is a conspicuous geographical feature in this region and Moore discussed it geographically, but not limnologically. Oth-

Fig. 19. Research construction to study hydrologic cycle at Coweeta. U.S. Forest Service.

erwise, the dominant aquatic environments are also rivers and streams, on which Moore wrote nothing. It may be an unfair comparison, but popularizer Virginia S. Eifert (1959) had published River world: wild life of the Mississippi, and Professor Robert Usinger, University of California, Berkeley, who had earlier edited Aquatic insects of California (1956), published four years after Moore's chapter a popular book, *The life of rivers and streams* (Usinger 1967).

Chapter 11, "Mid-continent states" (Carlander et al. 1963) includes Iowa, Missouri, Nebraska, Kansas, and Oklahoma. Aquatic environments in this region include many rivers, some lakes, and numerous ponds. The east and west boundaries of Iowa are defined by the Mississippi and Missouri Rivers, and the eastern boundary of Missouri is defined by the Mississippi, with part of Missouri's western boundary being defined by the Missouri River. The numerous other rivers of this region flow into one of these two major rivers. The discussion of rivers in this chapter extends over more pages (6.5) than do pages on other topics. Glaciers in the past did extend south into the three northernmost states of this region, and there are some natural glaciated lakes in addition to numerous man-made farm ponds. Fourteen biology research centers are mapped and briefly characterized (Carlander et al. 1963:318–319).

One center is the Iowa Lakeside Laboratory, on glaciated Lake Okoboji; its early history was summarized in Part 50 (Egerton 2014*a*:145). Its stone buildings were built by the Federal Civilian Conservation Corps during the 1930s (Lannoo 2012). Debby Zieglowsky-Baker compiled an impressive "Eighty years of research at Iowa Lakeside Laboratory: a bibliography" (1990), which contains ingredients for a history of limnology at that laboratory. Professor Michael J. Lannoo thinks (*personal communication*, 16 October 2015) that there was little limnology research done in northern Iowa after Birge and Juday's (1920) "A limnological reconnaissance of West Okoboji" until the 1960s, though Chicagoan Richard Bovbjerg (1919–) joined the Zoology Department, University of Iowa, in 1957 and was soon visiting the Lakeside Laboratory in summers. He published 24 papers—alone or with a collaborator, 1957–1981—on aquatic invertebrates (Zieglowsky-Baker 1990:191). Lannoo stated that limnology returned to the Lakeside Laboratory in the 1960s, after limnologist Roger Bachmann (b. 1934) joined the Zoology Department, Iowa State University in 1963. Bachmann was from Ann Arbor and had two degrees from the University of Michigan (B.S. 1956, Ph.D. 1962). Zieglowsky-Baker (1990:190) listed only three papers in which Bachmann was sole or senior author.

Illinoisan limnologist Sammuel Eddy (1897–1972) earned his M.A. and Ph.D. (1925, 1929) at the University of Illinois under Shelford, and in 1929, he joined the University of Minnesota faculty (Burgess 1996:38). His chapter 10 surveyed limnology in Minnesota, South Dakota, and North Dakota (1963). However, Eddy noted that few limnological studies had been made in the Dakotas. Minnesota has numerous glacial lakes which Eddy (1963:312–313) discussed, and he also devoted almost two pages to rivers. Although the major rivers had dams and impoundments which he also discussed, Eddy at least saw the need to discuss river limnology. An Eddy student was Raymond Lindeman (1915–1942), who wrote his Ph.D. dissertation on succession in Cedar Bog Lake, near the University of Minnesota (1941).

Milwaukeean Robert Pennak (1912–) earned his B.S., M.S., and Ph.D. from the University of Wisconsin (1934, 1935, 1938, under Juday), then settled at the University of Colorado, Boulder for his career. His "Limnological variables in a Colorado mountain stream" (1943), mentioned above, was on Boulder Creek, which runs through the town. He measured physical and chemical conditions and phytoplankton and zooplankton. His chapter 12, "Rocky Mountain States" (Pennak 1963), included Colorado, Utah, Wyoming, Montana, and Idaho. His general map of these states (1963:350) enumerated 32 locations of limnological interest, which he discussed. Those sites included Rocky Mountain, Yellowstone, and Glacier national parks. His map indicates the general location of the Arkansas, Colorado, Columbia, Missouri, and Rio Grande rivers, none of which carried a number indicating a discussion. His four regional maps indicate the paths of numerous rivers and streams, only five of which were named; the focus of his regional maps was to indicate locations of lakes and impoundments. Pennak was a productive researcher, and his chapter bibliography listed 11 of his own publications, but not his *Freshwater Invertebrates of the United States* (1953, edition 3, 1989).

Edmondson (1963), discussed above as Hutchinson's first student, wrote chapter 13, Pacific coast and Great Basin, which included California, Nevada, Oregon, and Washington. He had been at the University of Washington since 1949, and he was heavily involved in research on Lake Washington, on which his article devoted over two pages (1963:373–375). He also devoted about a page to the Columbia River, which was by then far from pristine; Grand Coulee Dam was largest of dams and reservoirs that created obstacles for migrating salmon. He did not discuss the status of salmon in the Columbia in 1963. Most of his biological discussion of the Columbia concerned plankton. For Oregon, he only discussed the unique Crater Lake in the Crater Lake National Park (1963:383–384). For California, he cited and discussed Norman Reimers (1957), "Some aspects of the relation between stream food and trout survival" and Reimers, Maciolek, and Pister (1955), Limnological Study of the Lakes in Convict Creek Basin, Mono County, California. Among other lakes and ponds which he discussed in California, he also discussed the novelty of the Salton Sea, which has salt water and is below sea level (1963:386–387). Otherwise, he gave a bibliography on California limnology because the literature was too voluminous for him to discuss it all. Instead of a specific discussion of Nevada limnology, he discussed the Great Basin (1963:388), which includes most of Nevada, but also parts of Utah and Oregon.

Hartford, Connecticut native Gerald Cole (1917–) earned his B.A. degree (1939) at the Middlebury College in Vermont, and his Ph.D. (1949) at the University of Minnesota, Minneapolis. In 1958, he joined the faculty of Arizona State University, Tempe. His chapter 14, The American southwest and Middle America (1963) included Arizona, New Mexico, Oklahoma, Texas, and Middle America (discussed below). He included two full-page maps, one on the U.S. states, with 45 enumerations of lakes and reservoirs discussed. After his general survey, he turned to particular lakes throughout the regions. Later, he published a Textbook of Limnology (Cole 1975, edition 2, 1979).

