Raymond Laurel Lindeman and the Trophic Dynamic Viewpoint

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Introduction

With its presentation of the Raymond L. Lindeman Award, The American Society of Limnology and Oceanography recognizes each year an outstanding paper written by an author no older than 35 years of age. Raymond Lindeman was an intellectually daring, determined young man whose insightful paper, "The Trophic Dynamic Aspect of Ecology" (Lindeman 1942) has inspired many others and serves as a cornerstone of ecosystem ecology. The gift to establish this ASLO award came from Lindeman's graduate school friend and colleague, the late Charles B. Reif, whose recollections of the young Ray Lindeman (Reif 1986) are a vivid personal account. The now-famous story behind the rejection and ultimate publication of Lindeman's Trophic Dynamic paper was told by Cook (1977) and is not repeated here. The main focus here is on the Minnesota years, on Raymond Lindeman the graduate student, because that part of the story has so far been relatively neglected. My main focus in delving into the Raymond Lindeman story was to clarify his scientific breakthroughs and to seek to understand how he came to them, who or what influenced him, and how his work departed from the prevailing practices. Background includes the aforementioned works as well as several other biographical and historical and interpretive studies (Lindsey 1980, McIntosh 1985, Kingsland 1991, Hagen 1992, Sobczak 2005, Brady 2008). This telling builds upon those previous works by the use of archived files of Lindeman's and others, as well as recent interviews of individuals who knew Raymond Lindeman.

Raymond Lindeman photographed in 1939. [Author recommends 1-column width]

Raymond Lindeman's graduate work began with a traditional examination of different forms of one species of rotifer but by the time he was writing his thesis Lindeman's work departed greatly from the scholarship of the era and embraced the entirety of the aquatic ecosystem. We remember Raymond Lindeman today for his quantitatively based, conceptually driven study of an ecosystem in its entirety, including plants, animals, and other living compartments as well as the nonliving compartments. Lindeman's postdoctoral advisor, G. Evylen Hutchinson (after whom ASLO has also named an award), referred to Raymond Lindeman as "one of the most creative and generous minds yet to devote itself to ecological science" (Hutchinson Addendum to Lindeman 1942). Today, we aquatic scientists continue to

be inspired by Raymond Lindeman's story while we build upon the science that he was so instrumental in creating. The presentation of the Lindeman Award is occasion to recall a life story both compelling and tragic.

Although Raymond Lindeman lived only a short time he "produced more of scientific importance in his brief life than most people have produced in a normal life span."(D. Lawrence letter to Robert E. Cook, January 11, 1975, Lawrence papers, University of Minnesota Archives). His 1942 Trophic-Dynamic paper is widely celebrated but the breadth of his accomplishments may sometimes be overlooked. Raymond Lindeman is best known for developing and advocating a conceptual approach, but he knew his organisms, and as we'll remember here, he built his theory on a solid foundation of his knowledge of natural history and paleoecology.

Publications by Raymond L. Lindeman.

Lindeman, R. L. 1939. Some affinities and varieties of of the planktonic rotifer Brachnionus havanaensis Rousselet. Transactions of the American Microscopical Society **58**:210-221.

Lindeman, R. L. 1941. The developmental history of Cedar Creek Bog, Minnesota. American Midland Naturalist **25**:101-112.

Lindeman, R. L. 1941. Ecological dynamics in a senescent lake. University of Minnesota, Minneapolis, MN. PhD thesis.

Lindeman, R. L. 1941. Seasonal food-cycle dynamics in a senescent Lake. American Midland Naturalist **25**:636-673.

Lindeman, R. L. 1942. Experimental simulation of winter anaerobiosis in a senescent lake. Ecology **23**:1-13.

Lindeman, R. L. 1942. Seasonal distribution of midge larvae in a scenescent lake. American Midland Naturalist **27**:428-.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-418.

Unpublished works.

Intra-specific variation in the rotifer *Brachionus diacanthus* Schmarda (B. angularis Gosse). Submitted to the *Transactions of the American Microscopical Society*, November 18, 1938. Retracted March 26, 1939.

Microfossils in the sediments of a senescent lake, and their succesional significance: a preliminary report. With Eleanor Lindeman.

Raymond Lindeman, born and raised on a Minnesota farm, showed early academic aptitude, and did his graduate work at the University of Minnesota with Dr. Samuel Eddy as his major professor. From there he moved to Yale to work as a Postdoc with Dr. G. Evelyn Hutchinson. His famous trophic dynamic paper took form at Minnesota, was finished at Yale, and was submitted to Ecology where it initially was rejected for publication. After several well-established scientists from Minnesota and Yale wrote in support of the manuscript it eventually was published. Raymond Lindeman's life came to a tragic early end before the paper actually appeared.

Chronology of events in the life of Raymond L. Lindeman. [Author recommends 1.5 column width]

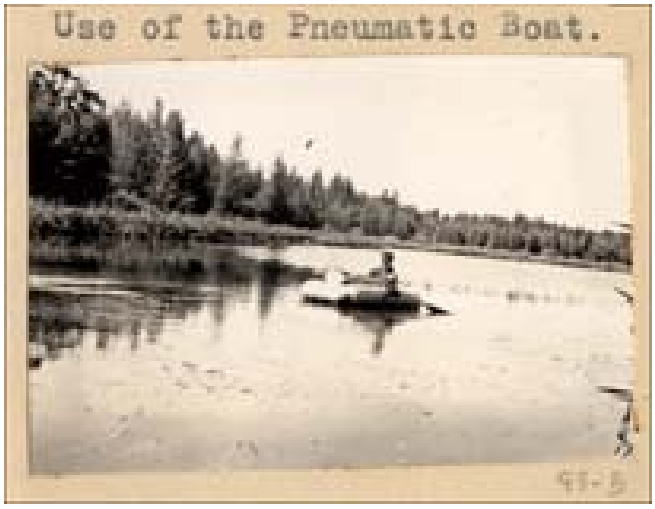
Date	Event
July 24, 1915	Born, Redwood Co., MN
1927	Entered High School
1932	Entered Park College
1935	Attended summer session, University of Minnesota, Itasca field station
Fall, 1936	Received B.A. from Park College, graduated second in class
Summer, 1936	Entered Graduate School University of Minnesota
December 21, 1936	First sampling trip to Cedar Bog Lake undertaken
Date uncertain	Hospitalized with jaundice
December, 1937	Attended LSA/AAAS meeting in Indianapolis, IN
February 26, 1938	Joined Limnological Society of America (ASLO forerunner).
Summer, 1938	Wed to Eleanor Hall
Summer, 1939	Attended Fri day Harbor Summer Session with Eleanor
December, 1939	Met Hutchinson at LSA/AAAS meeting in Columbus, OH
June 24, 1940	Last sampling trip to Cedar Bog Lake
Summer, 1940	Attended Hydrobiology Symposium at Madison and met Deevy.
November 11, 1940	First letter to Hutchinson
Nov 1940	First draft of trophic dynamic paper
December, 1940	Attended LSA/AAAS meeting in Philadelphia, PA, gave paper entitled, Food Chain Dynamics in a Senescent Lake and met Hutchison
February, 1941	Date on his PhD thesis
April, 1941	Awarded Sterling Fellowship to work at Yale
Summer, 1941	Instructor of five-week Field Biology summer course at St. Mary's College, Winona, MN
August, 1941	Arrived at Yale
September, 1941	Cover date on first draft Trophic Dynamic paper to include quantification of trophic levels in energy terms
October, 1941	Trophic Dynamic paper submitted
November, 1941	Trophic Dynamic paper rejected
December, 1941	Attended LSA/AAAS meeting in Dallas, TX and gave a paper with Hutchinson (see text box).
Christmas, 1941 – April 1942	Illness, little work accomplished including hospitalization for 3 weeks shortly after returning from Dallas.
March, 1942	Revised Trophic Dynamic paper was submitted and acceptance was received
April-May, 1942	Hepatic attack with hypertrophy and visceral edema
June 15, 1942	Underwent exploratory surgery
June 29, 1942	Passed away
October, 1942	Trophic Dynamic paper published in Ecology

