

LINDEMAN'S CONTRADICTION AND THE TROPHIC STRUCTURE OF ECOSYSTEMS¹

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Abstract. R. L. Lindeman's empirically based generalizations that both progressive efficiencies and percent of energy lost due to respiration increase with trophic level appeared contradictory, because he linked trophic levels in series to form a simple trophic chain. This model equates the energy not respired by the populations aggregated to form a trophic level to the productivity of the populations assigned to the next trophic level. This is clearly not the case for Cedar Bog Lake and ecosystems generally, because of nonpredatory losses and energy gains from other than the previous step in the trophic chain, e.g., bacterivory, detritivory, and feeding on organisms at more than one trophic level. Network analyses of energy-flow models make possible an objective and unambiguous definition of trophic level that does not suffer this contradiction. Trophic guild is proposed as an alternative to trophic level when what is meant is an aggregation of species with similar trophic resources.

Key words: energy flow; Lindeman; trophic dynamics; trophic guilds; trophic levels.

INTRODUCTION

Lindeman's (1942) classic paper, "The Trophic-Dynamic Aspect of Ecology," illustrates the difficulty of simplifying ecosystems without sacrificing essential information. On the one hand, he detailed the myriad pathways by which organisms were nourished in Cedar Bog Lake and recognized that trophic interactions in nature fit a "food cycle" model. On the other hand, he used G. E. Hutchinson's unpublished formulation of 1941 on trophic dynamics (hereafter cited as G. E. Hutchinson, *unpublished manuscript*), wherein trophic "levels" (Lindeman 1942) were groupings of populations, the productivity of any level was defined as the "rate of contribution of energy" from the previous one, and ecosystem trophic structure was reduced to a chain of feeding interactions.

The trophic-dynamic aspect of ecology emphasizes the production of organisms and dissipation of energy in ecosystems, while ignoring other functions, such as nutrient cycling and information processing. Regardless of the larger question of the value of this approach, there are problems internal to the Lindeman-Hutchinson formulation of trophic dynamics. Murdoch (1966) condemned trophic levels because they were not state variables, and many others have recognized the problems in assigning species and detritus to trophic levels (Rigler 1975, Cousins 1987). Rich (1984a) showed how Lindeman's top-down definition of productivity, which ignored the energy flows to decomposers, led to underestimates of Lindeman efficiencies. Hutchinson's formalization of trophic dynamics also led to an apparent contradiction between Lindeman's (1942) hypothesis of increasing progressive efficiencies (the ratio of the

productivity of one trophic level to that of the previous) and observations that respiration per unit productivity increased with trophic level.

The purposes of this paper are, first, to contrast the trophic chain model with Lindeman's energy-flow model of Cedar Bog Lake, as an example of the trophic structure of ecosystems in general. The second is to show how the contradiction between increasing respiration-to-productivity ratios and increasing progressive efficiencies with increasing trophic level, which Lindeman (1942) and Kozlovsky (1968) failed to resolve, is an artifact of connecting trophic levels to form a chain. The last purpose is to discuss two concepts of trophic level: a heuristic one that retains the traditional meaning with a new name, but abandons trophic chains and progressive efficiencies, and an analytical one that sacrifices the traditional meaning of trophic level for one that is objective, quantifiable, and compatible with the network of trophic interactions and energy flows in ecosystems.

TWO MODELS

Raymond Lindeman's writings (1941a, b, 1942) gave explicit expression to his understanding of the network of trophic interactions in Cedar Bog Lake, including the detrital and grazing food webs (Odum 1962).

Following non-predated death, every organism is a potential source of energy for myriads of bacterial and fungal saprophages. . . . These saprophages may also serve as energy sources for successive levels of consumers, often considerably supplementing the normal diet of herbivores. . . . —Lindeman 1942

This understanding was also reflected in the diagram of Cedar Bog Lake that he presented and discussed (Fig. 1). This was a network with cycles: energy moved