Neel's (1963) chapter 21 focused its 20 pages upon the "Impact of reservoirs" in seven adjacent states: Montana, North Dakota, South Dakota, Wyoming, Nebraska, Colorado, and Kansas. European settlers built numerous small dams on rivers in these states, but Neel only discussed reservoirs with 50,000 or more acre-feet, especially those on the Missouri River. He also compared reservoirs with natural lakes, and discussed the effects of reservoirs on streams below dams. John Dendy's (1963) chapter 22 was on "Farm Ponds" in the United States, most of which were man-made; he emphasized climate in managing them for harvestable fish. In antiquity, middle ages, and early modern times, fish ponds raised common carp *Cyprinus carpio*, an omnivore, for food. However, that European and Asian custom did not transfer well into North America, where few people wanted to eat bony carp. Denny provided a map showing which parts of 48 continuous states were suitable for raising trout, and numerous lists of fish suitable for ponds elsewhere. Carlander et al. (discussed above) also included sections on, reservoirs and farm ponds (1963:327–330).

Chapter 19, The St. Lawrence Great Lakes, was by U.S. Fisheries biologist Alfred Beeton, U.S. Fisheries Laboratory, Ann Arbor, Michigan and University of Michigan limnologist David Chandler (discussed above). Chandler was the only U.S. author who wrote two chapters, though as coauthor in this chapter. This chapter was also the only one involving two nations—Canada north of the lakes and the United States south of them. These lakes were very productive of fish before Europeans settled along their shores, since the amounts of fish which American Indians harvested annually had a negligible impact on fish populations (Bogue 2000:5–9). For European settlers, the fish were a bonanza, for the fishermen could not only harvest enough for their families and neighbors but they could also sell fish in the growing cities around the lakes (Bogue 2000:12–330).

Lake Erie is, by far, the smallest and shallowest Great Lake, which contributes to it being also the most productive of fish, for two reasons: nutrients get recycled rather than sinking into the depths and land near Lake Erie is farmed more intensively than land near other Great Lakes, with fertilizer washing into Lake Erie (Dymond 1964*b*:85, Bolsenga and Herdendorf 1993:258–266). In 1925, Lake Erie's cisco fishery collapsed, with annual catch declining from an average of 20 million pounds to 5.5 million, and in 1928, declining further to 1.9 million (Beeton and Chandler 1963:544–545). The U.S. Bureau of Fisheries began regular Great Lakes research beginning in 1927, under fisheries biologist John Van Oosten (1891–1966), which focused attention on catch data (Van Oosten 1930, Smith 1957, Hile 1966). The Franz Theodore Stone Laboratory at Put-in-Bay, near Toledo—run by Ohio State University—did likewise (Langlois 1949, Abrams and Taft 1971), and its director, ecologist Thomas H(uxley, called "Hux") Langlois (1898–1968), wrote a landmark synthesis, *The Western End of Lake Erie and Its Ecology* (Langlois 1954). The western end has the shallowest waters of Lake Erie and also has the greatest abundance of fish in the lake. The Ohio Lab focused attention upon limnological data. The Bureau attributed fishery collapse to overfishing, and the Ohio Lab attributed it to water pollution (Egerton 1985, 1987*b*). Neither group had the expertise to discredit the other group's claims. However, Langlois (1964) argued that pollution was driving Lake Erie toward disaster.

Lake Erie has a fairly dense human population along its shores, and it has had the most serious environmental problems. Two limnologically valuable bibliographies on it appeared simultaneously: a compact *Lake Erie Bibliography in Environmental Sciences* (Herdendorf et al. 1974); and a bulky *Annotated Bibliography of Limnological and Related Studies concerning Lake Erie and Influent Tributaries* (5 volumes [Biology, Chemistry, Physical, Engineering, Socio-Economic], Prantner et al. 1974), with different authors for each volume, but all listed here under Elaine Prantner, senior author of volume one.

The Erie Canal, connecting Buffalo on Lake Ontario with Albany on the Hudson River, was completed in 1825, though improvements continued until 1854 (Shaw 1966). Canada, not to be outdone, built the Welland Canal, connecting Lakes Ontario and Erie by going around Niagara Falls (Styron and Taylor 2004). It admitted ships by 1829 and was fully completed in 1833. Sea lampreys were later discovered in Lake Ontario. They apparently had entered by the Erie Canal, since the rapids in the St. Lawrence River had been a barrier to entry from there (Ashworth 1986:114). The first Welland Canal only admitted ships up to 100 feet long, and no lampreys seem to have reached Lake Erie until after enlargements for the third Welland Canal in 1881. By 1900, the commercial annual catch of fish in Lake Erie was 33 million pounds, an unsustainable rate. Sea lampreys were not found in Lake Erie until the 1920s, by which time the large fish to which sea lampreys attach were already scarce. Sea lampreys failed to flourish in Lake Erie, but reached Lake Huron by 1933,

