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Ecosystem Trophic Foundations: Lindeman Exonerata

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Systems analysis is basically a quantitative modeling approach to problems concerning whole complex systems. When faced with large, complex, and highly interacting systems, human judgement and intuition may lead to wrong decisions [Van Dyne, in *Ann. Rev. Ecol. Systematics* 3:348 (1972), with G. L. Swartzman].

INTRODUCTION

That the final statement of the structure of a biocoenosis consists of a pair of numbers, one an integer determining the level, one a fraction determining the efficiency, may even give some hint of an undiscovered type of mathematical treatment of biological communities.

G. Evelyn Hutchinson

Addendum to Lindeman (1942)

After a decade or so of relative quiescence, the field of ecology is again becoming an arena for lively debate, as new and sometimes radical concepts appear, and old, cherished ideas are vigorously challenged. One of the cornerstones of ecological thought and discussion over the past forty years has been Raymond Lindeman's (1942) concept of the trophic pyramid. Lindeman's idea is thermodynamic at its core: the total amount of energy ingested by host organisms cannot become fully available to the individuals that prey on them. That is, the amount flowing to the predators must be less than the influx to the host population. Thus, one is led to imagine a trophic pyramid of energy flow, where the amount of energy transferred during successive feeding events (as represented by the width of the pyramid) becomes progressively smaller at higher levels of feeding.

Now, there is no arguing with the second law of thermodynamics; it must prevail in the end. Also, the image of ecological feeding relations as a chain of trophic transfers possesses a descriptive

elegance that is hard to resist. Perhaps these two attributes of the Lindeman scheme account for its survival as a key element in modern ecological discourse. Few ecologists are given to speaking of an ecosystem without mentioning "herbivores" or "carnivores," as though populations fit neatly into one of the links of Lindeman's trophic chain. Yet most 10-year-old schoolchildren are taught that feeding relations in an ecosystem resemble more a complicated web (e.g., Chapter 20) than a simple chain of transfers.

As Cousins (1985) remarks, "A hawk feeds at five trophic levels." In general, there appears to be no discrete mapping of real populations to integral trophic levels. While many are content to live with the conceptual ambiguities engendered by this mismatch, Cousins takes strong exception to the continued reliance on Lindeman's scheme by most ecologists: "The trophic concept is not just wrong at its edges: it is erroneous in fundamental ways that create many difficulties for ecological science."

Cousins is primarily concerned that the attention paid to the Lindeman description of ecosystems comes at the expense of that given to other concepts, most notably Elton's pyramid of numbers (Ulanowicz, 1989). To a degree, he is correct in decrying the relative lack of interest in organism size, and this writer has elsewhere encouraged the study of particle size distributions and allometric relationships in ecology in lieu of taxonomic categorization (Ulanowicz, 1981; Ulanowicz and Platt, 1985). But Cousin's insistence that Lindeman was wrong and Elton was right is ill-considered. He is perhaps too influenced by positivistic doctrine. As *descriptions* of the real world, various constructs are rarely unequivocally right or wrong. Some are simply better descriptions of events than others (Ulanowicz, 1986).

LINDEMAN'S IDEAS IN THE CONTEXT OF THE ECOSYSTEM

As a quantitative description of behavior at the level of the community, the Lindeman scheme has much to recommend it. It is necessary to abandon only the notion that the mapping from taxa to trophic levels be discrete, and then most ambiguities concerning trophic status quickly vanish. That is, a given taxon need not be assigned wholly to a single trophic level, and vice versa. It is an observed fact that the hawk apportions its activity over five different trophic levels. So what is to keep one from turning that observation into quantitative description?

There are two (interrelated) ways of making a nondiscrete trophic description. We may choose to regard dynamics at the level of the community, where trophic compartments appear discrete and the activities of each taxon are divided among the trophic groups (Higashi, Burns, and Patten, 1992). Alternatively, our focus could be on the individual taxon, and each species could be considered to feed at some noninteger trophic level that is the weighted average of the number of links in the various pathways over which it obtains sustenance. The quantification of both mappings can be achieved with use of the same data—the matrix of feeding coefficients.

TROPHIC AGGREGATION SCHEME

Suppose that species j is any member of an n -component ecological community and that its total intake of some appropriate medium (energy, carbon, nitrogen, or other) is T_j . Measurement may reveal that an amount T_{ij} of this intake comes from another member i of the community. The dimensionless ratio $g_{ij} = T_{ij}/T_j$ is called the *feeding coefficient* of j on i . It describes the extent to which j *directly* depends on i for sustenance. The coefficient g_{ij} may be considered as the entry in the i th row and j th column of an n -dimensional square matrix, $G = (g_{ij})$, the matrix of feeding coefficients. By definition, the sums down the columns of G are all less than or equal to 1. A sum down column j of less than 1 implies that j derives some of its food from outside the community.