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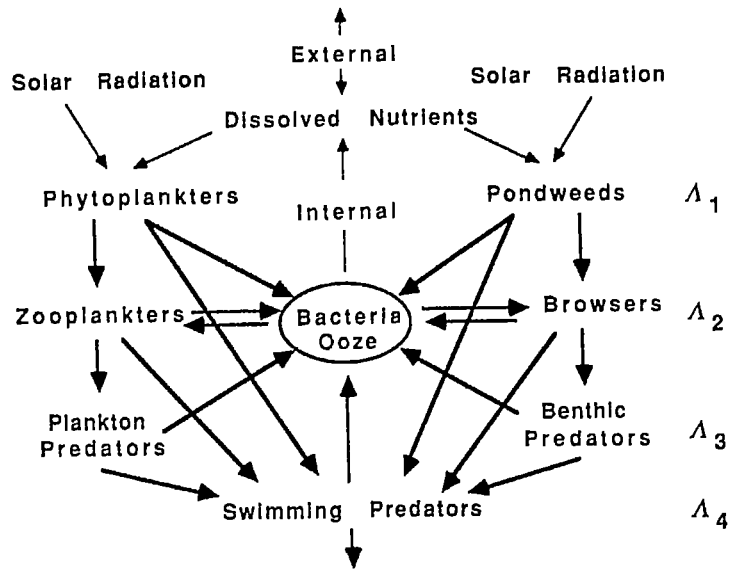


FIG. 1. Generalized lacustrine food-cycle relationships after Lindeman (1942).

to and from the consumers of the grazing chain and "ooze," the detritus and decomposers. Other populations fed on both herbivores and carnivores. Lindeman (1941b, 1942) described such flows as follows,

Zooplankters are primary consumers, feeding indiscriminately upon nannoplankters and suspended organic particles less than 10 mm in diameter.

—Lindeman 1941b

In general, predators are less specialized in food habits than are their prey. This ability . . . tends to make the higher trophic levels of a food cycle less discrete than the lower.

—Lindeman 1942

Most ecosystems share with Cedar Bog Lake features such as detritivory, bacterivory, and blurred trophic levels.

Lindeman simplified the trophic structure of Cedar Bog Lake using G. E. Hutchinson's (*unpublished manuscript*) trophic chain model (Fig. 2). First, each population was assigned to a single trophic level according to the number of times the energy embodied in the population was previously assimilated by organisms at earlier "stages," i.e., lower levels. To make assignments unambiguously requires ignoring the energy obtained by feeding at more than one trophic level or on the trophically unclassified decomposers. Lindeman (1942) understood that energy flows both to and from decomposers and that many populations in Cedar Bog Lake feed at several trophic levels. Nevertheless, he excluded these energy flows from his analysis. The resulting trophic levels could then be connected in series to form a chain. This decision reflects an overriding concern with the productive function of ecosystems, as opposed to its dissipative function (Rich 1984a, b).

Hutchinson formulated the dynamics of the trophic chain as follows:

The rate of change of the energy content Λ_n therefore may be divided into a positive and a negative part:

$$d\Lambda_n/dt = \lambda_n + \lambda'_n,$$

where λ_n is by definition positive and represents the rate of contribution of energy from Λ_{n-1} (the previous level) to Λ_n , while λ'_n is negative and represents the sum of the rate of energy dissipated from Λ_n and the rate of energy content handed on to the following level Λ_{n+1} .

—Lindeman 1942:402–403

The steady-state condition of trophic level i ($d\Lambda_i/dt = 0$) can be formulated, using Kozlovsky's (1968) notation, as follows:

$$\lambda_i = \lambda'_i = R_i + NP_i; \quad i = 1, \dots, n, \quad (1)$$

where R_i (respiration) is the rate of energy dissipated from Λ_i , NP_i (net productivity) the rate of energy content handed on to the following level, and λ_i (productivity) the rate of energy contribution from Λ_{i-1} (the previous level) to Λ_i . It is clear from the Hutchinson quote above that

$$NP_i = \lambda_{i+1}, \quad (2a)$$

and therefore, the steady-state condition can be rewritten as

$$\lambda_i = R_i + \lambda_{i+1}. \quad (2b)$$

Eq. 2b is an explicit statement of the simple structure of the trophic chain according to G. E. Hutchinson (*unpublished manuscript*) and Lindeman (1942).

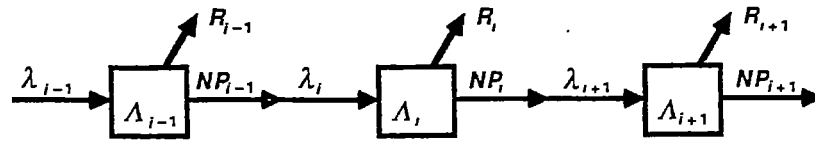


FIG. 2. Formalization of trophic structure according to Hutchinson (*unpublished manuscript*). R_i is respiration, NP_i net production, λ_i productivity and Λ_i energy content of trophic level i .