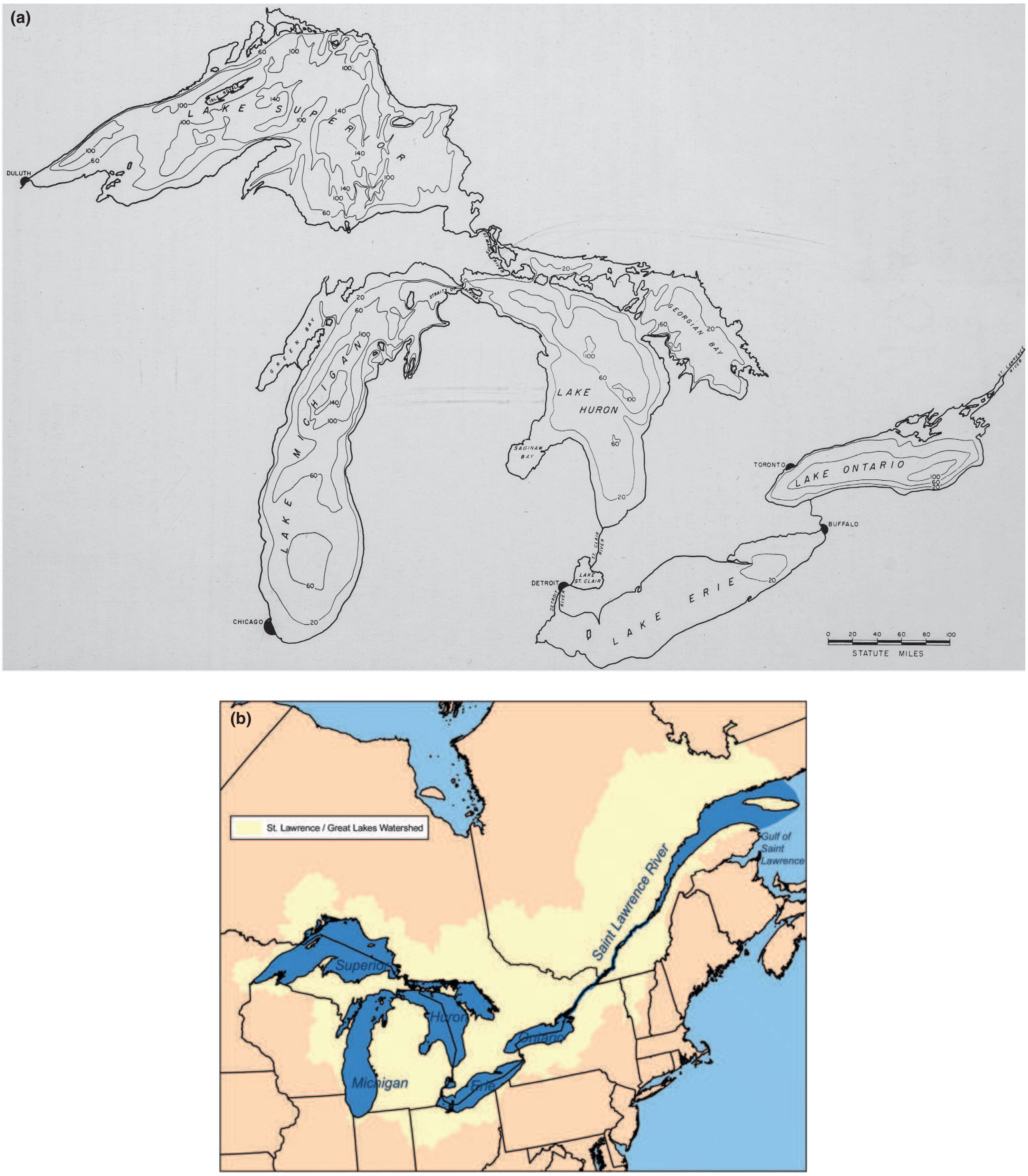


Fig. 20. (a) Great Lakes showing depth contours. Beeton and Chandler (1963:536). Courtesy University of Wisconsin Press. (b) The North American Great Lakes drainage basin. Color map. Wikipedia.

Lake Michigan by 1936, and Lake Superior by 1946 (Ashworth 1986:119, Grady 2007:277–281). Two important developments in the mid-1950s were: the establishment of the Great Lakes Fishery Commission (1954) that would control sea lampreys by erecting physical barriers and by spraying lampricide in the streams where they spawned; the establishment of the St. Lawrence Seaway in 1954–1959, which greatly facilitated the rate of invasions by foreign species (Hills 1959, Ashworth 1986:101–115). Dr. David Garton discovered zebra mussels at the Ohio State University's Franz Theodore Stone Laboratory, west end of Lake Erie, in 1988 and received Sea Grant research funds to study them.

At the 93rd meeting of the American Fisheries Society in 1963, Dr. Athelstan Spilhaus proposed establishment of what became U.S. Sea Grant Institutes. That proposal passed Congress in 1966 and was signed into law by President Johnson. It established a partnership involving government, academia, and industry. In 1971, Sea Grant programs were established at four universities in oceanic coastal states, in 1972 at the University of Wisconsin, in 1973 at the State University of New York (including Cornell University). However, it progressed more slowly to other Great Lakes states: Illinois-Indiana in 1982, in 1985 to University of Minnesota, in 1988 to Ohio State University. These programs received substantial research funds. Research reports appeared in various venues, one of which was the Great Lakes Fishery Commission's Technical Reports, which were made available to interested scholars for free, formerly in paper, most recently online. Some of these reports were narrowly technical, while others were relevant to limnology: Herbert F. Allen et al. (1969), "Limnological survey of Lake Ontario", Alfred M. Beeton (1963), "Limnological survey of Lake Erie, 1959 and 1960", Beeton et al. (1967), "Physical limnology of Saginaw Bay, Lake Huron", F. N. Egerton (1985), "Overfishing or pollution? Case history of a controversy on the Great Lakes", Lee Emery (1985), "Review of fish species introduced into the Great Lakes, 1819–1974", Michael J. Hansen (1990), "Lake Superior: the state of the lake in 1989", Stephen J. Nepszy (1988), "Parasites of fishes in the Canadian Waters of the Great Lakes". The Great Lakes Fishery Commission was interested in the relations of fish populations and the physical environment.

Canada

On the northern side of the Great Lakes, Toronto, Ontario, became a center of studies on limnology and fisheries (Beeton and Chandler 1963:545–546, Fry 1963:489–490, Johnstone 1977, Bocking 1997*a*:165–78). The Ontario Fisheries Research Laboratory, University of Toronto, and eventually, the Fisheries Research Board of Canada also conducted fishery and limnology research at the Great Lakes. (Collaboration between Ontario Fisheries and University of Toronto began in 1913, as discussed in part 50 (Egerton 2014*a*:146–147) An early Canadian limnologist, D(onald) S(trathearn) Rawson (1905–1961), was born near Toronto, and earned his academic degrees at the University of Toronto (B.A. 1926, M.A. 1927, Ph.D. 1929). His doctoral dissertation on bottom fauna of Lake Simcoe "is well known as a standard reference in limnology" (Rawson 1930; Northcote and Larkin 1963:459). Rawson then spent his career at the University of Saskatchewan (see below).