Lindeman the scientist and ASLO the society had nearly contemporaneous beginnings. Raymond Lindeman began his graduate student training in 1936, the same year in which the Limnological Society of America was formed. The LSA was an affiliate society of the American Association for the Advancement of Sciences, and it was the forerunner society to ASLO (Lauff 1963). The LSA became ASLO in 1948 (Redfield 1956). Lindeman attended the 3rd annual LSA meeting in Indianapolis in 1936, his second year in graduate school, and he joined the society shortly thereafter -- annual dues were $1 (P.S. Welch letter to RL, February 26, 1938, Lindeman papers, Yale University). At this time LSA membership was ~300 individuals (Lauff 1963). He also attended the 1939 LSA meeting in Columbus Ohio,

and it was here that he met Hutchinson for the first time. Lindeman also attended a third LSA meeting in Dallas in 1941 where he gave a talk that he co-authored with Hutchinson. Scientific societies were important then like they are today – not just for communicating science but for allowing individuals to make new contacts and explore career opportunities.

Lindeman's Life

Raymond Laurel Lindeman was the eldest child of Otto and Julia Lindeman, nee Ash. Friends and family called him Ray but we will refer to him here by his full first name. The family rented and farmed property near Clements, Minnesota (FM Interview). Raymond had three siblings. A brother, Myrl Arlo, was two years Raymond's junior. His two sisters were named Ethel B. and Lila Mae (nicknamed Pat). Another member of the Lindeman household was Floyd Mertz, a hired hand. The pursuit of knowledge ran strong in the agrarian Lindemans. Both parents attended an agricultural school (PL Interview) and Otto was sometimes the first of his neighbors to introduce new practices to the farm (FM interview). Myrl obtained a Bachelor of Mechanical Engineering with high distinction in 1941 and a Master of Science in Mechanical Engineering in 1942, both from the University of Minnesota (University of Minnesota, Registrar records). Myrl died, like Raymond, from problems associated with his liver (FM Interview). Ethel specialized in bookkeeping and financial analysis (PL Interview). Ethel helped type Raymond's thesis. Pat's education included a BS with distinction from the University of Minnesota in 1950 (University of Minnesota registrar records). She taught nutrition in community colleges in California for more than 30 years. The family provided direct support to Raymond's research; Pat recalls the Lindeman family helping process his mud samples using tweezers and white bowls (PL Interview). On two occasions Floyd Mertz accompanied Raymond into the field for the regular Cedar Bog Lake sampling (FM Interview). A photograph of Raymond in his inflatable boat on the lake derives from one of these occasions. Raymond was close to his mother. Julia was with him and his wife in New Haven in his final days.



Raymond Lindeman using his "Pneumatic Boat" to sample in July, 1937. The date was indicated on a copy of this photo in the collection of Mr. Floyd Mertz, who sampled the lake with Lindeman on two occasions (FM interview). The photograph from the Raymond Laurel Lindeman Papers, Manuscripts and Archives, Yale

University Library. [Author recommends 1-column width]

As a boy, Raymond had few friends his own age, and he had an early, avid scientific interest, keeping a large butterfly collection in his bedroom (PL Interview). Raymond attended a "country school with eight grades in one room" (PL Interview). His teacher had him take 8th grade tests in 6th grade and Raymond passed them all (PL Interview). Raymond entered Redwood Falls High School in 1927 at age 12 and graduated in 1932. A common and recurring theme among those who recalled Raymond was his intense and not easily satisfied curiosity about the natural world. From multiple sources, we get some inkling about the way Raymond Lindeman threw himself into the subject. He was a "nice fellow but all business," (FM Interview). "Ray was always a very serious and intense worker," said Don Lawrence (D. Lawrence letter to Robert E. Cook, January 11, 1975, Lawrence papers, University of Minnesota Archives). According to Reif (1986), "In all social situations Ray was always polite, serious, and proper, " and "[o]nce Ray decided on a course of action his awareness of time was switched to hold".

His work habits approached relentlessness, perhaps to the point of degrading his already compromised health. For example, Don Lawrence recalled that "he and his wife would work intensively in the field and in the lab for several weeks until he began vomiting blood. Then he would spend some weeks in the hospital on bland diet and then go to work again."(D. Lawrence letter to Robert E. Cook, January 11, 1975, Lawrence papers, University of Minnesota Archives). Alec Hodson, another faculty member during Raymond's graduate school years said, "If it weren't for his wife, who was always around to help him with his work and to see that he got some food into his stomach, I seriously think he would have forgotten to eat."(Finley 1977). Raymond often skipped class to work on his own ideas, but his grades did not suffer (Reif 1986).

An appetite for hard work apparently did not spill over to all life's endeavors. Floyd Mertz recalls that Raymond seldom was involved in the work of the farm, and he never saw Raymond get on a tractor (FM Interview). Raymond was clearly capable of spending long hours outdoors, but from these observations of Floyd Mertz it seems his energy was focused on natural history, not agriculture. From brief comments in his correspondence it seems Raymond had mostly suspicion when it came to organized religion. For example, one letter when discussing potential prospects related to a job opening at Catholic University, Lindeman wrote, "I would like to be able to teach the Truth as I see it and not as some holy so-and-such sees it for me…" (RL letter to C. Reif, August 20, 1940, Lindeman papers, Yale University Archive). Reif (1986) comments that Raymond's political views were left of his own.

Raymond graduated second in his class from Park College, Missouri (Reif 1986). At Park, he was a member of the Chorus, Glee Club, and the manager of the Student Book Exchange (Application for Fellowship for Study in Scandinavian Countries, approximately March 15, 1939, Lindeman papers, Yale Archives). Raymond's enjoyment of singing was also noted by his graduate student friend and officemate (Reif 1986). Apparently Raymond first met his eventual graduate school advisor, Samuel Eddy, while Raymond was doing summer undergraduate studies at the Lake Itasca field station in 1935. An undated, handwritten draft of a letter from Lindeman to Eddy accepts an assistantship to attend graduate school and thanks Eddy for his interest, referring to Itasca in 1935 (Letter from RL to Eddy, Lindeman papers, Yale Archives). A group photograph of Raymond at Itasca survives. University of Minnesota Registrar records confirm he attended during summer, 1935

before he graduated from Park. It is interesting today to note that even in the mid-1930s summer programs such as field stations had a strong influence on the career trajectories of young ecologists. A poem Raymond wrote at Itasca even seems in some ways to foreshadow the trophic-dynamic approach, what with its "hunting and hunted microbes" and its "dynamic worlds". The poem's central theme is the search for understanding amid nature's splendor. This desire ran strong in Raymond Lindeman.

This group photograph hangs at the Itasca Biological Station. It was taken either in 1935 or, more likely, 1937 when Raymond penned the poem presented elsewhere. RL is the second from the right in the back row. Other individuals are not identified. [Author recommends 1.5 column width]

Minnesota's Lake, Itasca,
Hears the great pines bend and sway,
Hears the wild deer's muted whistle
Greet its mate at close of day;
To us now who watch and listen
Cascades through both ear and lens
Fragments of primeval secrets
To o'erwhelm our narrowed kens!
Here we search the placid waters,
Find a microcosmic sea
Wherein hunting, hunted microbes
Eat and live and die, as we.
Here we wander through the forest
Magnitude past all belief;
Yet one shrub is universal
To the aphid in its leaf.
Here beside the lake, Itasca
We have found a rendezvous;
With all Nature's prized beauty
Here about our feet astrew.

