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LINDEMAN'S TROPHIC-DYNAMIC ASPECT OF ECOLOGY: "WILL YOU STILL NEED ME WHEN I'M 64?"

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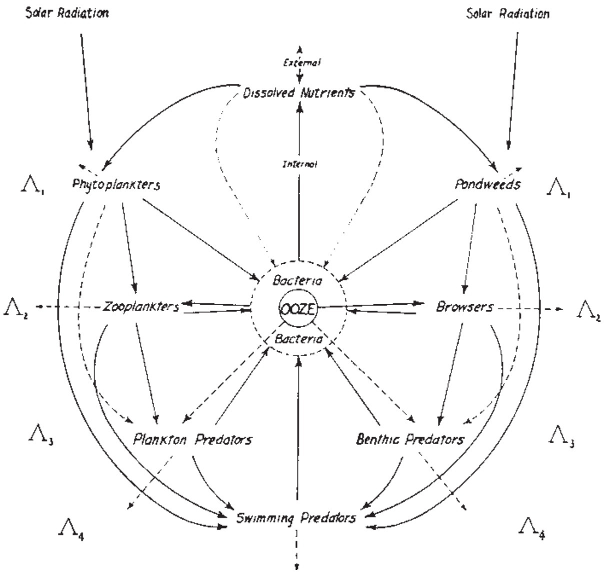
In the fall of 1941, only six years after the word "ecosystem" was coined, Raymond Lindeman submitted "The trophic-dynamic aspect of ecology" (the final chapter from his Ph.D. thesis) to the journal *Ecology* (Cook 1977). Lindeman's thesis work at the University of Minnesota was ambitious in that it explored the mechanisms underlying bog succession. Specifically, Lindeman studied the succession of Cedar Creek Bog in Northern Minnesota, and provided a novel conceptual template for studying not only succession, but also energy flow in aquatic ecosystems. Lindeman's approach to studying aquatic ecosystems was initially supported by G. Evelyn Hutchinson, and later embraced by Eugene Odum and a generation of aquatic ecologists. Lindeman's *Ecology* manuscript is now considered foundational work in the histories of ecology and limnology (Real and Brown 1991; Wetzel 2001), and seminal work in ecosystem ecology (Golley 1993).

This work was one of the first papers to implement Arthur Tansley's newly proposed ecosystem concept in a quantitative manner and was groundbreaking in several ways (Cook 1977; Golley 1993). Lindeman's paper argued that trophic structure affects community patterns and succession; hence, a quantitative food web is essential to understanding temporal change in aquatic ecosystems. Remarkably, the paper recognized the central role of bacteria and detritus in ecosystem energy flow placing "ooze" as the hub of all trophic interactions (Lindeman 1942; Golley 1993; Figure 1). The work's most enduring contribution is that it provided a common currency (organic matter or energy flow) for studying interactions among trophic levels and for comparing disparate aquatic ecosystems, thus establishing a theoretical orientation in ecology (Cook 1977).

Lindeman was fortunate that his *Ecology* manuscript was reviewed by arguably two of the leading limnologists in the world: Chancey Juday at the University of Wisconsin and Paul Welch at the University of Michigan (Cook 1977). Unfortunately, neither Juday nor Welch recognized the merits of Lindeman's work and both rejected the manuscript for publication in *Ecology* (Cook 1977). Juday wrote: "The chances are that the author's beliefs and imaginary lakes would be very different entities if he had a background of observations on fifty or a hundred of the 10,000 lakes claimed by the state of Minnesota, instead of only one, and that a special type." Welsh wrote: "Limnology is not yet ready for generalizations of this kind. The basic background data for such a paper is far too

Figure 1. Generalized food-cycle relationships for aquatic ecosystems showing energy flow among four trophic levels and highlighting the central role of bacteria (Lindeman 1942). Reprinted with permission from Ecological Society of America.