Without loss of generality, all sustenance from outside the community may be assumed to be primary production. Imports from outside the system other than primary production can be accommodated by slight changes in the matrix algebra that follows.

A convenient property of G is that its algebraic powers provide quantitative information about *indirect* transfers in the system. For example, when we multiply the feeding coefficient matrix by itself, the result is denoted as G^2 . The (i,j) th component of this product matrix represents the fraction of the whole diet of j that derives from i over all pathways of exactly two transfers. Similarly, it may be shown by mathematical induction that the (i,j) th entry in the matrix G^m represents the fraction of total input to j that left compartment i and flowed to j over all pathways of exactly m transfers.

Recalling that the components of G are all less than or equal to 1, its successive powers tend to consist of progressively smaller components and, in fact, when no recycling is present in the system, the powers of G will truncate (produce a matrix of all zeros) in at most $n - 1$ steps. This opens the possibility that the sum of all the powers of G might form a convergent series, and it turns out that $I + G + G^2 + G^3 + \dots = (I - G)^{-1}$, where I represents the multiplicative identity matrix (with 1's along the principal diagonal and zeros elsewhere).

The limit, $(I - G)^{-1}$, is called the *structure matrix* (Leontief, 1951) and may be calculated directly by matrix inversion. It contains information on all pathways of all lengths that exist in the system. In particular, Levine (1980) pointed out that the j th column of the structure matrix depicted how compartment j ultimately depended on all the other species in the community, so the sum of the j th column should yield the *average trophic position* of that species.

To apportion the given species among discrete trophic levels requires that we deal with each power of the G matrix in its turn. Let a_1 be a row vector wherein the i th component is taken to be the fraction of total input to i that enters from outside the system or, in other words, the degree to which species 1 acts as a primary producer. Multiplying a_1 on the right by G gives another row vector, call it a_2 , whose i th element measures the fraction of total input to 1 which arrives after having passed through one other compartment, that is, the degree to which i acts as an "herbivore." Proceeding in a similar manner, multiplication of a_1 by G^{m-1} yields a vector a_m with elements that quantify the degree to which each compartment acts at the m th trophic level. If there are no cycles in the flow network, this series of row vectors will terminate within $n - 1$ steps, and it becomes possible to form a *trophic transformation matrix*, A , whose i th row is composed of the elements of a_i .

The trophic transformation matrix A was derived by Ulanowicz and Kemp (1979) in an effort to systematize earlier efforts at trophic apportionment by Homer and Kemp (unpublished manuscript; see also Wiegert and Owen, 1971). We read the composition of the i th trophic level along the i th row of A , whereas apportionment of the j th species among the discrete trophic levels is spelled out by the corresponding elements of the j th column. The web of feeding relations can be mapped into a concatenated straight chain using A as a linear transformation (see Ulanowicz, 1986).

An example of the aggregation process can be performed on the simple, hypothetical network in Fig. 21.1. Compartment 1 receives all its input from outside the system, compartment 2 receives 50%, and 3 "produces" 25% of its throughput. The row vector a_1 , therefore, looks like (1.0, 0.5, 0.25, 0), and this vector constitutes the first row of A . The feeding coefficient matrix is formed by dividing each intramural transfer by the throughput of the receiving node. For example, $g_{24} = 15/40 = 0.375$. The G matrix looks like

$$G = \begin{bmatrix} 0 & 0.5 & 0.5 & 0.125 \\ 0 & 0 & 0.25 & 0.375 \\ 0 & 0 & 0 & 0.5 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

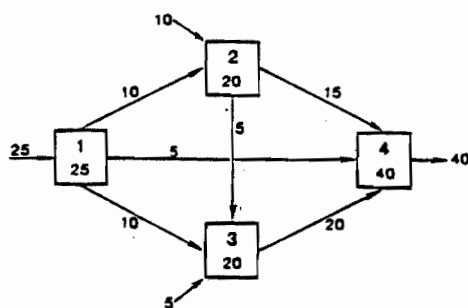


Figure 21.1 Hypothetical network of flows (arbitrary units) among four compartments. Unit 4 receives medium at three different trophic levels.

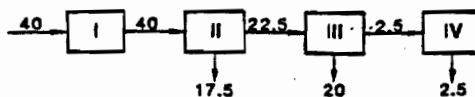


Figure 21.2 Results of trophic aggregation of the flows depicted in Fig. 21.1.