Ontario does have coastal waters at Hudson Bay and James Bay, but most of its fisheries are in fresh waters, and so its aquatic science has emphasized limnology. In 1920, an Ontario Fisheries Research Laboratory (OFRL) was established in the University of Toronto's Department of Zoology. Its director in 1922–1946 was Professor William J(ohn) K(nox) Harkness (1896–1960), who earned two degrees at the University of Toronto (B.A. 1922, M.A. 1923). He began fisheries research while an undergraduate (Dymond 1964*a*:3–4); OFRL emphasized the importance of limnology for fisheries in support of its funding (Bocking 1997*a*:153–154). In 1946–1960, Harkness at the Ontario Department of Lands and Forests increased the catch limits in the Ontario waters of the Great Lakes, arguing that fish populations were controlled by environmental conditions, not by size of spawning stocks (Bocking 1997*c*:164).

However, zoologist Henry A. Regier (b. 1930), who had earned his B.A. degree (1954) at the Queen's University and his M.S. and Ph.D. (1959, 1962) at the Cornell University, also at the Department of Lands and Fisheries, argued in 1962 that walleye had declined in Lake Erie due to overfishing, and Jack Christie (1963), at the Department on Lake Ontario argued that overfishing caused decline of that lake's whitefish. Regier had an academic career at the University of Toronto and also worked closely with the *Fisheries Research Board of Canada*. He wore his fisheries hat more often than his limnology hat, but he was concerned with the environmental conditions in which commercially significant fish species lived. He was a very productive scientist, and three of his publications from 1973 indicate his concerns: he and W. L. Hartman published Lake Erie's Fish Community: 150 Years of Cultural Stresses (Regier and Hartman 1973), in which they discussed fishing pressure vs. environmental factors for at least 10 species. Their map told part of the story; there were five cities on the U.S. shore of Lake Erie and none on the Canadian shore (Regier 1962). He was sole author of "Sequence of exploitation of stocks in multispecies fisheries in the Laurentian Great Lakes" (Regier 1973), in which he expanded his research to encompass all five Great Lakes. He and Francis Henderson then expanded the reasoning from the two other papers to achieve a general model in "Towards a broad ecological model of fish communities and fisheries" (Regier and Henderson 1973). Subsequently, he extended his reasoning in another direction in Science for the Scattered Fisheries of the Canadian Interior (Regier 1976).

Two other limnologists at the University were Dymond and Fry. Toronto native John R(ichardson) Dymond (b. 1887) earned two degrees at the University of Toronto (B.A. 1912, M.A. 1920). English native F(rederick) E(rnest) J(oseph) Fry (1908–1989) immigrated to Toronto and earned three degrees at the University (B.A. 1933, M.A. 1935, Ph.D. 1936) and became a professor there (Bocking 1997*a*:159–162). Fry wrote the chapter 17 survey on Ontario (1963). Two new limnologists at the University of Toronto during the 1960s studied water quality (Bocking 1997*a*:167–168). English immigrant Frank H(arold) Rigler (b. 1928) earned his Ph.D. at the University of Toronto (1954) and then joined the faculty. He studied phosphorus significance, including its pollution problems and its impact on algae growth. Winnipeg native Harold H. Harvey (b. 1930), earned his B.S., M.S., and Ph.D. degrees (1953, 1956, 1963) at the University of British Columbia. At Toronto, he studied declining fish populations and acid lake water in lakes near Sudbury and traced the problem to sulfur dioxide pollution from medal smelters (Bocking 1997*a*:167–168). His fish physiology studies included impacts of acid rain on fish.

OFRL research at Lake Nipissing began in 1921, and it established a laboratory there, 1929–1935, then it moved to Lake Opeongo in Algonquin Park, where Fry and others conducted research (Fry 1963:489). A five-year experiment there was adding fertilizer to Opoeongo's relatively infertile waters. A creel census began there in 1936 and was still ongoing when Fry wrote. In 1960, the Great Lakes Institute was established at the University of Toronto for cooperative research among academic departments. The Royal Ontario Museum of Zoology "has always been closely associated with the University of Toronto and is now an integral part of it" (Fry 1963:490), but later it separated from the university. It served as a repository for animals being studied, including fish and aquatic invertebrates. Ontario is enormous, and there are aquatic research facilities at other universities, including Queen's University, Kingston on Lake Ontario. Fry provided a brief survey of such facilities.

Vianney Legendre, at the Service de la Recherche, Ministère de la Chasse et des Pêcheries, Montreal, Quebec, wrote the chapter 17 survey on Quebec. His map of Quebec enumerated 20 biological stations, listed on the facing page (1963:510–511). Otherwise, his is a bibliographic survey. He was quite interested in the history of Quebec natural history studies (1963:495–506). For example, French navigator Jacques Cartier (1491–1557) discovered and named St. Lawrence Gulf in 1534 and returned there in 1535–1536 and named fish caught or seen: mackerel, mullet, sea bass, eels, lampreys, smelts, salmon, pike, trout, suckers, bream (Pouliot 1934:11–139, cited from Legendre 1963:496). Thomas Herriot (1560–1621), leading physical scientists in Elizabethan England, described on his 1585 trip to New England the gar *lepisosteus*, and Samuel de Champlain (1567–1635) independently discovered it in what is now Lake Champlain in 1609. In other words, both the French and British natural history traditions had simultaneous beginnings in Canada; did that continue? Quebec City native Joseph Bouchette (1774–1841) was in the service of the British, as his father had been, and in 1815, he published in London both an English and a French edition of his Topographical Description of the Province of Lower Canada, that is, Quebec, which discussed aquatic products for southern Quebec. The Natural History Society of Montreal was founded in 1827 and published its Proceedings in 1828–1883. We skip down to Claude Mélançon, who wrote "many books on Quebec aquatic animal groups" (Legendre 1963:506), of which Legendre cited two on Quebec fish (1936) and amphibians and reptiles (1950). Plant geographer Pierre Dansereau (1911–2011) wrote the first essay on correlation between Quebec fish and fresh-water plants (1945) and Cécile Lanquette's M.S. thesis at the University of Montreal (1946) was "the first elaborate study of Quebec fresh-water plankton" (1963:509). Legendre's survey also included a three-page table of institutional reports—government and non-government—on Quebec fresh-waters.