The Limnology and Oceanography
Bulletin

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fragmentary. If Dr. Lindeman could put this paper aside for ten years, then bring it out and see how it looks in the light of what we hope will be the added accumulation of limnological information, he might possibly congratulate himself that he deferred its publication." Lindeman received a rejection letter from the editor of *Ecology*, Thomas Park, in November 1941.

G. Evelyn Hutchinson, Lindeman's post-doctoral advisor at Yale University, recognized that Lindeman's approach to studying aquatic ecosystems as described in the "Trophic-dynamic aspect of ecology" was powerful and would allow comparative analyses among aquatic ecosystems (Golley 1993). Hutchinson was discouraged by the reviews and promptly wrote a passionate letter to Park in defense of Lindeman's work (Cook 1977). Hutchinson wrote: "I feel that a number of far-reaching hypotheses that can be tested by actual data and which, if confirmed, would become significant generalizations, are far more valuable than an unending number of marks on paper indicating that a quantity of rather unrelated observations has been made." Swayed by Hutchinson's letter, Park ultimately accepted a revised version of Lindeman's manuscript recognizing that "time is a great sifter in these matters and it alone will judge the question." Ray Lindeman died in June 1942 at age twenty-seven prior to the paper's publication. In an obituary attached to the end of the publication, Hutchinson wrote: "Knowing that one man's life at best is too short for intensive studies of more than a few localities, and before the manuscript was completed, that he might never return again to the field, he wanted others to think in the same terms as he found so stimulating, and for them to collect material that would confirm, extend, or correct his theoretical conclusions." In 2002, "Trophic-dynamic aspect of ecology" was cited by members of the American Institute of Biological Sciences as the third most influential journal article with respect to their career training (Barrett and Mabry 2002).

The fields of ecology and limnology were apparently not ready for the generalizations proposed by Lindeman after all, as the paper and its approach were not widely embraced (outside of Yale) during the decade following its publication. Finally, in 1953, with the publication of Eugene Odum's *Fundamentals of Ecology*, Lindeman's model for studying energy flow in aquatic ecosystems was promoted and widely distributed, thus greatly influencing an emerging body of research on energy and nutrient cycling in aquatic and terrestrial ecosystems (Golley 1993). Odum's writings and those of his numerous colleagues and students rapidly made the study of energy flow the principal approach for studying diverse biological processes and comparing diverse ecosystems (Golley 1993). John Teal's classic study of "Energy flow of the salt marsh ecosystem of Georgia" (1962) embodies the effectiveness of Lindeman's approach 20 years after the original publication. Using Lindeman's work on Cedar Creek Bog as a template, Teal (1962) quantified a salt marsh's allochthonous and autochthonous organic matter production and assessed the fate of these pools of potential energy for marsh heterotrophs. Teal found that much of the organic matter produced within and delivered to salt marshes could not be accounted for in secondary production within the salt marsh ecosystem and hypothesized that as much as 45% of the organic matter entering the ecosystem might be transported to adjacent ecosystems. Lindeman's approach to studying energy flow in a closed bog ecosystem was now being used to study open lotic ecosystems that required quantification of organic matter inputs and outputs. Odum's "outwelling hypothesis" that terrestrial organic matter inputs were subsidizing secondary production in estuaries and coastal waters was a logical extension of the findings of Teal and others. It promoted much debate in the literature, thus extending Lindeman's bog-ecosystem model to include all aquatic ecosystems (e.g., springs, swamps, salt marshes, streams, and sloughs).