Multiplying a_i on the right by the remaining three powers of G yields the succeeding rows of the A matrix:

$$A = \begin{bmatrix} 1.0 & 0.5 & 0.250 & 0 \\ 0 & 0.5 & 0.625 & 0.4375 \\ 0 & 0 & 0.125 & 0.5 \\ 0 & 0 & 0 & 0.0625 \end{bmatrix}$$

Reading across the second row reveals that the "herbivore" trophic level contains 50% of compartment 2's throughput, 62.5% of 3's, and 43.8% of 4's. Conversely, looking down column 4 reveals that species 4's activity appears 43.8% at the second trophic level, 50% at the third, and 6.3% at the fourth. All columns of A sum to unity, meaning that all the activity of each taxon is accounted for in the trophic levels.

As an alternative to calculating the structure matrix, $(I - G)^{-1}$, we may compute the average trophic position of each of the four boxes in Fig. 21.1 by multiplying each member in the i th row by the value i and summing the results down the columns. This procedure yields trophic positions of 1.0, 1.5, 1.875, and 2.625 for compartments 1 through 4, respectively.

Figure 21.2 depicts the result of aggregating the network in Fig. 21.1 using the transformation A .

CYCLING CAUSES COMPLICATIONS

At this point we could conclude that the relationship between feeding webs and trophic chains is neither as impossible nor as ambiguous as many would portray it to be. We may pass readily from one depiction to the other. True, the discrete trophic compartments are mathematical constructs, but they are unique, quantifiable, and no less "real" than the results of, say, principal component analysis in mechanics or statistics.

There remains, however, one major constraint on the process: the starting network must contain no internal cycles. When cycles are present, the powers of G form an infinite sequence. It then becomes unclear how and where to artificially truncate the number of rows in the A matrix. Of course, material and energy *cycling* are critical features of any ecosystem.

To apply the trophic aggregation scheme to realistic networks with cycles, Ulanowicz (1983) has suggested that the given arbitrary network be decomposed into two constitutive networks—one containing only cycled medium and another portraying only once-through flow in the system (this having the topological structure of a graph "tree"). Removing the cycles involves (1) enumerating all the simple directed cycles, (2) weighting each cycle by an appropriate amount, and (3) subtracting each cycle from the network in such a way so that none of the residual flows becomes negative. The enumeration is accomplished using an algorithm best described as "backtracking with node ordering," and the weighting of the cycles is in proportion to both the magnitude of the smallest arc and the probability that any quantum of medium will complete the specified circuit (Ulanowicz, 1983).

For example, Fig. 21.3 schematically depicts the carbon flows ($\text{g C m}^{-2} \text{ y}^{-1}$) among 17 ecosystem components of a tidal marsh gut in the vicinity of the Crystal River Nuclear Generating Station in Florida. This network may be decomposed into a nexus of pure cycles, as in Fig. 21.4, and a tree of transfers with dissipation (Fig. 21.5). Devoid as it is of complicating cycles, the web in Fig. 21.5 may now be aggregated into a Lindeman-type chain, as in Fig. 21.6.

We might argue that the chain in Fig. 21.6 illustrates the underlying trophic dynamics of the Crystal River system (Ulanowicz, 1986). However, there are difficulties with this portrayal. The cycles that have been excluded do participate in the trophic-dynamic process. Therefore, their exclusion from the chain in Fig. 21.6 is bound to result in distorted values of calculated trophic efficiencies. Such inaccuracy is not overwhelming in the present case, for which cycling accounts for only about 10% of total activity. However, when dealing with network flows of certain materials, cycling can constitute 80% to 90% of total activity, thereby rendering the trophic structure of the residual flows meaningless. Efforts to map the extracted cycles back onto the aggregated residual flows usually lead to a confusing jumble of feedback loops.

There is another, more subtle difficulty with aggregating the residual flows as in Fig. 21.6. In some of the trophic chains condensed from the residual flows of complicated networks, the resultant number of trophic levels turned out to be almost twice the number that had been expected. Closer inspection of the transformation revealed that the residual tree contained a few pathways wherein medium flowed up a feeding chain to a high-level predator, was transferred to the detrital compartment, and from there ascended up another feeding pathway that was independent of the starting route. By regarding the transfer from high carnivore to detritus as equivalent to a legitimate feeding relationship, we artificially increase the lengths of some pathways. By chance, the trophic aggregation in Fig. 21.6 does not appear to contain such artificially long trophic pathways.

To summarize the dilemma, trophic aggregation seems to work well in systems with only unidirectional (acyclic) flow. However, all real living systems involve recycling. Cycles inordinately complicate the trophic aggregation process, and efforts to extract them distort the quantitative results.

TROPHIC AGGREGATION WITH BIOGEOCHEMICAL CYCLING

Resolution of the problem is surprisingly easy. Those who are astonished by the simplicity of the solution are urged to meditate on the wonders of hindsight. Lest the reader be carried away by these considerations, however, it is noted that the general problem of combining cycles with trophic aggregation has not here been solved. Rather, the special structure of ecosystem networks permits a particular resolution to the problem.