Ecologists concerned with trophic dynamics have generally followed Lindeman's precedent and assigned populations to trophic levels and connected these levels in series to form acyclic trophic chains or trees (branching chains). They naturally concluded that low transfer efficiencies, $(\lambda_i - R_i)/\lambda_i$, for years estimated roughly at 10%, were the cause of a short supply of energy by the fourth or fifth trophic level. However counterintuitive it might seem, Pimm and Lawton (1977) and Pimm (1982) have shown that food chain lengths are not correlated with energy availability as estimated by primary production and the metabolic efficiencies of species populations in the chain. This lack of correlation may result from the large percentage of primary and secondary production that is not actually assimilated by consumers and predators, respectively (Richman 1958, Slobodkin 1962), but rather assimilated and dissipated by decomposers which are not traditionally included in food chains and webs. A second, related problem is that reducing a realistic network of energy flows to a chain or chains of feeding relations by not including the decomposers neglects information about the actual amount of energy available to organisms. When Lindeman reduced the food cycle of Cedar Bog Lake to a trophic chain, a contradiction arose between his empirical findings and this oversimplification of ecosystem trophic structure.

THE CONTRADICTION

In his analysis of the Cedar Bog Lake productivity data, Lindeman (1942) found increasing progressive efficiencies, the ratio of the productivity of one trophic level to that of the previous, as his trophic levels became further removed from the source of primary production. That is,

$$\lambda_i/\lambda_{i-1} < \lambda_{i-1}/\lambda_{i-2} \tag{3}$$

He offered this finding as a general principle and it has been known since as Lindeman's progressive efficiency hypothesis (PEH). This hypothesis has been rejected by many, including Hutchinson (1978), as being unlikely. It is reasonable to question the generality of the PEH, but not to reject a priori Lindeman's data showing this trend or the possibility of this relationship occurring in nature. The reason his data should be accepted is addressed below.

Lindeman (1942) also reviewed observations of dissipation or respiration losses relative to productivity (i.e., respiration efficiencies). He concluded:

Considering that predators are usually more active than their herbivorous prey, which are in turn more active than the plants upon which they feed, it is not surprising to find that respiration with respect to growth in producers (33 per cent), in primary consumers (62 per cent) and in secondary consumers (> 100 per cent) increases progressively. These differences probably reflect a trophic principle of wide application: the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle.

—Lindeman 1942:404

This generalization can be written as follows:

$$R_{i-1}/\lambda_{i-1} < R_i/\lambda_i \tag{4}$$

The contradiction between these two observations, Inequalities 3 and 4, is as follows. Dividing Eq. 2b by λ_i gives,

$$R_i/\lambda_i + \lambda_{i+1}/\lambda_i = 1, \tag{5}$$

and since R_i/λ_i and λ_{i+1}/λ_i sum to unity, an increasing trend in one ratio necessitates a decreasing trend in the other. Both ratios cannot increase with trophic level.

Lindeman (1942) recognized the possible contradiction between increasing respiration-to-productivity ratios and increasing progressive efficiencies. He tried to reason away this contradiction with reference to predator-prey encounter probabilities:

... this generalization of increasing efficiency in higher consumer groups would appear to contradict the previous generalization that the loss of energy due to respiration is progressively greater for higher levels in the food cycle. These can be reconciled by remembering that increased activity of predators considerably increases the chances of encountering suitable prey.

—Lindeman 1942:407

This might be interpreted as saying that an increase in respiration, R_i , can be offset by an increase in productivity, λ_i , but because Eq. 5 is a statement about ratios, Lindeman's reasoning fails to resolve the contradiction. Likewise, these ratios are not "relatively independent," as suggested by Kozlovsky (1968): given $\lambda_n = A_n$ in the latter's notation, Lindeman was clearly concerned with R_n/A_n and A_{n-1}/A_n , not A_{n-1}/NP_n as stated by Kozlovsky. Respiration-to-productivity ratios and progressive efficiencies are dependent, i.e., Eq. 5 holds, as long as Eq. 2a ($NP_i = \lambda_{i-1}$) is true. Koz-

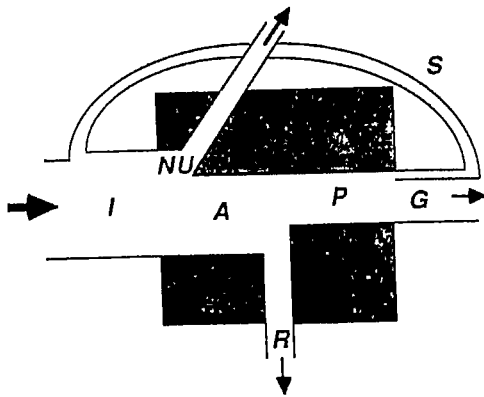


FIG. 3. Components for a "universal" model of ecological energy flow after Odum (1968). *I* is ingestion, *A* assimilation, *R* respiration, *P* production, *G* growth, *S* storage and *NU* energy not utilized.

lovsky's "extremely simple explanation" for the contradiction is wrong.