Four decades after the publication of "Trophic-dynamic aspect of ecology" and several years after the inception of the "microbial loop" (Pomeroy 1974), Lindeman's model of energy flow had become central to the study of inland waters (see preface of Wetzel 1983) and was at the base of one of stream ecology's most influential conceptual models: the River Continuum Concept (RCC; Vannote et al. 1980). Although not cited nearly as much as the RCC (now approaching 1600 citations!), Lindeman's seminal work on a lentic-bog ecosystem provided the template for examining the energy flow of stream ecosystems at multiple scales. The RCC's classic conceptual figure builds on Lindeman's food web depiction (Fig. 1) by placing microbes at the center of feeding relationship diagrams. Vannote et al.'s RCC (1980) and Wetzel's leading limnology textbook (1983) inspired a tremendous body of research on energy flow in inland waters throughout the 1980s and 1990s (see Wetzel 2001). By the end of the 20th Century, Lindeman's blueprint for studying energy flow was being used at a wide range of spatial scales across freshwater and estuarine ecosystems.

Experimental studies of energy flow in lake ecosystems close to Cedar Creek Bog have verified the power and longevity of Lindeman's approach and further quantified the important role of terrestrial energy subsidies to aquatic biota (Pace et al. 2004 and references within). Experimental manipulations of allochthonous energy flow in low-order, forested streams in the southeast U.S. are grounded in Lindeman's approach (Hall et al. 2000), and have greatly advanced it (Eggert and Wallace 2003 and references within). A growing body of food web studies using stable isotope analyses has provided new, and potentially powerful tools for examining energy flow from lower to higher trophic levels (e.g., Bastviken et al. 2003). We now know that the world's large rivers and estuaries are routinely net heterotrophic confirming the importance of terrestrial-derived energy inputs to downstream-ecosystem metabolism (Frankignoulle et al. 1998; Cole and Caraco 2001). However, net ecosystem production in higher-trophic levels remains uncertain as spatial scale increases in aquatic ecosystems (Thorp and Delong 2002). This net heterotrophy paradox has roots that extend decades into the past (e.g., Teal 1962; Vannote et al. 1980), but has received renewed attention after the documentation of community changes and declines in higher trophic levels in many riverine, estuarine, and marine ecosystems (Pauly et al. 2002; Thorp and Delong 2002; Jacobs et al. 2003). Lindeman's approach can be incorporated into efforts to understand the mechanisms underlying these food web changes and, in some cases, efforts to restore food webs.

San Francisco Bay's freshwater Delta provides one such case study for examining energy flow within a large-scale aquatic ecosystem that has experienced significant food web alterations. Recent research here helps address basic questions regarding energy flow in riverine and estuarine ecosystems, and, more specifically, questions regarding the multiple mechanisms underlying declines in native fish and shifts in forage food (Jassby et al. 2002; Lopez et al. 2005; Sobczak et al. 2005). The San Francisco Bay's Delta is a complex mosaic of tidal, freshwater and estuarine habitats that consists of 1127 km of leveed waterways and 57 human-made islands at the confluence of the Sacramento and San Joaquin Rivers, which drain a 1.6 x 10^5 km^2 catchment (Jacobs et al. 2003). California's Delta is at the heart of the state's water conveyance projects that provide drinking water for twenty million people and irrigation water for much of the Central Valley's agriculture. The Delta's engineered and highly-disturbed waterways are also a complex aquatic ecosystem supporting 130 species of fish, including many that are threatened (e.g., winter-run Chinook salmon) or endangered (e.g., Sacramento splittail; Jacobs et al. 2003; Lopez et al. 2005). Historical declines in higher trophic levels including native fishes and zooplankton may be the result of multiple stressors. Did alterations in food resources at the base of the Delta's food web contribute to declines in higher trophic levels? The Delta's large spatial scale and complex hydrology provide inherent problems to addressing this seemingly basic ecological question. Further, the Delta's migratory and spatially variable fish populations complicate an inventory of fish populations. Large-scale ecosystem restoration plans (comparable to the Florida Everglades' restoration in scope) aim to stabilize or increase the Delta's declining native fish populations (Jacobs et al. 2003). Lindeman's blueprint for examining aquatic food web structure provided a tractable solution to this problem: examine the energetic base of the Delta's food web and determine if it is sufficient to support higher trophic levels.