To whom Fortune does so favor
That we revel here discern
Dynamic worlds are set before us
Let us humbly seek to learn.
—Raymond Lindeman

Poem by Raymond Lindeman. From http://www3.cbs.umn.edu/itasca/about/poem.shtml. [Author recommends 1 column width]

Raymond met his bride-to-be, Eleanor Hall, at Park College. She was a partner in science as well as life. Eleanor's father was a Professor of Political Science at Albion College (Reif 1986). They were wed in Michigan in the summer of 1938. She apparently then transferred to Minneapolis; attending the University of Minnesota from Fall 1938 through Winter 1941. She received a Bachelor of Arts in Zoology with a minor in French on the same date Raymond received his PhD (University of Minnesota, Registrar records). Raymond's sister Pat described Eleanor as a "very, very loving person" (PL Interview). Eleanor is often described as being with Raymond in the field as well as during long hours in the lab. Don Lawrence wrote, "It is certain that Ray could not have accomplished what he did without the devoted help of his wife. They had no children so she spent all her available time on his projects." (Letter from Don Lawrence to Robert Cook, January 11, 1975, Lawrence papers, University of Minnesota Archives). She was the algal specialist of the pair. Raymond mentions her expected contributions to their anticipated future work in his NRC fellowship application written during his Postdoctoral year at Yale , "My wife will work jointly with me in this research. She is a competent diatom taxonomist, and her quantitative analyses of these microfossil indicators will enable us to extend the scope and value of this research beyond that which I could accomplish if working alone" (Application for National Research Fellowships in the Natural Sciences, National Research Council, February 17, 1942, Lindeman papers, Yale Archives).

Late in November 1941, Eleanor consulted with Dr. Ruth Patrick on some difficult diatom species identifications, receiving confirmation of most of her IDs (letter from RL to Ed Deevy, December 2, 1941, Lindeman papers, Yale Archives). With Lindeman, Hutchinson and Patrick at once at Yale, this was a confluence of three scientists after whom ASLO has named awards. After leaving Minnesota the Lindemans attempted to publish a manuscript based on Eleanor's algal data, but they were thwarted when Samuel Eddy withheld permission to utilize the associated basic limnological survey data (Various RL letters to Chuck Reif and Samuel Eddy, Lindeman papers, Yale Archives). Following Raymond's death, Eleanor returned to the University of Minnesota and attended graduate school from Fall, 1942 through Spring, 1944 (records of the University of Minnesota registrar -- the field of study is not recorded). Eleanor remarried to a medical researcher, had children, and did extensive traveling with her husband and family especially in South America, eventually living in northern California (PL Interview).

Raymond and Eleanor collecting benthos at Cedar Bog Lake for their winter anaeorbiosis survival experiment. November 15, 1939. A path through the ice is apparent. Raymond Laurel Lindeman Papers, Manuscripts and Archives, Yale University Library. [Author recommends 1 column width]

Raymond and Eleanor Lindeman lived what sounds like a Spartan existence even given the circumstances of Depression-era graduate-student life. The young couple first resided in a trailer on private property at 410 Harvard St., SE (Application to American Scandinavian Foundation, approximately March 15, 1939, Lindeman papers, Yale Archives), a few minutes by foot from Room Z11 of the Zoology building, an office Raymond shared with Charles Reif (Reif 1986). The plumbing for the trailer was located in the basement of a home next door and an extension cord furnished their power (letter from D. Lawrence to Robert E. Cook, January 11, 1975, Lawrence papers, University of Minnesota Archives). Today, the location where Lindeman's trailer once sat is occupied by a Superblock of University dormitories, and hundreds of students reside there temporarily year after year. The Lindemans later moved to an apartment farther from campus (Reif 1986). Raymond and Eleanor did not own a car, which necessitated monthly transportation arrangements through friends and family to permit the Cedar Bog Lake sampling. Six individuals in addition to Eleanor are acknowledged in Lindeman's thesis as providing help in the field. Eleanor kept canaries in the trailer (PL Interview and letter from Chuck Reif to RL, July 5, 1938, Lindeman papers, Yale Archives). Raymond's annual stipend at the University of Minnesota was $600. Money obviously was tight, and there are many references to the toughness of the economic times in the Lindeman correspondence.

As will be covered in more detail below, near the end of Raymond's graduate

studies, he met Hutchinson and Deevy (one of Hutchinson's students), and then applied for and received a Sterling Fellowship to work at Yale. In between, in the summer of 1941, Raymond was a summer Instructor at St. Mary's College, Winona, Minnesota. St. Mary's was four-year, liberal arts men's college run by the De La Salle Christian Brothers, a Roman Catholic teaching congregation. Sometime late in August, 1941 the Lindemans arrived at New Haven. Shortly after arriving, Raymond wrote to his former advisor:

> "Sorry not to have written before, but I've been awfully busy revising again, with Hutchinson's help, my essay on the trophic-dynamic viewpoint in ecology. I think a copy will reach you in a week or so, and would like to have your reactions to it. We arrived in New Haven about a month ago, and are now very nicely located. The department is very interesting: the offices and equipment (with exceptions) are not as good as at Minnesota but there are many more full-time technicians around. I guess they put their money into high salaries and technicians rather than equipment, which is better from some points of view. I can't praise Dr. Hutchinson too highly – he's the most congenial, unassuming and friendly sort of fellow imaginable – and without reservation the most incredibly brilliant. He knows the European literature like a book and comes around for a chat every day with Tommy Edmondson (working on rotifers), Tom Austin (working on zooplankton – has published with Tressler) and myself. There's lots to be learned here just by keeping one's ears open. We're organizing a general ecology seminar group, from as many fields as we can find fellows interested – soils, botany, oceanography, etc., and hope to have some spiraited [sic] discussions"
> (letter from RL to Samuel Eddy, September 28, 1941, Lindeman papers, Yale Archives).

By October even the financial situation had improved: "By the way, about two weeks from now you'll be receiving a little financial "present" from us if we have any left by the time we get down to the R's on our debtor list!" (letter from RL to Chuck Reif, October 22, 1941, Lindeman papers, Yale Archives). The stipend at Yale was $1800/year, triple his graduate school salary. Professionally, the time at Yale was occupied with further sample analysis by Eleanor and him, revisions of the Trophic-Dynamic paper along with submission, rejection and resubmission followed by acceptance (Cook 1977), attendance of the Dallas meetings, then shortly afterward declining health (see Timeline).

Had he been blessed with robust health, Raymond Lindeman would be in his mid-90s as I write this, but sadly, his story unfolds differently. Several serious ailments afflicted him and altered the course of events. The first was an injury which occurred when he was young when he accidentally spilled iodine into his right eye, which resulted in corneal corrosion and meant this eye was capable only of distinguishing dark from light (Reif 1986). This would have had some impact on his work. When applying for a Sterling Fellowship at Yale, Raymond listed his equipment needs this way, "50x dissecting microscope, monocular preferred" (RL letter to Hutchinson, February 17, 1941, Lindeman papers, Yale archives). A discoloration of the right eye socket is apparent in one portrait presented in this article, but not another and according to Reif (1986) his favoring of his left eye often imparted to him a kind of quizzical look when he was in conversation. His other

ailments more significantly affected his work and ultimately led to his early death. In addition to these being debilitating they also were a factor relative to the WWII draft, which was drawing many equal-aged young men of his time into global combat. Raymond suffered both from chronic colitis, or sometimes it is said, stomach ulcers. Raymond's digestive problems plagued him often and sometimes greatly restricted his activities. According to Don Lawrence, Raymond subsisted entirely on a bland diet (Finley 1977). Reif (1986) recalls them sharing meals, including corn and eggs, cooked over a Bunsen burner in the lab, and that when given a chance to select the menu for a home-cooked meal Raymond requested salmon cakes. Raymond spent one summer ill in his bedroom on the farm, where the family took food to him (PL Interview).