In simple chains of trophic levels, where Eq. 2a is true, Inequalities 3 and 4 are always contradictory; increasing respiration-to-productivity ratios and increasing progressive efficiencies with increasing trophic level are impossible. Therefore, either Eq. 2a is not true and there is something wrong with the simple chain-of-trophic-levels models, or there is something wrong with the empirical observations upon which Inequalities 3 and 4 are based.

I will not consider the veracity of Lindeman's generalization about respiration costs (Inequality 4), even though his estimates are likely flawed. Rather, assume for the sake of generality that the observations discussed by Lindeman (1942) are possible. While it would be acceptable to do likewise for productivities (Inequality 3), it is enlightening to consider them further.

Lindeman's (1941a, b) data could have accurately documented increasing progressive efficiencies, because he estimated productivity values from measurements of standing stocks of the species populations constituting his trophic levels. This estimate of productivity (λ_i) reflected more accurately assimilation by those populations (A_i) than what was produced by prey (NP_{i-1}) because it neglected nonpredatory losses (production not consumed and not respired by consumers) and egestive losses (production consumed but not incorporated). In principle, these losses can be corrected for, as Lindeman attempted. But, the standing stock biomass or energy content of every population is a product of the energy it gains from all its trophic resources, whether or not they have been assigned to the previous trophic level. It is clear from Fig. 1 that populations Lindeman assigned to trophic level i obtained energy from sources other than the populations he assigned to level $i - 1$. Eqs. 2a and 2b, therefore, did not hold for Cedar Bog Lake. More importantly, these equations will not be true of any ecosystem where

species populations cannot be unambiguously assigned to trophic levels. And, this is the case more often than not.

The problem is the simple chain-of-trophic-levels model and Eq. 2a. Connecting trophic levels, formed by aggregating species populations, in a simple Hutchinsonian chain forces the user to ignore, as did Lindeman, the energy obtained from populations at trophic levels other than the previous, or to attribute the energy inaccurately to populations assigned to the previous trophic level. Lindeman's contradiction is not one between progressive and respiration efficiencies; rather it is one between empirical observations, the trophic level concept, and the trophic chain model.

TROPHIC LEVELS AND TROPHIC GUILDS

Odum's (1968, 1983) "universal energy flow model" makes explicit what Hutchinson's trophic chain model does not, that a species population feeding at more than one trophic level must be partitioned into different levels. Trophic levels are represented as "... discrete energy levels, in which case the biomass and energy channels represent all or part of many populations supported by the same energy source" (Odum 1968). To operationalize Odum's concept, each portion of a population's biomass is allocated to the proper trophic level defined by the number of times that portion of energy was previously assimilated by organisms since the energy was fixed by primary producers in the system. In terms of his model (Fig. 3), ingested energy (I) is all of the inflows to any level, including cannibalism by species constituting part of the previous trophic level. Some of this energy is egested, i.e., not used (NU); the remainder is assimilated (A) and either respired (R), or utilized for production of new biomass (P). Odum (1968) wrote that NU energy was still available at the same level, but his diagram of the universal model did not reflect this. All biomass is available for transfer to the next trophic level, but only some portion of it (G) will be consumed and assimilated during the time interval over which the measurements are made; this is the true productivity, (λ). Energy not transferred and energy transferred but not assimilated by the next trophic level is stored (S) and represents the energy content of biomass.

Ecology now has the means to partition species populations into energy levels, thus making operational an analytical concept of trophic level. Recent attempts to implement this idea partition the energy flow through each compartment into several classes according to how many steps of intercompartmental transfer (i.e., how many trophic levels) energy experienced before it arrived at the compartment (Ulanowicz and Kemp 1979, Levine 1980, Ulanowicz 1986). Ulanowicz and Kemp (1979) presented a two-step transformation algorithm to partition and reaggregate compartments of an energy-flow model into a canonical chain of trophic levels. Cycles cause, however, computational problems

for this algorithm. Ulanowicz (*in press*) changed this algorithm so that the cycles are first deleted. Levine (1980) and Braner (1985) used the theory of Markov processes to calculate, respectively, trophic level distribution of each compartment and trophic position (average path length from external input). Higashi et al. (*in press*) generalize the basic idea of partitioning, develop the notion of trophic-path partitioning of standing stocks and flows, and derive a method for "unfolding" any given food network along the direction of trophic process from the bottom (source components or primary producers) to higher trophic levels. This is achieved by partitioning all network components, both standing stocks (compartments) and flows, according to the past history of the energy in the system. This method does not require arbitrary decisions about the trophic level of species populations or functional groups, especially decomposers and detritivores, nor deletion of cycles from the ecosystem network (T. P. Burns et al., *unpublished manuscript*).