Pimm (1982) and later May (1983) both remark on the rarity of cycles in the *feeding webs* of most ecosystems (however, see Patten, 1985, and Polis' results in Chapter 20). By and large, feeding relationships have been supposed to resemble topological trees. My own experience with topological analysis of many ecosystem model networks has tended to support Pimm's and May's observation. For example, of the 119 cycles identified in Fig. 21.3, only two comprised of small

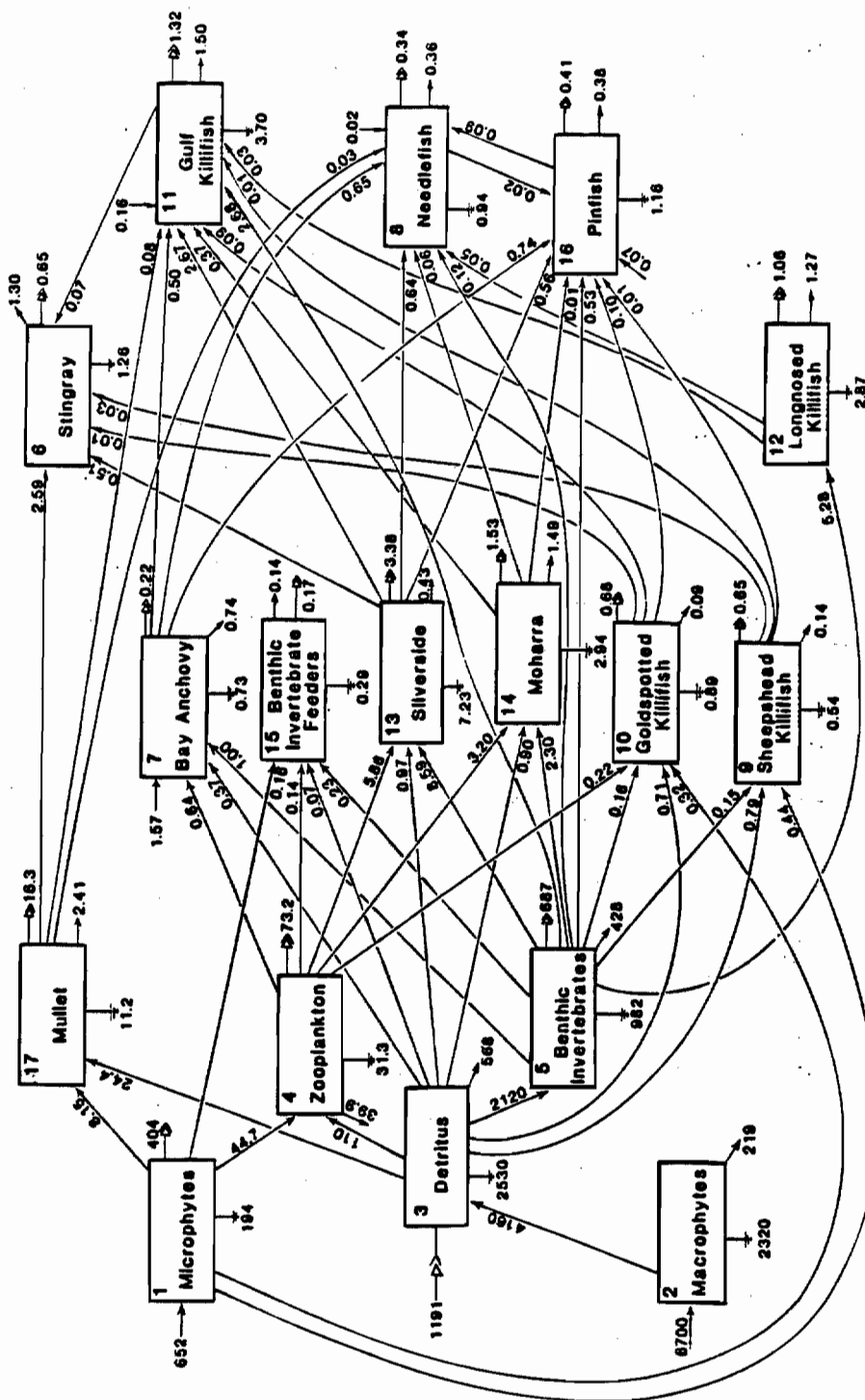


Figure 21.3 Schematic of carbon flows ($\text{mg C m}^{-2} \text{ day}^{-1}$) among taxa of a marsh gut ecosystem, Crystal River, Florida. The linked (\rightarrow) arrows depict returns to detritus. Ground symbols represent respirations (after M. Homer and W. M. Kemp, unpublished manuscript).