Date unknown but this portrait was included in Lindeman's application for an NRC Fellowship, which was dated February 17, 1942. In contrast to the better known portrait shown in Figure 1, this one shows little overt sign of the boyhood injury to his right eye save perhaps a slight narrowing. The photograph does not appear to be retouched. Raymond Laurel Lindeman Papers, Manuscripts and Archives, Yale University Library. [Author recommends 1 column width]

As problematic as his digestive issues were, it was pathologies of his liver that ultimately proved most serious. Raymond suffered from a form of hepatitis that resisted both clear diagnosis and treatment. It led to episodes of jaundice in 1937 and early 1942. In a lighthearted passage to his close friend, Reif wrote, "They'll be cooping you up as an alien if you don'[t] change your color scheme soon" (Letter from Chuck Reif to RL, February 13, 1942, Lindeman papers, Yale Archives). Early in March, Raymond was reporting "I've been out of the hospital for two weeks, but haven't yet gotten back to normal routine. The attack was quite serious and left me with a good bit of cirrhosis and hypertrophy (considerably enlarging my midriff), so that I'll have to be rather careful from now on" (letter from RL to Chuck Reif, March 3, 1942, Lindeman papers, Yale Archives). The most medically complete description of his fatal illness seems to be from an April 13, 1942 letter Raymond penned to Don Lawrence: "The trouble is obscure – hepatic cirrhosis of unknown etiology, with a possibility that it may become progressively worse in spite of everything" (Letter from RL to Don Lawrence, April 13, 1942, Lawrence papers, University of Minnesota Archives). Just a month later during his downhill slide of 1942, he wrote this to Reif, "confidentially, there is a better than even chance I won't survive the summer. My liver trouble has gotten irregularly worse, in spite of the best doctors, and after 4 months is beginning to show visceral oedema. I expect to have an exploratory

operation soon in the more or less desperate hope that they can find out what the cause is and then try for a cure. Eleanor is working at the Yale Library and s[h]ould be able to continue if worst follows worse" (Letter from RL to Chuck Reif, May 16, 1942, Lindeman papers, Yale Archives, underlines original). Today, we know that the causes of hepatic cirrhosis include alcoholism, hepatitis B and C and fatty liver disease, as well as other unknown causes. From all reports, Raymond Lindeman was a teetotaler whose work habits left little room for dalliances, so it seems safe to rule out the first of these causes. The end came on June 29, 1942. Raymond Lindeman donated his body to the Department of Anatomy, Yale.

Influences

The conceptual advances of his 1942 Trophic Dynamic paper are why Raymond Lindeman's name is celebrated today, but this famous paper is part of a fascinating journey of intellectual growth and transformation. What influences and inspirations eventually led to this breakthrough? Looking into this background lets us appreciate that the conceptually elegant Trophic-Dynamic Viewpoint was advanced in full knowledge of the messiness and complexity of natural ecosystems. According to his NRC Postdoc application (Yale archives), Raymond's coursework at Minnesota consisted of: Protozoology (Turner), Animal Behavior – physiology (Minnich), Animal Ecology – terrestrial (Eddy), Aquatic Ecology (Eddy), Entomology (Mickel), Parasitology (Riley), Histology (Pliske), Ichthyology (Eddy), Biostatistics (Treloar), Rotifer Problems (research) (Eddy) and Research in Aquatic Biology (Eddy). Notably missing from this list of coursework is the name of W.S. Cooper, an individual as we will see who was a big influence on Raymond Lindeman.

Raymond Lindeman's advisor at the University of Minnesota was Samuel Eddy (1897-1972), Professor of Zoology and Curator of Fishes at the Bell Museum of Natural History. Eddy worked to document the fish species of Minnesota (Eddy and Surber 1943), and later of all of North America (Eddy 1957). He also published multiple works on vertebrate anatomy. He taught courses in ecology, anatomy and fishing (in Physical Education). Eddy's hometown was Decatur, IL. He attended James Millikin University where he was introduced to aquatic invertebrates. He left school for a time to pursue farming and then returned to finish his Bachelor's degree. He received a Ph.D. from the University of Illinois in 1930 with a thesis entitled, "A Study of Freshwater Plankton Communities". From there he went to the Illinois Natural History Survey, published a number of studies on plankton in Lake Michigan and elsewhere, and subsequently joined the University of Minnesota Zoology faculty in 1929.

Eddy was what we'd likely call today a traditional zoologist. His interests were in species identification, anatomy, and biogeography. "My principal hobby in high school was to dissect every animal I could collect and to keep careful notes on my dissections. I read every book in our public library." (Eddy 1961, p. 122). Eddy led an extensive survey of Minnesota lakes, which was performed during 1929-34 under the WPA and CCC auspices. Charles Reif, Raymond's close friend and fellow Eddy student, spent his summers at these camps in the northern part of the state, collecting data for his thesis and helping to manage the survey. Leadership of the survey was later transferred to someone else, which from correspondence between Lindeman and Reif seems to have been a serious blow to Eddy. Eddy's writings around the time when Lindeman was in his lab indicate a keen interest in fish growth rates and productivity, a clear overlap with the energetics approach being taken by Lindeman. The letters Eddy wrote to Lindeman at Yale are short and professional

and lacking in personal exchanges, with more than one letter from Eddy asking Lindeman if Raymond had brought one or more laboratory items from Eddy's lab to Yale. From this distance, we can guess that Samuel Eddy's influences on Lindeman included a deep knowledge of the natural history of lake organisms, a respect for scientific rigor, and professionalism.

Eddy was clearly supportive of Lindeman, for example in writing recommendation letters for Postdoctoral applications (RL letters to Samuel Eddy, 1942, Yale archives), but Lindeman's conceptual orientation seemed to have little overlap with the intellectual style of his major professor. In the year after Lindeman left Eddy's lab, Eddy was finishing his book with Surber (Eddy and Surber 1943), which contains an extensive introduction on lake dynamics. The section begins, "Fishes represent the end of a long cycle through which the elements of fertility pass from raw substances in the water and lake bottoms to food for the higher forms of fish life", a verbal parallel to Lindeman's food cycle diagram (see below). But, there is nothing of substance from Lindeman's thesis in this section, perhaps because its intended audience was the public. Lindeman's papers are cited in Eddy's much later (1966) account of lakes in the north central U.S. as examples of studies of productivity relations. The trophic dynamic theory is mentioned here but not otherwise remarked upon. From this great distance, it is hard to discern any significant intellectual influence that Eddy had on the conceptual and theoretical advances associated with Lindeman's most famous Cedar Bog Lake studies, or that Lindeman's theoretical advances made much of an impact on Eddy's thoughts.