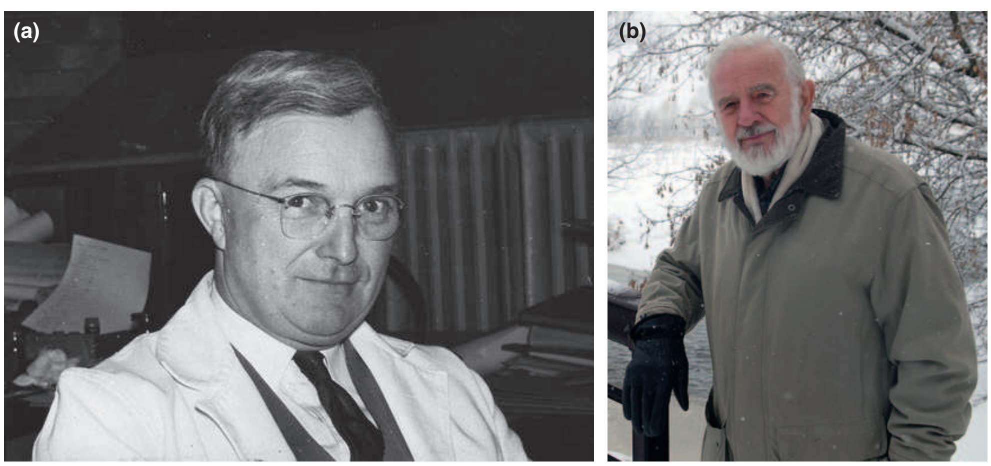


Fig. 21. (a) D(onald) S. Rawson. (b) Henry A. Regier. a—Wikipedia; b—Courtesy H.A. Regier.

New Brunswick native M(orden) W(hitney) Smith (1905–1980), Biological Station, Fisheries Research Board of Canada, St. Andrews, New Brunswick, wrote a 14-page chapter 18, "The Atlantic provinces of Canada" (Smith 1963), on Newfoundland, New Brunswick, Nova Scotia and Prince Edward Island. Smith explained that Newfoundland includes a large part of eastern Labrador. He devoted five pages to physical and climatic features of these provinces and seven pages to limnology, followed by a list of limnological personnel and locations and bibliography.

F(rederick) R(onald) Hayes (1904–1982) was born in Parrsboro, Nova Scotia, and studied zoology at the Dalhousie University, Halifax, and the Liverpool University, Liverpool, England, 1922–1929 (Mills 2013). He returned to the Dalhousie University as an Associate Professor, then Professor, 1930–1964. He and his students and associates investigated since 1945 factors influencing lake productivity. They added radioactive phosphorus to small (4 ha) Bluff Lake, Nova Scotia and attempted to determine its turnover time. In 1964–1969, Hayes served as Chairman, Fisheries Research Board of Canada. His The Chaining of Promethus (1973) "wittly and perceptively explored the subordination of Canadian science to governmental administration" (Mills 2013).

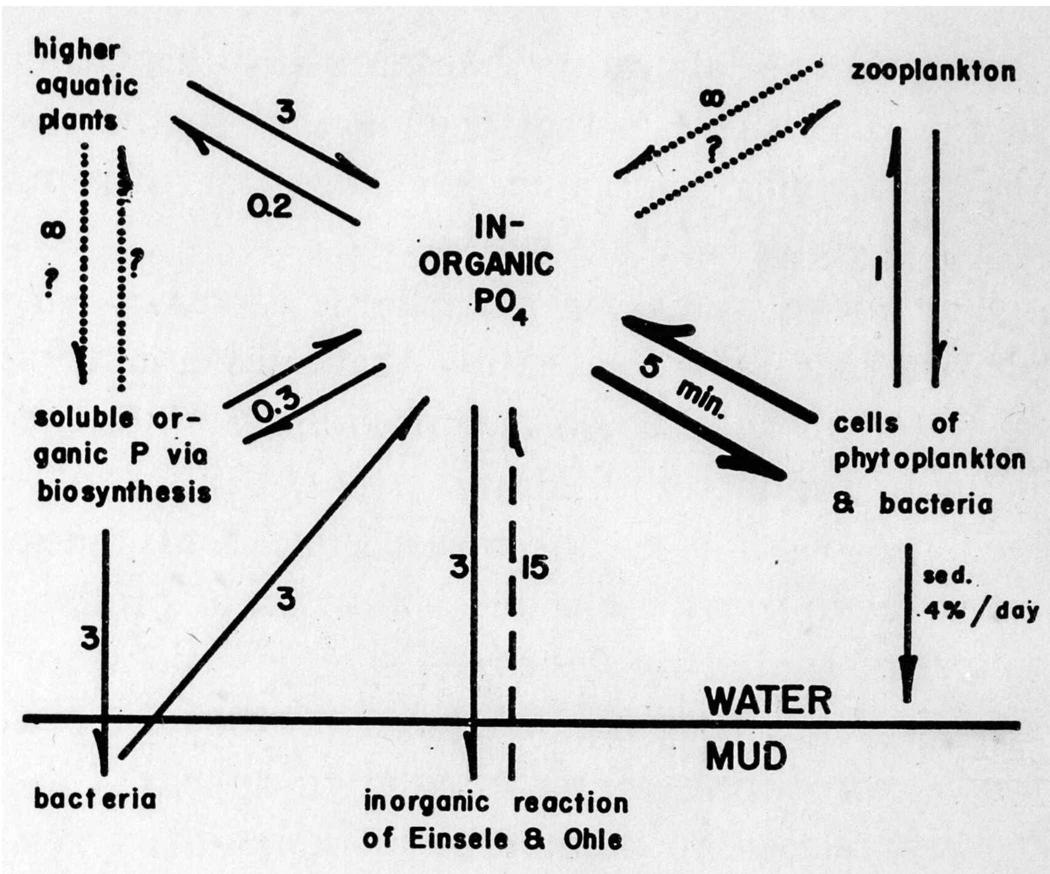


Fig. 22. Transformations of phosphorus in Bluff Lake, with turnover times for different equilibria. Hayes and Phillips (1958:473). Courtesy John Wiley and Sons.