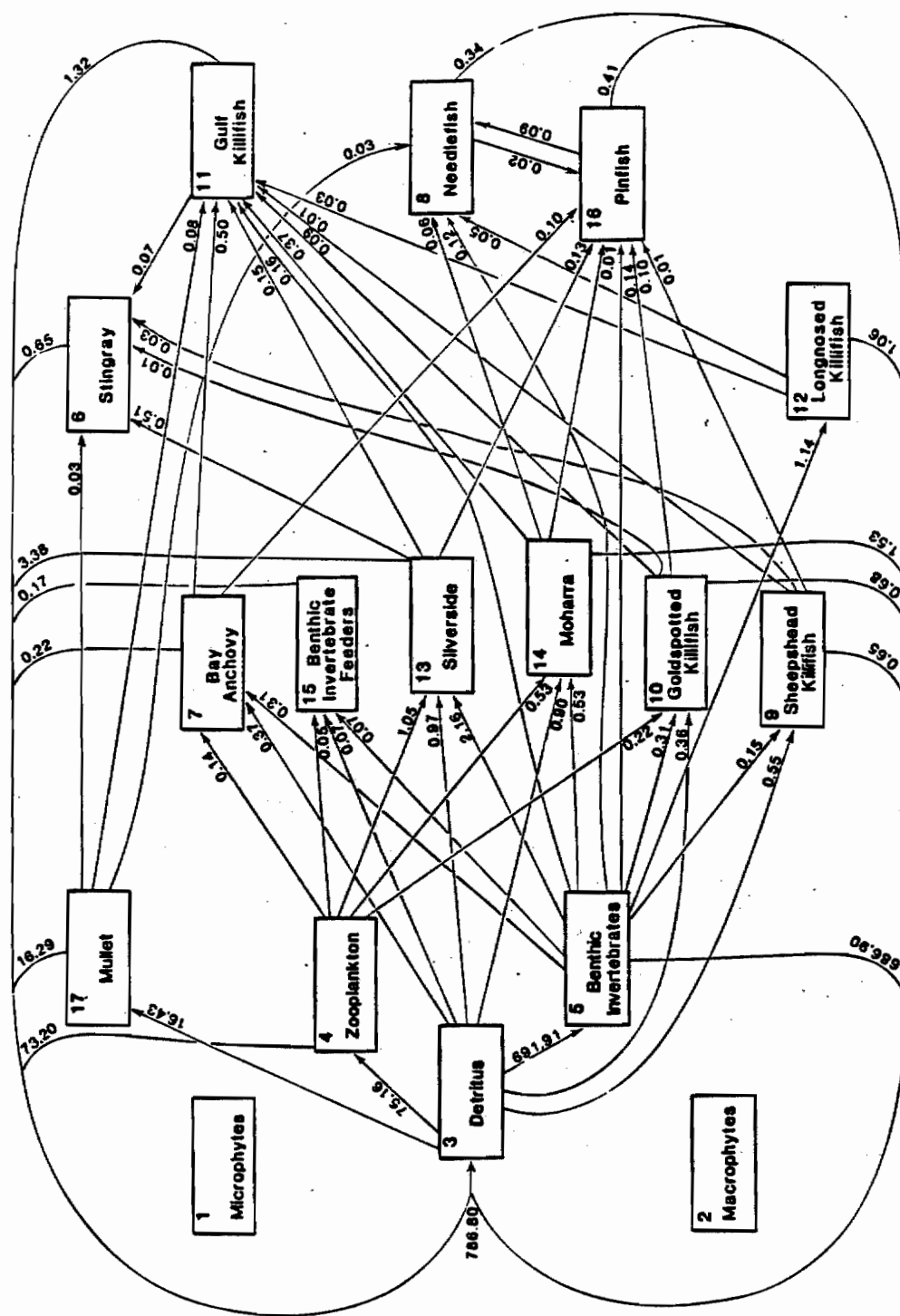


Figure 21.4 Composite nexus of all cycled flow inherent in the network in Fig. 21.3. See Fig. 21.3 for further details.