Raymond's publication list is short but the topics included are broad, including biogeography, paleolimnology, succession, and trophic dynamics. His first publication (Lindeman 1939) was a classical zoological work describing several new forms of the rotifer Brachionus havanaensis. This style of work is unmistakably in the footsteps of Eddy. Lindeman worked through some of Eddy's own plankton samples for this paper, and the taxonomic-autecological approach taken there was closely aligned with the fish studies Eddy was doing at the time. In the publication Raymond credits Eddy's inspiration for the study and in correspondence Lindeman also says that Eddy had begun work on a monograph of Brachionus but had abandoned it due to pressures of other duties, opening up the chance for Lindeman to take over (RL letter to E. Ahlstrom, February 17, 1939, Yale archives).

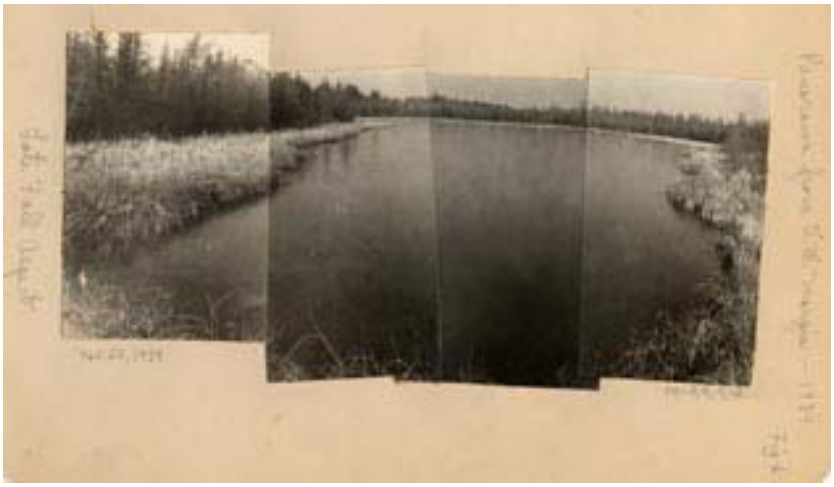
This 1939 paper of Lindeman's is actually one of two he submitted to the Transactions of the American Microscopical Society on the forms of Brachionus. The other (see list of publications) was submitted in November of 1938, but after acceptance Raymond withdrew it in March of the following year because he became aware of a larger study by D.E.H. Ahlstrom on the entire genus. As Editor, J.E. Ackert invited Raymond to send a substitute manuscript. Raymond declined. It seems apparent that Raymond's efforts by now were being devoted fully to the Cedar Bog Lake study. None of the rotifer work made it into Lindeman's thesis. The record does not permit us to see clearly how the rotifer work fit into his thinking when he was forming his research directions in the early part of his graduate school years. Was it ever seriously considered as his main topic, or was it an opportunistic foray that presented itself to him? Raymond began his regular sampling of the Cedar Bog Lake ecosystem in December of 1936, only six months into his graduate work, which seems to clearly indicate that he saw the study of the whole lake ecosystem not just the rotifers as his main interest right from the beginning.

William S. Cooper was a significant influence. Cooper was a student of Henry Chandler Cowles at the University of Chicago, receiving his Ph.D. in 1911. Cooper

came to Minnesota in 1915 by way of Stanford when F.E. Clements was the Head of the University of Minnesota Botany Department (Lawrence 1979). Clearly, succession was a topic often discussed during Lindeman's graduate school years. Cooper's research interest in Minnesota centered on the postglacial history of the Anoka Sand Plain, the geological feature on which Cedar Bog Lake is located (Cooper 1935, Lawrence 1979). In the words of Don Lawrence, "I think Dr. Cooper was more real help to Raymond than Eddy because Cooper had recently advised another student [Russell Artist] in a pollen analysis study of the bogs of the Anoka Sand Plain, another of which (Cedar Bog Lake) Lindeman was studying." Further, in a letter to E.S. Deevy in November, 1939, Raymond wrote, "Dr. Cooper has been promoting as much cooperative work as possible on this beautiful natural area, and my own work is largely in response to his suggestion" (Yale archives). Cooper, Lawrence and others, including Raymond, were freely mixing their scientific interests with preservationist goals, and Lindeman's project was undertaken at an early stage of maintaining the site for future generations (Hodson 1985).

The creek and bog as well as the water body now called Cedar Bog Lake were an exciting find and judged to be a valued location for research. Cooper was the first scientist to "discover" Cedar Bog Lake while on an aerial reconnaissance trip on April 6, 1930 only six years before Raymond performed his first sampling. The bog and lake were first referred to as "Decodon Bog" and "Decodon Lake" respectively owing to the extensive growth of this plant in the lake margins. Since at least Lindeman's writings the lake has been called Cedar Bog Lake. By 1937 the Minnesota Academy of Science had formed a committee to investigate the preservation of this site. About 200 hectares -- or about one tenth of the currently preserved area -- around Cedar Bog Lake were purchased with private funds around 1940. Lindeman's published papers and his correspondence make it clear that his main interest in this particular ecosystem had to do with its dystrophic state. He often referred to the lake as being in "late successional state" and one of the major questions he wished to answer was the pattern of productivity associated with the succession from open water to land. Raymond had the overall goal of connecting long-term changes in productivity relations to his measurements of energy in and out of ecosystem components. Thus, the extensive bog around the lake was one of its major values as a study area. The preserved land was transmitted to University of Minnesota ownership in 1942, and has since grown to 2200 hectares (for a more complete history, see http://www.cedarcreek.umn.edu/about/history/historylong.shtml). The area was then known as "Cedar Creek Forest". For many years the land was called the "Cedar Creek Natural History Area." Today it is named the Cedar Creek Ecosystem Science Reserve, and a laboratory building there is named in Lindeman's honor (see Recognitions below). The synergisms of scientific investigation and conservation that are part of this story are ones that continue to be strong defining characteristics of modern ecology.

An aerial photo of Cedar Bog Lake taken in 1966 by Don Lawrence. This view looks SW. Cedar Creek meanders across the top half of the photo. http://www.cedarcreek.umn.edu/about/history/Lawrence1966Photos/. [Author recommends 1.5 column width]



A panoramic view of Cedar Bog Lake assembled by Raymond Lindeman. This view looks north. [Author recommends 2-column width]

Cooper was a popular teacher. Perhaps Cooper's most important influence on Raymond was his regular seminar held at the Cooper home, which seems to have been a forum where wide-ranging discussions about many ecological topics occurred. For example, in February of 1941, Raymond wrote to Hutchinson that, "The theoretical section on the 'ecosystem' has been undergoing more or less constant revision. Our joint bio-ecology "seminar" group meeting weekly at Dr. Cooper's home is providing much stimulation and helpful criticism, all of which is tending to clarify the concept and principles."

There is one other highlight of Lindeman's graduate school years that is preserved in the historical record. In the summer of 1939 Raymond received

University support in the form of a Sigerfoos Fellowship to attend a summer program at Friday Harbor. He and Eleanor made the trip out west. Near the end of the summer, he collected some samples for Don Lawrence of Mount Saint Helens ash deposits from several Seattle-area lakes. He received credit for a course in Marine Plankton and a course in Marine Research.

There is a rich correspondence between Raymond and Edward S. Deevy through the years 1939-1942 (Yale archives). Deevy was Hutchinson's second PhD student, receiving his degree in 1938. His work "converted the field of paleolimnology into a quantitative science" (http://www.nap.edu/readingroom.php?book=biomems&page=edeevey.html). Deevy's interactions with Lindeman arose indirectly out of the Columbus LSA meeting (see Timeline). This was where Raymond first met G. Evelyn Hutcinson, who read Deevy's paper there because Deevy was unable to attend. Lindeman and Deevy finally met in 1940. Through their progressively less and less formal correspondence, Deevy advised Raymond on his application for a Sterling Fellowship to work at Yale. Deevy told him to stress the "zoological" rather than "ecological" aspects of his application because he thought the department would be more receptive that way. The correspondence between Raymond and Deevy clearly shows the strong interest that Raymond had in the field of paleolimnology and lake succession.