T. G. Northcote and New Zealand immigrant P(eter) A(nthony) Larkin (1924–), at the Institute of Fisheries, University of British Columbia, Vancouver, wrote chapter 16, Western Canada (1963), which covered the enormous region of British Columbia, Alberta, Saskatchewan, Manitoba, and a southern portion of both the Northwest Territories and Nunavut. Larkin earned his B.A. and M.A. degrees (1945, 1946) at the University of Saskatchewan and his Ph.D. at the Oxford University

(1948). Larkin became Chief Fisheries Biologist, British Columbia Game Commission, 1948–1955, then joined the University of British Columbia faculty in 1955. Northcote and Larkin acknowledged that a survey of the limnology on the Western Planes was practically a scientific biography of D. S. Rawson, who went to the University of Saskatoon in 1929 (Anonymous 1961, Northcote and Larkin 1963:451, Bocking 1990*a*, 1997*b*, Hammer 2006, Egerton 2015*a*:38–39). Rawson was very active in researching the productivity of Canadian lakes in Saskatchewan and elsewhere and training graduate students to do so. Rawson also connected lake productivity to fish yield. The Limnological Society of America sponsored a symposium on Problems of Lake Biology at which Rawson spoke on "Some physical and chemical factors in the metabolism of lakes" (1939). He suggested that lakes could be divided into eutrophic and oligotrophic, and various intermediate stages, depending upon magnitudes of physical and chemical factors which he discussed: geology, temperature, oxygen, carbon dioxide, acidity, calcium, nitrogen, phosphorus, iron, silica, and organic materials. Evaluating those factors was complicated, but one should also consider K. M. Strom's admonition to keep a dynamic view by

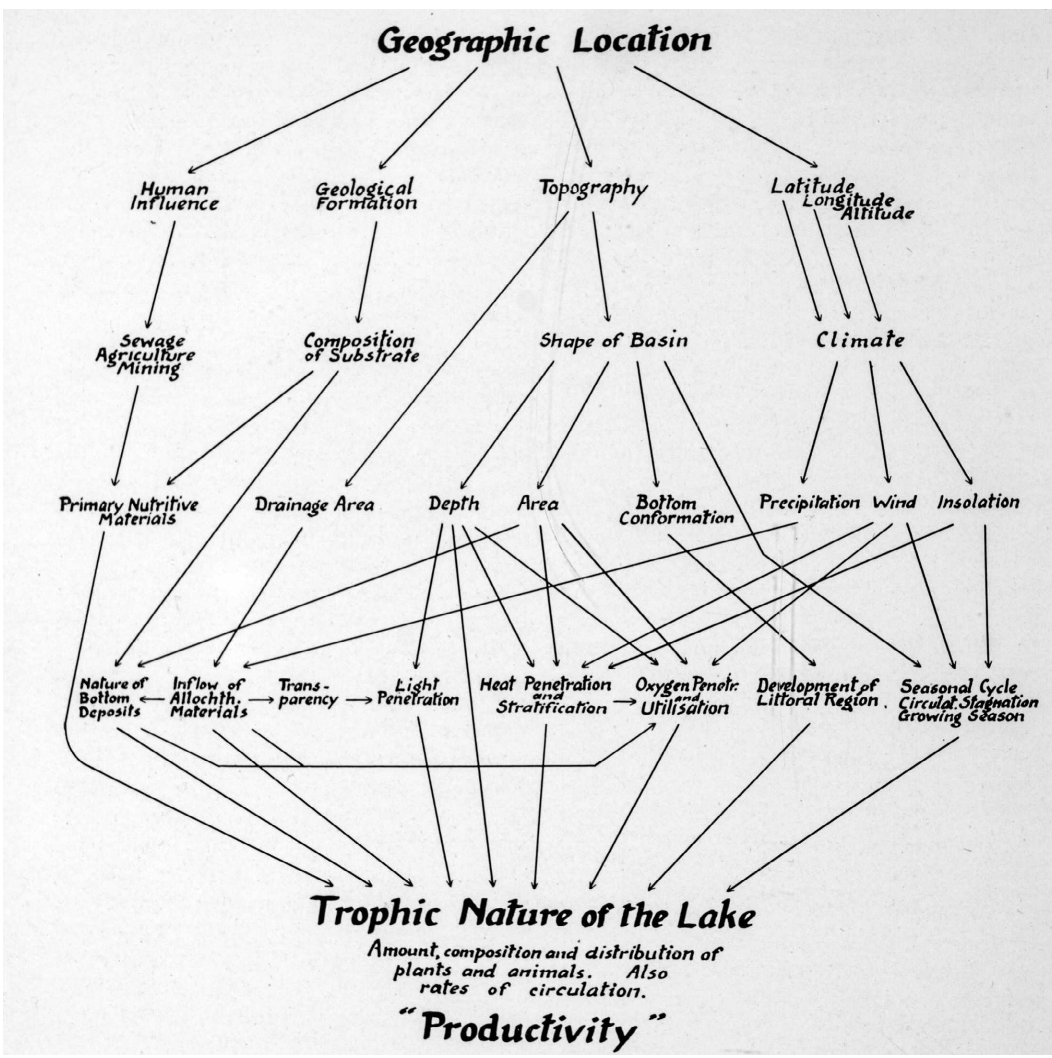


Fig. 23. Interrelations of factors affecting the metabolism of a lake. Rawson (1939:10). Courtesy American Association for the Advancement of Science.

considering time and rates of production. In Rawson's (1939:23) paper, he hoped that "the dissolved organic matter will provide an index to productivity."