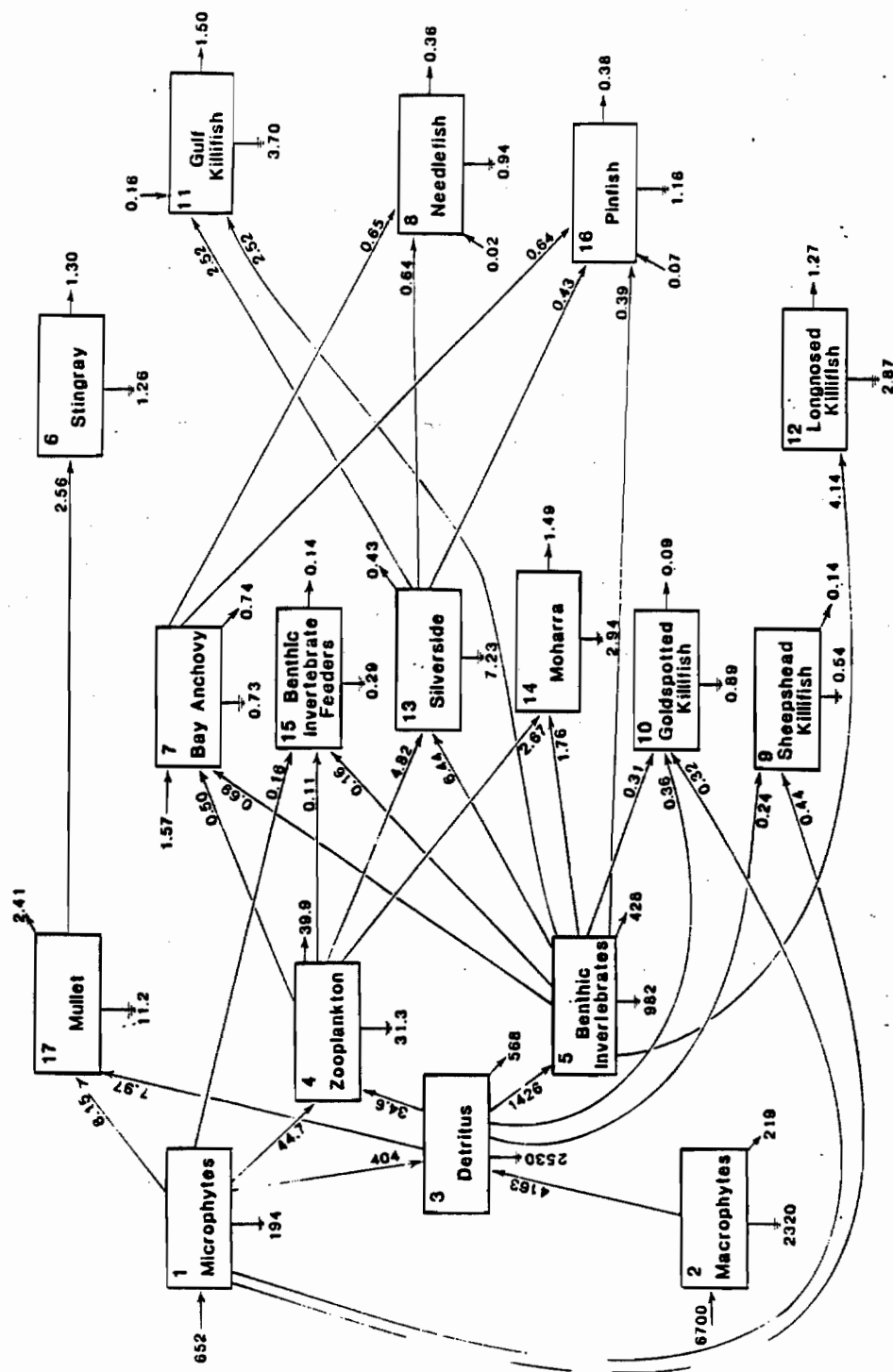


Figure 21.5 The acyclic network of carbon flows remaining after cyclic flows (Fig. 21.4) have been subtracted from the original flows (Fig. 21.3).

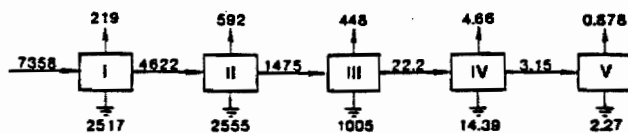


Figure 21.6 Results of trophic aggregation of the flows depicted in Fig. 21.5.

flows do not involve the detrital pool. That is, cycling in this model at least appears overwhelmingly biogeochemical in nature.

Coupling this last observation with the earlier remark about the inaccuracies occasioned by treating flows to detritus as "trophic" transfers (even though organisms of the microbial loop do "feed"), it becomes justifiable to exclude nonliving, nonfeeding compartments from the trophic aggregation. Operationally, this is easy to accomplish. We identify all the living compartments and list them first in the n -compartment series of taxa. Assuming that there are L taxa of feeding organisms, the trophic analysis can be carried out using only the $L \times L$ initial submatrix of the full network after any (presumably inconsequential) cycles in this submatrix have been removed by the methods described earlier. The trophic analysis performed on the submatrix of living species, free as it is from nonfeeding transfers, should prove satisfying to the intuition.