No list of influences on Raymond would possibly be complete without mention of G. Evelyn Hutchinson, his Postdoctoral Advisor. Raymond would have been aware of Hutchinson's work through his reading and training as a graduate student. His personal introduction was facilitated by Ed Deevy, His first letter to Hutchinson was written on November 11, 1940 about the time of the first preserved draft of the Trophic Dynamic paper and there are a total of eight other preserved letters in the correspondence between them. These seem to be a complete record of the correspondence undertaken at this time of fertile intellectual activity by Lindeman. Raymond described his interests in this first letter as being "centered around senescent lakes and lake succession" rather than stressing energetics or food cycle relationships. He also lists plans for future study, and they indicate Raymond's focus on combining paleo- and modern time scale studies. Raymond says his plans include: spectroscopic analysis of sediments, pollen analysis for chronology, microfossil analysis, analysis of chlorophyll, phosphorus and nitrogen to better understand the food cycle, and population dynamics (paraphrased from the original letter RL to Hutchinson November 11, 1940, Yale archives). In a later letter (November 26, 1940), Raymond states, "my primary research interest is at present in food cycles and community dynamics". Raymond and Hutchinson met the following month at an LSA meeting.

They corresponded back and forth during the following nine months, during which Raymond's thesis was completed and accepted by his committee. At the same time his Trophic-Dynamic paper was being revised. He and Eleanor moved to New Haven in August. The scientific content of their letters emphasizes two things. First, they compare thoughts on spectroscopy for measuring nutrients; both of them are planning to utilize this technique in their upcoming work and the technical details were of mutual interest. Second, they stake out contrasting positions on the nature of productivity and succession in climax lake communities. Hutchinson's correspondence refers to his paper with Wollack (1940) and Raymond's viewpoint is spelled out in his correspondence as well as his thesis (Lindeman 1941a, pp. 175-179). Their argument concerns patterns of organic matter accumulation –

Hutchinson's work on Lindsay Pond suggested to him that lake succession rather quickly reaches a point where this accumulation is fairly constant with time, that lakes reached a kind of equilibrium, whereas Raymond's Cedar Bog Lake studies convinced him that no such equilibrium was reached. What seems most notable in correspondence between Raymond and Hutchinson is an absence of discussion of the developing Food Cycle ideas that are core to the famous Trophic-Dynamic paper. This manuscript was submitted to Ecology only 1-2 months after Raymond and Eleanor arrived at New Haven, and thus Hutchinson's greatest input might have occurred during this brief window.

Now that we have insight into the persons Raymond Lindeman encountered and learned from in his graduate career and later, it is time to attempt to put Lindeman's studies into a broader scientific context.

The Trophic Dynamic Viewpoint

Historians have often noted Lindeman's work and its position in the development of ecology. McIntosh (1985) stressed Lindeman's focus on the concept of succession, and he wrote about the work's role in the adoption of energy-based principles by later ecologists. Kingsland (1991) discusses the way Lindeman attempted to connect short-term, observable dynamics to longer-term patterns of succession. Hagen (1992) provided an overview of Lindeman's writings and emphasizes the connection with Hutchinson. Golley (1993) paid particular attention to how Lindeman's work related to early formulations of the ecosystem concept, "Lindeman concluded the lake was an ecosystem. He was the first to implement Tansley's concept explicitly in a quantitative effort to define the system and describe and understand its dynamic behavior (p.50)". This same theme also was touched upon by Kingsland (1995). Kohler (2002) emphasized the way Lindeman advanced the trophic level concept of Elton and takes special note of the detailed knowledge of Cedar Bog Lake that Lindeman brought to his synthesis.

Now we will consider how Lindeman used his Cedar Bog Lake data in relation to the literature of the time to generate a two-part breakthrough. Part one was the formalized description of the system as represented in the well-known Food Cycle diagram with OOZE in the central spot, the kind of "wiring diagram" that Lindeman thought was appropriate. Breakthrough part two was the quantification of stocks and rates that layered on top of that diagram.

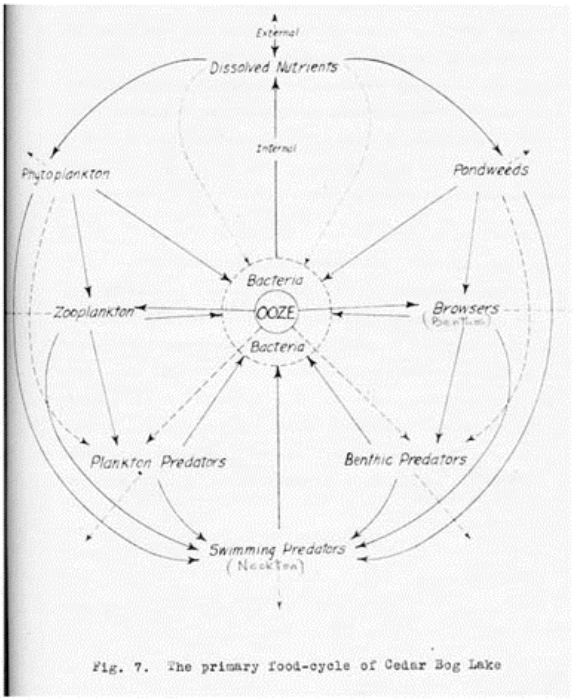


Fig. 7. The primary food-cycle of Cedar Bog Lake

Lindeman's Food Cycle diagram here, copied from his thesis , is identical to the one which appeared in Lindeman . The version in Lindeman is somewhat modified. [Author recommends 1.5 column width]

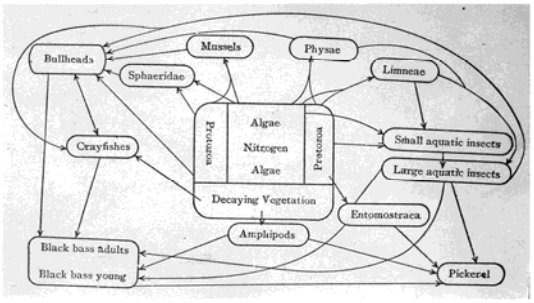
The seminal trophic dynamic paper (Lindeman 1942) was initially rejected in part because reviewers thought its conclusions went too far beyond the data, especially in that Cedar Bog Lake was just one lake of many. This criticism may lend the impression that Raymond Lindeman was a theorist unacquainted with natural history detail. However, Raymond's Cedar Bog Lake study was remarkable in its scope and meticulous in its detail. Raymond Lindeman got his hands and feet dirty. Between December 21, 1936 and June 24, 1940, Raymond (or when he was ill, assistants) made 28 sampling trips to Cedar Bog Lake, amassing a data set on water column temperature and oxygen, the macrobenthic community, net and nannoplankton, pond weeds, and swimming predators including fish. He utilized a transect of sites across the long dimension of the lake. He did not measure nutrients or estimate bacterial abundance though from his writings it's clear he placed great importance on these. Fish and other swimming predators were estimated from samples taken after winter kill. Intensive sampling of one or another of these different categories of organisms was not at all unusual for the day, but to attempt a comprehensive accounting of all of these interacting players all at once was. He used this painstakingly gathered information to create a composite accounting of the biomass of organisms within various ecosystem components. Mostly, he utilized wet centrifuged mass of collected samples to convert to dry mass and eventually to convert these to g-cal. This effort yielded a record of the seasonal patterns associated with these major groups (Lindeman 1941b, a). Perhaps the most detailed subset of his data concerned the macrobenthos. In his thesis, he presented counts of these organisms from a total of 286 samplings for which he, Eleanor and other helpers sieved and then hand-sorted organism. In his thesis, he crunched his data to present individual populations and groupings of populations into g m-2. It was but one lake, but Raymond Lindeman knew Cedar Bog Lake intimately.