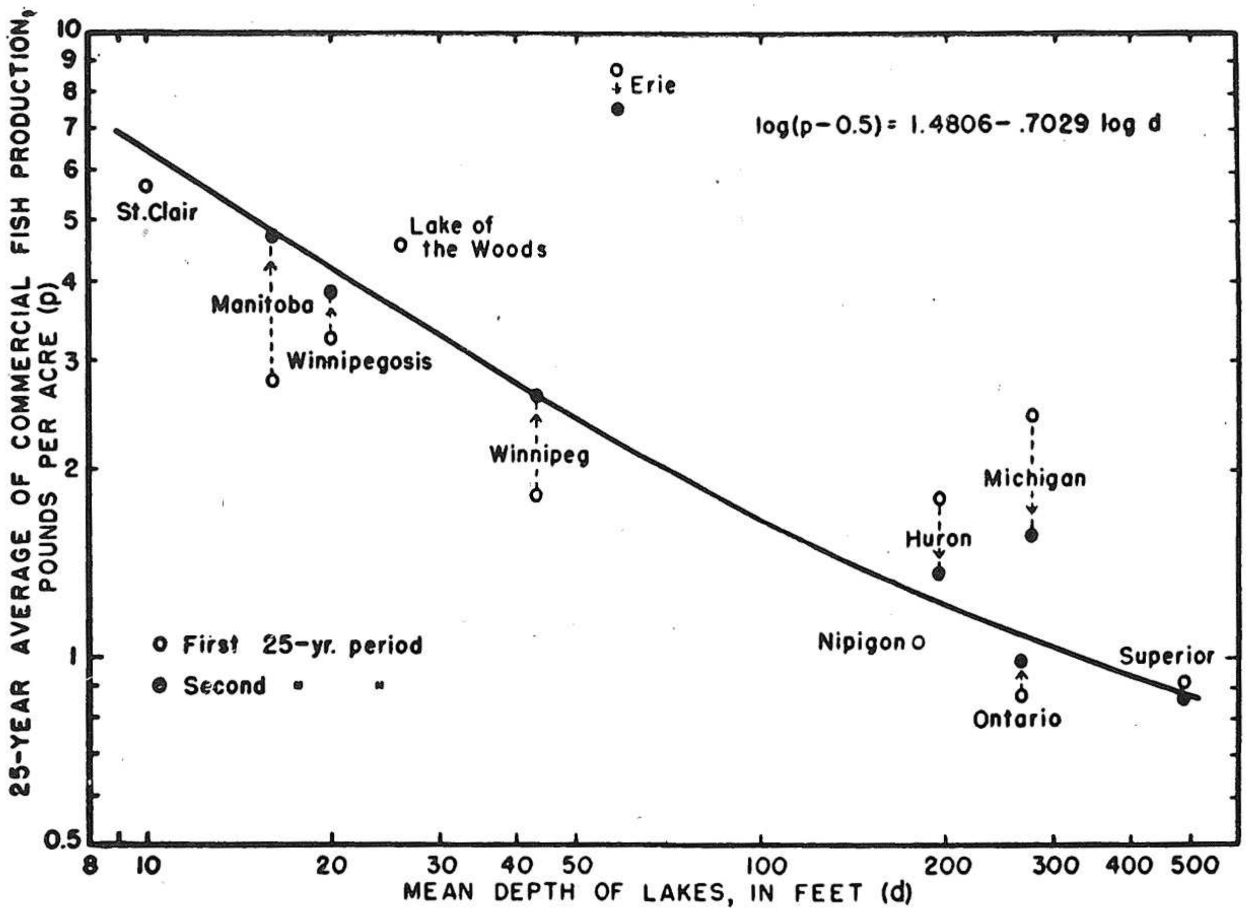


Fig. 24. Logarithmic plot of the relation between mean depth and average fish production for one or two 25-year periods in ll large lakes. One of the Great Lakes, Lake Michigan, lacks any shore in Canada. Rawson (1952:517).

Authors of a survey, "The morphoedaphic index, a fish yield estimator—review and estimation" (Ryder et al. 1974), discussed five of Rawson's papers, published in 1944–1960, but not his earlier papers of 1939 and 1942. Two papers he published in *Ecology* compared similar Canadian lakes (Rawson 1942, 1952). He served as the President of the Limnological Society of America in 1946–1947 and the President of the Canadian Committee for Freshwater Fisheries Research in 1950.

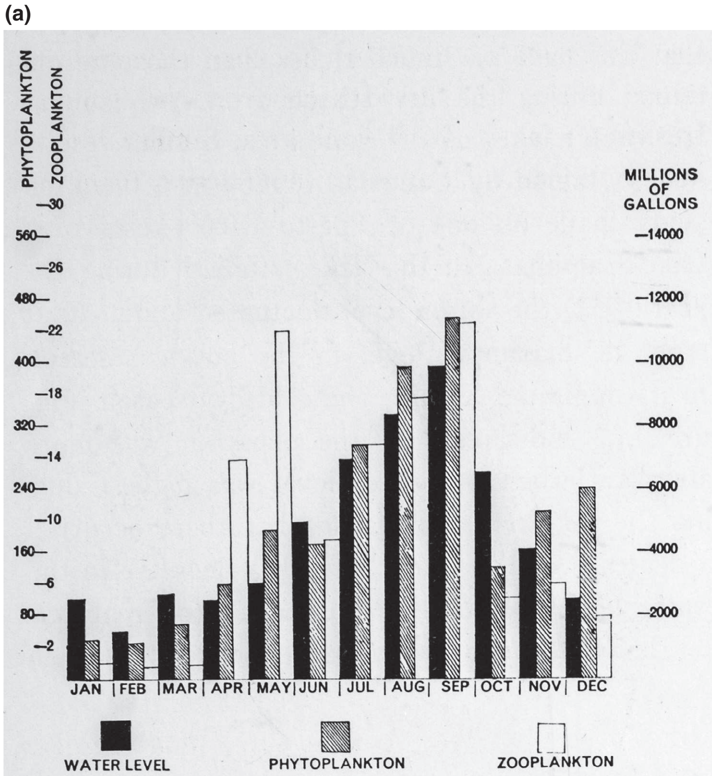
Canadian limnology continued, though I lack enough references to follow its history, except for the University of Toronto fisheries ecologist Henry A. Regier (b. 1930), whose story will appear in part 60 of this history, on the American Great Lakes. A final example illustrates Canadian progress. D. W. Schindler and eight coauthors at the Department of Fisheries and Oceans, Freshwater Institute, Winnipeg collaborated on experimentation: Long Term Ecosystem Stress: the Effects of

Years of Experimental Acidification on a Small Lake (1985). The location was "Lake 223, a small Precambrian Shield lake surrounded by virgin boreal forest in the Experimental Lakes Area, and typical of poorly buffered small lakes of northwestern Ontario" (Schindler et al. 1985:1395). They found, among other things, that some laboratory experiments were not validated by lake experiments.

