Environmental Case Study

Measuring Energy Flows in Cedar Bog Lake

In 1936, a young graduate student named Ray Lindeman began his Ph.D. research on a small, marshy pond in Minnesota called Cedar Bog Lake. His pioneering work helped reshape the way ecologists think about the sytems they study. At the time, most ecologists were concerned primarily with descriptive histories and classifications of biological communities. A typical lake study might classify the taxonomy and life histories of resident species and describe the lake's stage in development from open water to marsh and then to forest. Blind in one eye, Lindeman couldn't do the microscopy necessary to identify the many species of algae, protozoans, and other aquatic organisms in the lake. Instead, following the ideas of two contemporary English ecologists, Charles Elton and A. G. Tansley, he concentrated on biological communities as systems and looked at broad categories of feeding relationships, for which he coined the term *trophic levels* (from the Greek word for eating) (fig. 3.1). Aided by his wife, Eleanor, Lindeman spent many hours collecting samples of aquatic plants and algae, grazing and predatory zooplankton and fish, and the benthic (bottom-dwelling) worms, insect larvae, crustaceans, and sediment. Back in the laboratory, he measured the plants' photosynthetic rates, the animals' respiration rates, and the total energy content of organic compounds in each of the different trophic levels.

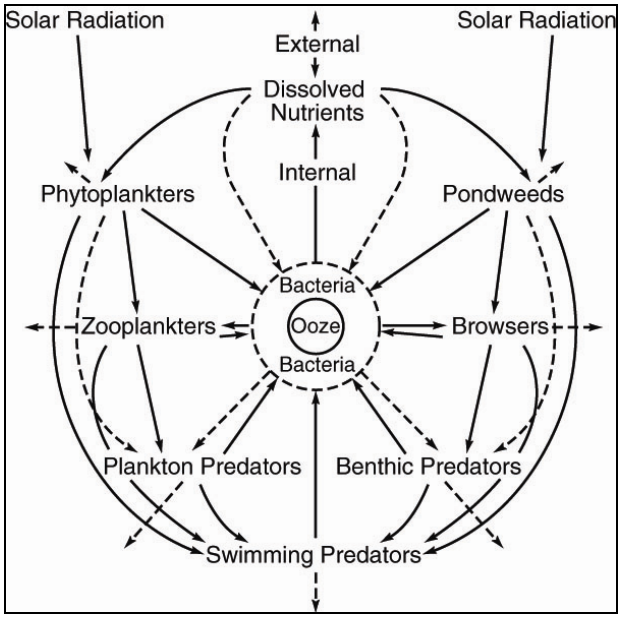

Figure 3.1 Feeding relationships in Cedar Bog Lake. After R. Lindeman, 1942. The trophic-dynamic aspect of ecology. *Ecology* 23(4):399–417.

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Describing the system in terms of energy flows was a radical departure from ecological methods at the time. Lindeman made a careful balance sheet of the total energy content in the biomass at each trophic level, the energy used in respiration, and the energy content of organic matter deposited in the sediment. To his surprise, he found that each successive feeding level contained only about 10 percent of the energy captured by the level below it. The remainder is lost as heat or deposited in sediments, he argued, because of the work that organisms perform and the inefficiency of biological energy transformations. In his dissertation, Lindeman showed that energy represents a common denominator that allows us to sum up all the processes of production and consumption by the myriad organisms in a biological community.

Lindeman also broke from standard procedure by representing the relationships in his study lake as a mathematical model: He used a series of equations to describe thermodynamic relationships and the efficiency of energy capture and transfer. Ironically, Lindeman's most important paper was rejected by the journal *Ecology* as being too theoretical and too quantitative. It was only after the intercession of G. Evelyn Hutchinson from Yale, with whom Lindeman had a postdoctoral fellowship after finishing his studies at Minnesota, that his mathematical model and energy analysis of Cedar Bog Lake was finally published. Unfortunately, Ray Lindeman died of liver failure before his article appeared. It has since become a landmark in ecological history.

In the years since Lindeman's work, the idea of taking a systemic view of a biological community together with its physical and inorganic environment has become standard in ecology. Energy flows and nutrient cycles are central to the way we understand the workings of ecological systems. Constructing quantitative models to describe, explain, and explore ecological processes has become routine.