Lindeman's accomplishments hinge on the way that he organized the potentially unruly raft of data into an elegant "Food Cycle". Raymond's thesis contains a fascinating 10-page section he called the "History of Food Cycle

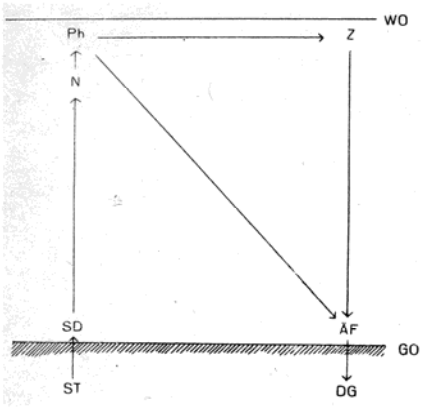
Concepts" where he describes the way his newly gained point of view arose from a lineage that started with Möbius (1877) and extended through some of the well-known forerunners of modern ecology and limnology. In these thesis pages it is possible to gain some appreciation for how Lindeman viewed those authors who influenced him and the departure he wanted to make from the past. Lindeman felt that Möbius was the first to enunciate the two "fundamental concepts" of productivity and community. On the other hand, according to Lindeman, Möbius failed to discuss the role of predation or of the "food-cycle". The concept of food-cycle was extremely important in Lindeman's writings. By this he meant the cycling of nutrients in and among the dissolved phase, autotrophs, microbes, and larger organisms, or in other words the integration of biotic and abiotic matter.

From here, Lindeman considered "The Lake as a Microcosm" of Forbes (1887), and he quotes from there the entire paragraph that begins, "As one example of the varied and far-reaching relations into which the animals of a lake are brought in the general struggle for life, I take the common black bass." Forbes's articulation of what we might today call the food web linkages of the bass, its prey and the species supporting those prey is in fact quite similar to a large fraction of Lindeman's writings, which concern themselves with placing each species of Cedar Bog Lake into the context of what it eats and what eats it. The gap Lindeman perceived in Forbes was the lack of discussion of plants. Lindeman also somewhat mysteriously included the following text referring to Forbes's microcosm, "nor did he fully enlarge upon the potent significance of his title." Lindeman, unfortunately, does not himself enlarge upon this thought and it not at all clear what he had in mind here and what aspects of "microcosm" he felt needed amplification beyond Forbes. The last sentence in Lindeman's paragraph about Forbes will be of interest to modern limnologists who have made the degree of autotrophy vs. heterotrophy an active research question, "The fact that Forbes did recognize lakes as relatively autotrophic microcosms represents a distinct contribution to the development of our concepts of nutritive cycles and of productivity." Lindeman had nothing but praise for F.A. Forel, whose Le Leman he next quotes and discusses. In Lindeman's view, Forel provided a "brilliant exposition of the general nature of food cycles" which "will serve even today as an introductory account of trophic relationships."

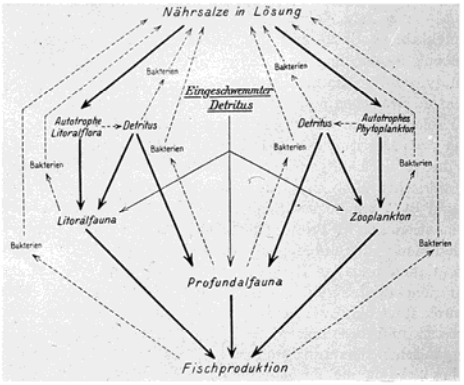
The remainder of Lindeman's "History of Food Cycle Concepts" section is organized around a set of diagrams from previous authors (Lindeman 1941b has a much-abridged version of this section). This discussion then leads to the presentation of the thesis version of Lindeman's impactful "OOZE" Food Cycle Diagram. The six forerunner diagrams that Lindeman reprinted and commented upon in his thesis illustrate in a powerful way what he absorbed from previous writings. They are arranged chronologically and begin with Shelford (1918) and continue through Alsterberg (1924), Thienemann (1926) based on Naumann (1924), Strøm (1928), Rawson (1930) and Wassmund (1930). These all were attempts at formalizing the workings of the lake ecosystem, and through this thesis section we get some insight into how Lindeman himself thought his own approach differed from these others.



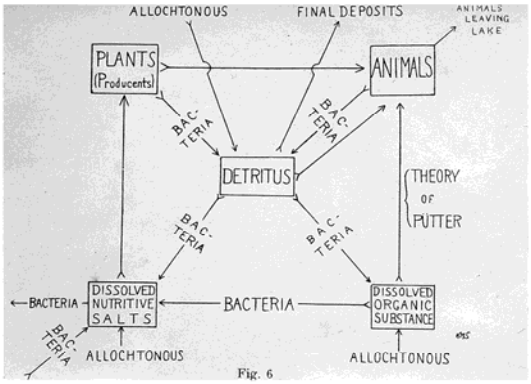
A. Shelford 1918



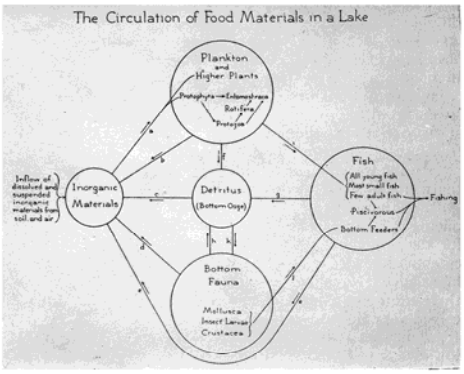
B. Alsterberg 1922, 1924



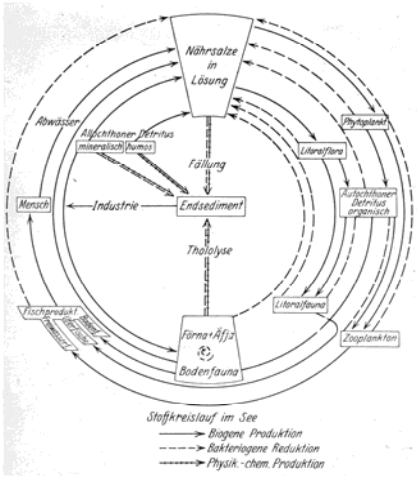
C. Thienemann 1926



D. Strøm 1928



E. Rawson 1930



F. Wassmund 1950

Food cycle diagrams from Lindeman . [Author recommends full page]

Working his way through these diagrams one after the other, features or perceived failings he noted included: the representation of only food chains with no feedback cycles through detritus (Shelford), the inclusion of allochthonous inputs (begins with Thienemann), an overemphasis on fish (Rawson), the central position of detritus (Strøm) and the inclusion of human influences (Wassmund). Looking carefully at all these six forerunning diagrams, it is Thienemann's that is the closest to Lindeman's. In fact, the correspondence is striking. Both show separate and symmetric cycles, one for open water and one for the littoral zone. Both begin with dissolved nutrients and end with fish. Lindeman collected the ooze and bacteria into a single central position whereas Thienemann represented detritus and bacteria in

multiple places, but the functional connections through these pools are essentially the same. There are some differences in that Lindeman shows all pools feeding into the bacteria/ooze complex whereas in Thienemann's diagram detritus comes solely from the autotrophs. Lindeman's view of lake ecosystems, on which his theoretical advances all rested, was strikingly similar to what Thieneman had suggested years earlier. Lindeman's depiction is more elegant in its simplicity and it seems more than an artistic stroke that he moved detritus to a central position, akin to Strøm's representation, and thus emphasized the essential connection of life and nonlife. Lindeman was at least strongly considering working with Strøm as a Postdoc because his papers contain an application for a fellowship to the American Scandinavian Foundation that mentions an intention to work in Strøm's laboratory (Yale archives).