Mexico, Central America, and West Indies

Canada's progress in limnology and ecology kept pace with that in the United States because both spoke the same language and had been part of the same scientific culture. In contrast, Mexico, Central America, and the West Indies mainly spoke Spanish, and U.S. and Canadian scientific influence did not have much impact until after World War II. Cole's chapter 14 (discussed above) also included a discussion of Mexico and Central America, with a good map that identified locations, but without enumerations of places discussed (1963:399). On Mexico: "We know little about limnology over much of this vast country," though he cited over a dozen relevant papers by Mexican biologists. José Sarukhán (1981:35) published a brief survey of Mexican ecology, in which he commented:

(a)



(b)

Average physical and chemical conditions of Lake Caonillas during the two main climatic seasons

		Hot wet season (May to Oct.)	Cold dry season (Nov. to April)
Temperature (°C)	Surface	29.6	26.4
	Bottom	27.4	23.5
Color (ppm)		26	28
*p*H	Surface	7.56	7.40
	Bottom	7.04	6.95
Visibility (ft)		3.66	3.83
Total alkalinity (ppm)	Surface	89.8	87.0
	Bottom	101.7	93.0
Carbonate (ppm)	Surface	13.3	14.33
	Bottom	0.0	0.0
Bicarbonate (ppm)	Surface	76.4	72.8
	Bottom	101.7	89.7
O_2 (ppm)	Surface	8.5	10.7
	Bottom	2.4	3.6
Free CO_2 (ppm)	Surface	0.0	0.0
	Bottom	5.0	5.6

Fig. 25. (a) Seasonal fluctuations of phytoplankton and zooplankton and water level of Lake Caonillas during 1952. (b) Average physical and chemical conditions of Lake Caonillas during the two main climatic seasons. a—By Amalia Avramidou; b—Candelas and Candelas (1963:438). Courtesy University of Wisconsin Press.

> *The area of ecology that has had the most recent development, marine and aquatic ecology, was originally the pursuit of isolated individuals. It has experienced a major stimulus in the last five to seven years from federal and international agencies interested in the exploitation of marine and freshwater resources. As a result, a number of young biologists have been attracted to the field, many of whom are still in the stages of postgraduate training or, having completed it, are just starting to develop their research.*

For El Salvadore, Cole cited eight relevant papers (1963:416–417), all by U.S. zoologists, which was typical for the Central American states. The Handbook of contemporary developments in world ecology contains only one chapter on a Central American country, COSTA RICA (Fournier-Origgi 1981). It provides an excellent general summary, but does not discuss limnology.

Chapter 15, The West Indies, was by two biologists at the University of Puerto Rico, Gustavo A. Candelas and Graciela C. Candelas. In addition to a general map, they provided maps of the five largest islands of the West Indies, showing rivers, lakes, and reservoirs. They also provided good geographical information. However, "A review of the literature has shown a conspicuous lack of research in relation to freshwater habitats in the Caribbean" (Candelas and Candelas 1963:440). Their respectable bibliography included only one such work, from Gustavo Candelas, Studies on the freshwater plankton of Puerto Rico (1956), and none from Graciela Candelas. Gustavo's research was conducted at Lake Caonillas, a reservoir. They emphasized research opportunities which the West Indies provided for limnologists. Herminio Lugo Lugo surveyed developments in Puerto Rican ecology (Lugo 1981) without mention of limnology. He did cite N. L. Britton et al. (1916–1943): *Scientific Survey of Puerto Rico and the Virgin Islands* (18 volumes), New York Academy of Sciences, which presumably contains ecological information, and perhaps limnological information.

Conclusions

During the last two-thirds of the 1900s, Hutchinson and Hasler were world leaders in limnology. Immigrant Hutchinson's contributions to science were not limited to limnology, but in limnology, he authored or co-authored numerous articles and surely published the longest treatise organized and largely written by a single ecologist, and he supervised the doctoral dissertations of a number of other outstanding ecologists. Utah native Hasler published a few general commentaries, but stuck more closely to limnology. He also authored or co-authored numerous articles and two books and supervised masters' theses and doctoral dissertations of more students than Hutchinson, though fewer of his students assumed leadership positions than did Hutchinson's students. The distinctive feature of Hasler's school was his emphasis upon experimental limnology, in rivers and lakes. Hasler was also an institution builder, symbolized by the Laboratory of Limnology which he had built on the University of Wisconsin-Madison campus, on the shore of Lake Mendota, which is now the most scientifically studied lake in the world. He also brought the first American meeting of the International Association for Limnology to the University of Wisconsin campus in 1962. The valuable influence of both limnologists was widespread and continues. During the mid-1930s, Hasler on the Piankatank and York Rivers and Hurst at Coweeta, independently initiated experimental studies of rivers. Rawson in Saskatchewan trained limnologists in a comparable way for Canadians as Hutchinson and Hasler were doing in the United States.

The Erie Canal, connecting the Hudson River and Lake Ontario, and completed in 1825, may have allowed sea lampreys to invade that lake, where they maybe remained for a century without progressing further. The Welland Canal, connecting Lakes Ontario and Erie, was initially completed in 1833, but only after enlargements later were sea lampreys discovered in Lake Erie, from which they invaded Lakes Huron, Michigan, and Superior. The crisis of sea lamprey attacks on large fish prompted Canada and the United States to establish the Great Lakes Fishery Commission that developed and applied barriers and a lampricide to control sea lampreys and then undertook other projects. Completion of the St. Lawrence Seaway in 1959 opened a floodgate for further alien invasions into the Great Lakes. In 1966, the U.S. Congress established U.S. Sea Grant Institutes, to provide funding and guidance of research on coastal fisheries and environments, which included states bordering the Great Lakes.

"Missing in action" describes limnology at most rivers during the six decades of this survey. Limnology arose from the study of life in lakes, and was easily extended into the study of ponds and reservoirs. To study rivers and streams required new strategies, which attracted very few adventurous limnologists. Many rivers during this period were polluted. Clarence Tarzwell (1963) addressed aspects of this problem in chapter 24, Sanitational Limnology. Limnology in Spanish-speaking middle America only began after World War II and had made little progress by 1963.

This is a partial survey, based upon historical narratives known to me. Perhaps, others will be inspired to broaden the scope of such narratives.

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