We still have the difficulty of what to do with transfers between the discrete trophic levels just created and the nonliving entities that remain. Cousins (1985) notes that during the International Biological Program it became standard practice to pool all the detrital material into a single compartment and assign this grouping to trophic level 1. For many ecosystems, this assumption is plausible. For example, in mesohaline marshes only about 5% of the primary production of emergent vegetation is consumed while the grasses are still alive, but the dead stalks of *Spartina* form the basis for a rich web of detrital feeders. It seems artificial to separate the grasses into living and detrital boxes. Of course, there is a difference in the quality of detritus issuing from organisms at different trophic levels, but, given the high degree to which the various nonliving organic elements are mixed in the environment, the assignment of detritus to any level other than the first appears hard to justify.

To summarize the various steps in the trophic aggregation algorithm:

1. Separate the compartments into living and nonliving subsets. List the living populations first.
2. Remove any cycles from the web of feeding organisms (this is usually a very small amount of the total activity).
3. Aggregate members of the feeding web into discrete trophic compartments.
4. Gather all nonliving components into a single compartment and assign this node to trophic level 1.

A schematic of the trophic aggregation matrix for this process is given in Fig. 21.7. L represents the number of living compartments and NL the number of nonliving nodes. As can be seen in the lower-right submatrix, all detrital compartments are aggregated into the n th position in the trophic sequence. This is merely a computational convenience, and the position in the matrix bears no relation to the trophic assignment of this aggregation, which is 1.

The results of this algorithm applied to the Crystal River network depicted in Fig. 21.3 is shown in Fig. 21.8. The detrital compartment, D , is placed directly under trophic level I to reflect its assigned level. All detritivory proceeds along the pathway $D \rightarrow \text{II}$ ($2256 \text{ mg C m}^{-2} \text{ d}^{-1}$), while direct grazing by herbivores ($54.6 \text{ mg C m}^{-2} \text{ d}^{-1}$) flows over $\text{I} \rightarrow \text{II}$. The topology of the combination of trophic aggregation with biogeochemical cycling is remarkably similar to the way Odum (1957) originally conceived of ecosystem flows occurring in Silver Springs, Florida. This trophic aggregation is said to be canonical with respect to the algorithm that generated it because, when the output network is used as input to the program, it will remain unchanged by the operations performed on it. That is, it is irreducible according to the aggregation formula used.

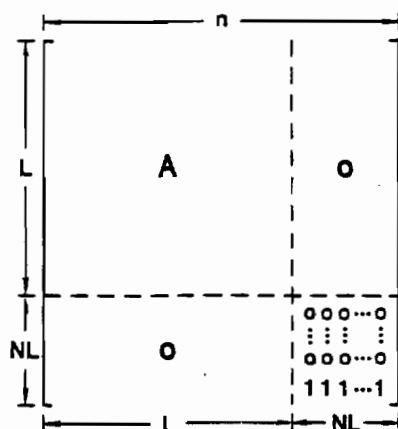


Figure 21.7 Partitioning of the trophic aggregation matrix according to two subgroups of species: *L*, living, and *NL*, nonliving.

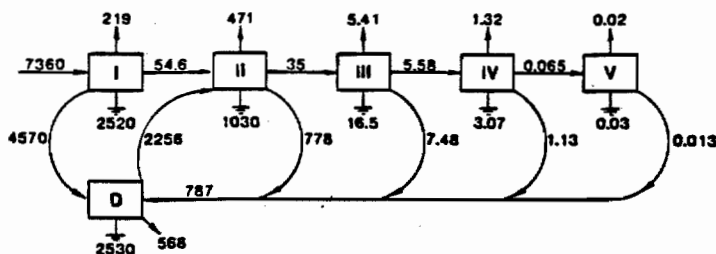


Figure 21.8 Results of trophic aggregation based on the 16 living species in Fig. 21.3. Component *D* represents the pool of all nonliving organic material.

One of the most interesting features of trophic levels is their overall efficiencies. That is, how well does each level pass on medium to the next member in the food chain? Unfortunately, there is some ambiguity concerning the efficiency of the first trophic level in Fig. 21.8. Do we divide the output of *I* by its input, the detritivory by the input to *D*, or some combination thereof? While individual ratios may be especially meaningful to those interested in certain topics (for example, detritivory), a more comprehensive trophic efficiency can be obtained by combining compartments *I* and *D* as in Fig. 21.9. Now the backbone, or *Lindeman spine*, of ever-decreasing trophic transfers (the "trophic pyramid" of earlier parlance) is readily visible and open to interpretation or comparison with the spine of other systems.