By his choosing to include and comment upon these different representations of aquatic ecosystems, we can see today that Raymond was grappling with the intellectual challenge of representing the complex and messy natural world -- many details of which he knew all too well -- as a clean, abstract concept amendable to further calculation, analysis and comparisons. His interpretation imposes a severe symmetry and an almost artistic formality on the ecosystem. Visually, it emphasizes the essential unity and interdependence of the biotic and abiotic realms. Lindeman published two versions of the Food Cycle Diagram in addition to the one in his thesis. In Lindeman (1941b) there are minor wording differences ("plankers" instead of "plankton"). In his Trophic-Dynamic paper (1942), Lindeman took one more step, adding the input of solar radiation explicitly (into Phytoplankters and Pondweeds) and noting trophic levels with Greek Lambdas and subscripts. The mathematical connotations of the Greek letters, added to the existing scaffolding of the Food Cycle Diagram is a clear illustration of how his work grew in quantitative directions when he moved to Yale.

The grasping of the entire ecosystem at once was one part of the Lindeman breakthrough. From noting the design and initial date of his sampling program, it seems to have been his goal almost from his first days in the Eddy lab. We can therefore see his Food Cycle diagram as a vital and important step, one which was taken after many trips to the field in all seasons, after hours of picking organisms out of ooze, after serious contemplation of observations of change on short and long time scales, and after reading and thinking about the works of those who came before him. The second part of the Lindeman breakthrough was his quantifying those observations in a way that corresponded with his diagram. Others were writing about the entire ecosystem and thinking about organizing different components into a logical and coherent fashion, but Raymond was the first to provide a quantitative accounting of all of these components in a single ecosystem, which allowed him to search for pattern within them.

At the writing of his thesis late in 1940 and early in 1941, the Cedar Bog Lake data was being presented in units of grams per unit surface area. He had moved part way to distilling the essence of the data he had painstakingly collected, but he knew more could be done,

> "The energy relationships within the ecosystem can thus potentially be expressed by a series of mathematical formulae. Although the present author feels utterly incapable of applying such lofty principles of analysis to the aquatic ecosystem, Haskell's approach is presented, with a keen appreciation of the potential power of the "energy-availing" perspective to open new horizons of ecological thought, in the hope that it may guide

future workers toward a more fundamental concept of ecological processes." (Lindeman 1941a, pp. 164-165)

At this time he was just beginning to express the ecosystem in energetic terms. His Seasonal Food Cycle paper (Lindeman 1941b) contains tables both in mass and in energy terms. He acknowledges Juday, Hutchinson, Deevey and Hodson for comments on this manuscript. In the first half of 1941 he was continuing to develop the Trophic-Dynamic viewpoint (called "Trophodynamic as late as February 1941). Two early versions of his manuscript (February and March, 1941) show little further progress in the analysis and presentation of data. By the next surviving draft (September, 1941), just a few weeks after his and Eleanor's arrival at Yale, the Quantitative Food Cycle Relationships section of his manuscript had greatly matured, and the whole manuscript was about a month away from submission. Now trophic levels were represented by Greek Lambdas. He was taking pains to separate standing stocks from rates and to distinguish gross from net production. Also by this time he had "interpolated" (his term) the biomass values into gram-calories per square centimeter. Hutchinson's influence in this maturation of quantitative approaches to the data and adoption of energetics seems undeniable, but the record is silent on how much each of them contributed. The surviving correspondence between the two is absent of any discussion whatsoever about quantifying trophic levels or thinking in energy terms.

No matter how the Trophic-Dynamic viewpoint came together, it did a remarkable thing:

"This paper was the first one to indicate how biological communities could be expressed as networks or channels through which energy is flowing and being dissipated, just as would be the case with electricity flowing through a network of conductors. Though the concept is now regarded as both basic and obvious, like the principle of competitive exclusion, it roused extraordinary suspicion."
(Hutchinson 1979, pp. 246-247)

Hutchinson's and Lindeman's continuing discussions regarding the patterns of productivity associated with succession formed the basis of a joint oral paper, presented at the December LAS meeting in Dallas. The confluence of energetics and succession theory would occupy many ecologists in the future. The young Raymond Lindeman's Trophic Dynamic Viewpoint truly changed the way ecologists think:

"During his long days on the water collecting his data and mulling over what they meant, he saw that by combining the stage-setting with the biotic community it supported, and treating it as an integrated unit through which energy from the sun is utilized and dissipated in graduate steps, he could reduce all the biological happenings to energy terms."
(Lindsey 1980, p. 5)

Abstract for LAS/AAAS meeting, December, 1941 (Yale archives).
Biological Efficiency in Succession

Examination of available quantitative data indicates that, in general, productivity increases during successional development. In lakes, photosynthetic efficiency and so productivity rise to a prolonged eutrophic stage-equilibrium, then decline with lake senescence, and finally rise again in the terrestrial stages of hydrarch succession. The evidence available for xerarch succession is less complete but suggests a series of stages of increasing efficiency, as the water-retaining capacity of the soil is built up. The most fundamental classification of biological formations and their successional stages may well turn out to be a numerically orderable classification based on biological efficiencies. The primary photosynthetic efficiency is very low, in climax forests probably of the order of 0.16%. The efficiency rises with the level in the food chain in any community. In aquatic communities, meager data suggests that an increase occurs in the efficiency of consumer levels during succession.

G.E. Hutchinson and R.L. Lindeman – Yale University

Recognitions

In addition to the ASLO award which is the impetus of this essay, Lindeman's achievements have been formally recognized in several other ways. Raymond Lindeman's name is associated with several sites on the University of Minnesota properties. A small seminar room (Room 200) of the Ecology Building on the St. Paul campus is named in his honor, and a plaque hangs at the entrance to the room. This is an appropriate recognition when we consider the great importance that the W.S. Cooper seminars had to the young Raymond Lindeman. The University of Minnesota Minneapolis campus includes a Scholars Walk, where pedestrians pass by a series of graphical presentations representing notable works of science, art and other forms of scholarship that arose from scholarship at the University (http://www.scholarswalk.umn.edu/discovery/wall_names.html). Lindeman's Food Cycle Diagram and associated text is displayed there. Many years ago there was some discussion about renaming the now-gone Zoology building for him, but that didn't occur (Lawrence papers). The Lindeman Research and Discovery Center was dedicated at the Cedar Creek Ecosystem Science Reserve in 2007, and it houses dry labs, faculty and staff offices, meeting rooms and meeting space. Years ago there was discussion about renaming Cedar Bog Lake "Lindeman's Pond" but that did not occur, some thinking that the name Cedar Bog Lake was already strong associated with Lindeman (Lawrence papers). Finally, the annual Raymond Lindeman Memorial Seminar in the Department of Ecology, Evolution and Behavior brings notable speakers to the campus in remembrance of the young, dedicated graduate student from Redwood County.

Acknowledgements

I thank Susan Jones, Ann Krogman, Robert Megard, Peggy Rinard, Gaston (Chip) Small, and Mary Spivey for comments on the manuscript. Mitch Haustein assisted with searching the Yale archives materials. ASLO provided financial support.

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