The strategy to study the base of the Delta's food web required a team of researchers willing to share multiple backgrounds and scientific approaches to studying energy flow (see Likens 1998 on ecosystem ecology- team building). The outcome of this collaboration was a group of complementary papers that characterized the base of the Delta's food web and energy flow to higher trophic levels. Allochthonous detritus dominates organic matter supply to the Delta and supports the majority of ecosystem respiration; however, allochthonous detritus is not strongly coupled to the Delta's metazoan food web (Sobczak et al. 2002). Autochthonous phytoplankton production, a small component of the Delta's organic matter budget, is the dominant energy source for metazoans and zooplankton (Müller-Solger et al. 2002; Sobczak et al. 2002). Zooplankton growth and reproduction are routinely limited by low phytoplankton biomass (Müller-Solger et al. 2002) even in many of the Delta's shallow water habitats (Sobczak et al. 2005). Phytoplankton production in the Delta has declined over 40% from 1975 to 1995, suggesting the long-term loss of an important food resource (Jassby et al. 2002). Phytoplankton biomass is highly variable in time and space, and appears to be related to turbidity and low growth rates, water transport and residence time, and benthic grazing by the invasive clam *Corbicula fluminea* (Jassby et al. 2002; Lopez et al. 2005). Our collective findings have provided multiple lines of evidence (and thus strong inference) regarding a linkage between declines in phytoplankton production and declines in higher trophic levels. These findings contribute to an evolving conceptual model of riverine and estuarine food webs (e.g., Thorp and Delong 2002) and aid ecosystem restoration efforts. Restoration actions geared at augmenting higher trophic levels need to consider disparities in phytoplankton biomass and bioavailable organic matter among Delta habitats (Lopez et al. 2005; Sobczak et al. 2005). In addition, restoration efforts aimed at promoting the energetic base of the Delta's food web must critically examine the role of multiple stressors to the Delta's native fish populations, such as predation and freshwater flow modification (Sommer et al. 2004).

Why is Lindeman's model paper for studying aquatic ecosystems still important 64 years after its publication?

While limnological methods and analytical tools have changed dramatically in the 64 years since Lindeman's work was submitted to *Ecology*, Lindeman's approach to studying aquatic ecosystems is clearly central to many of today's most important limnological research efforts (Bastviken et al. 2003; Eggert and Wallace 2003; Pace et al. 2004; Sommer et al. 2004). Further, limnologists and oceanographers are now being asked to contribute to global change models that require new knowledge regarding energy flow: what is the fate of terrestrial organic matter inputs into the world's aquatic ecosystems (Findlay and Sinsabaugh 2003); what is the age and source of the terrestrial-world's detrital subsidies to coastal ecosystems (Raymond and Bauer 2001; Mayorga et al. 2005); what is the role of humans in altering energy flow to the world's coastal ecosystems (Cloern 2001)? These current challenges facing limnologists and oceanographers occur over large portions of the globe and a shifting mixture of physical, chemical, and biological factors likely control their underlying processes. Lindeman's insight on energy flow helps researchers aggregate and organize some of the complexity of aquatic ecosystems, thus greatly increasing the likelihood that we will successfully answer these pressing questions. Further, limnologists and oceanographers will be increasingly asked to contribute to ecosystem restoration projects that aim to sustain or augment biodiversity and important native populations (Wetzel 2001; Pauly et al. 2002). Lindeman's approach for studying aquatic ecosystems may be an essential organizational component of ecosystem restoration programs designed to manage higher trophic levels.

Responding to Lindeman's critical reviewers in fall 1941, Hutchinson wrote: "In field ecology, it is necessary to have data collected over many months or years, and for comparative purposes studies are needed on localities very widely separated in space. To obtain the kind of data required takes two or three years' work on a single locality; to suggest that any one individual should wait until he has completed investigations on fifty or one hundred lakes is ironical rather than practical. It is therefore most important that all ecologists should have the opportunity to acquaint themselves with the theoretical possibilities that may guide them in their collection of data."

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