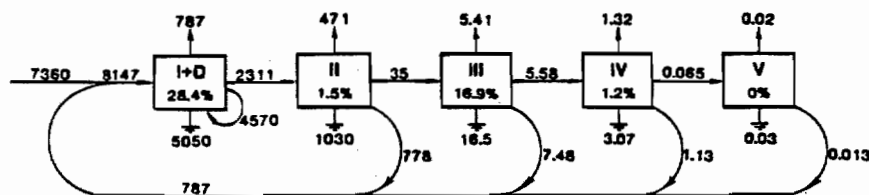


Figure 21.9 The trophic chain of Fig. 21.8 with the detrital pool and primary producers combined. The percentage figure in each box represents the trophic efficiency at that level.

CONCLUSIONS

Earlier ambiguities concerning the relationship between taxonomic category and trophic function appear to have their origins in the relatively imprecise ways in which the community of ecosystem processes was once described. More recently, the increasing number of measured networks of ecosystem processes has provided a quantitative context within which it has become possible to identify precisely the underlying trophic foundation of an ecosystem. To every complicated web of feeding relations and associated biogeochemical cycles, there corresponds a unique chain of trophic transfers in the sense of Lindeman. The ascending chain of trophic transactions is partitioned according to only the feeding processes taking place in the ecosystem. Hence, it appeals to our intuitive notion of what is meant by trophic levels. Furthermore, biogeochemical returns of medium may readily be appended to the trophic transfers to provide an accurate but uncomplicated picture of the system's underlying trophic dynamics. This ability to map arbitrarily complicated networks of ecosystems' flows into a common topological form permits the comparison of what might otherwise have appeared to be hopelessly disparate ecosystems.

Lindeman was able to see beyond the immediate form of ecosystem relationships to perceive the underlying thermodynamic generator for much of organized behavior. It is a tragedy that his genius passed so prematurely from the scene, for it has taken almost half a century for ecologists to begin to give concrete shape to his powerful insight.

ACKNOWLEDGMENTS

The author wishes to thank Steven Cousins for sending him a lucid, well-written critique of Lindeman's concepts, which engendered the present approach to the problem of how to incorporate cycling into the trophic aggregation process. Cousin's help stands as an example of how those on opposing sides of scientific issues can benefit from friendly, rational dialogue. The author is also indebted to Daniel Baird and John Field for helpful discussions concerning the trophic status of detrital material and the role of cycling in trophic dynamics. This work was supported in part by a grant from the Tidewater Administration of the State of Maryland's Department of Natural Resources.

REFERENCES

- COUSINS, S. 1985. Ecologists build pyramids again. *New Scientist* 107 (1463):50-54.
- HIGASHI, M., BURNS, T. P., and PATTEN, B. C. 1992. Trophic niches of species and trophic structure of ecosystems: Complementary perspectives through food network unfolding. *J. Theor. Biol.* 154:57-76.
- LEONTIEF, W. W. 1951. *The Structure of the American Economy*, 2nd ed. Oxford University Press, New York. 257 pp.
- LEVINE, S. 1980. Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* 83:195-207.
- LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.
- MAY, R. M. 1983. The structure of foodwebs. *Nature* 301:566-568.
- ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Mon.* 27:55-112.
- PATTEN, B. C. 1985. Energy cycling in the ecosystem. *Ecol. Mod.* 28:1-71.
- PIMM, S. L. 1982. *Food Webs*. Chapman and Hall, London. 219 pp.

- ULANOWICZ, R. E. 1981. Models of particle-size spectra. In Platt, T., Mann, K. H., and Ulanowicz, R. E. (eds.), *Mathematical Models in Biological Oceanography*. UNESCO Press, Paris. 156 pp.
- ULANOWICZ, R. E. 1983. Identifying the structure of cycling in ecosystems. *Math. Biosc.* 65:219-237.
- ULANOWICZ, R. E. 1984. Community measures of marine food networks and their possible applications. In Fasham, M. J. R. (ed.), *Flows of Energy and Materials in Marine Ecosystems*. Plenum, New York. 733 pp.
- ULANOWICZ, R. E. 1986. *Growth and Development, Ecosystems Phenomenology*. Springer-Verlag, New York. 203 pp.
- ULANOWICZ, R. E. 1989. Energy flow and productivity in the oceans. In Grubb, P. J., and Whittaker, J. B. (eds.), *Toward a More Exact Ecology*. Blackwell Scientific Publications, Oxford, pp. 327-351.
- ULANOWICZ, R. E., and KEMP, W. M. 1979. Toward canonical trophic aggregations. *Am. Nat.* 114:871-883.
- ULANOWICZ, R. E., and PLATT, T. 1985. *Ecosystem Theory for Biological Oceanography*. Canadian Bulletin of Fisheries and Aquatic Sciences 213, Ottawa. 260 pp.
- WIEGERT, R. G., and OWEN, D. F. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *J. Theor. Biol.* 30:69-81.