A *trophic level* is then a composite of those portions of the energy content of each component that have been assimilated an equal number of times. If an ecosystem has cycles of matter-energy, then the number of trophic levels is infinite at some very low probability. The question is no longer how many trophic levels are there; rather it is by what trophic level does some significant percentage of the energy flow into an ecosystem dissipate. This does not depreciate questions why or how the number of species populations that predate one upon the other is or is not limited in ecosystems.

This analytical concept of trophic level also preserves progressive efficiency (λ_{+1}/λ_i) as a meaningful index of trophic dynamics, because trophic levels receive energy only from the previous one. Energy flows into successive trophic levels, productivities strictly decrease by dissipation according to the second law of thermodynamics, but not so trophic levels' energy contents, biomasses, or numbers (Higashi et al., *in press*). The resulting energy-flow pyramid accurately quantifies the dissipative function of the ecosystem, because it includes all known flows to and from decomposers. Changes in respiration and progressive efficiencies with trophic level are dependent upon the particular trophic network, but they are constrained, in accordance with Eq. 5, to sum to unity. In ecosystem networks with cycles, progressive efficiencies (or a sequence of them) eventually become constant (repeat) with increasing trophic level (T. P. Burns et al., *unpublished manuscript*). Because most ecosystems have some energy cycling, progressive efficiency might, as envisioned by Lindeman (1942), serve as an index of the maturity or successional status of ecosystems, increasing as the ecosystem more efficiently utilizes energy (Margalef 1968, Odum 1969).

The traditional usage of trophic level, an aggregation of species populations deriving its energy from another such aggregation that is one trophic transfer closer to

the primary producers, is consistent with Lindeman's (1942) empirical findings if trophic levels are not constrained to receive energy from only the previous level. What was G. E. Hutchinson's (*unpublished manuscript*) productivity (λ) now represents explicitly all of the inputs to all of the populations grouped together regardless of the trophic status of their proximal resources. Energy flows from decomposers, if this diverse assemblage of organisms is not partitioned into different groups, and those from other than the previous level are included in the productivity measure. Likewise, the energy available for transfer is not necessarily equal to that entering the next trophic level. A large percentage of energy in biomass is not assimilated by predators, but is available for other uses by productive consumers and dissipative decomposers, and thus must be added to predation losses to determine Lindeman efficiencies correctly for these traditional trophic levels (Rich and Wetzel 1978, Rich 1984a, b).

This heuristic concept of trophic level (Fig. 4) allows accounting for all possible trophic interactions in energy-flow models of ecosystems. It recognizes that chemical energy can move between traditional trophic levels in many ways, including cycles (e.g., autotroph to herbivore to carnivore to decomposer to detritivore to carnivore), until it is dissipated or lost from the system. Eqs. 2a and 2b are no longer true generally, because of the possibility of obtaining nourishment from multiple trophic levels. As a result, Lindeman's contradiction disappears, as does the constraint of Eq. 5 on the relationship between respiration and progressive efficiencies.

Unfortunately, because the heuristic concept of trophic level lumps together populations which only generally obtain nourishment from similar resources, their progressive efficiencies are valueless as indices of trophic dynamics. They no longer indicate for each level "the degree of utilization of its potential food supply or energy source" (Lindeman 1942:407), because each potentially has energy sources that are not part of the previous trophic level. Trophic levels formed by grouping species populations together represent a mixture of energy of varying age and history of movement within the system. Because there is no unambiguous meaning to a sequence of such groupings, they should be called something other than trophic levels; I suggest trophic guilds, where guild has its original ecological definition as "... a group of species that exploit the same class of ecological resources in a similar way" (Root 1967).

A *trophic guild* is, then, a group of species that exploits the same class of trophic resources in a similar way; the qualification "in a similar way" allows for separating groups with common trophic resources according to how they obtain their energy. Yodzis (1982) first used the term trophic guild to describe dominant cliques, a set of species in a given ecosystem with the property that every pair in the set has some food re-

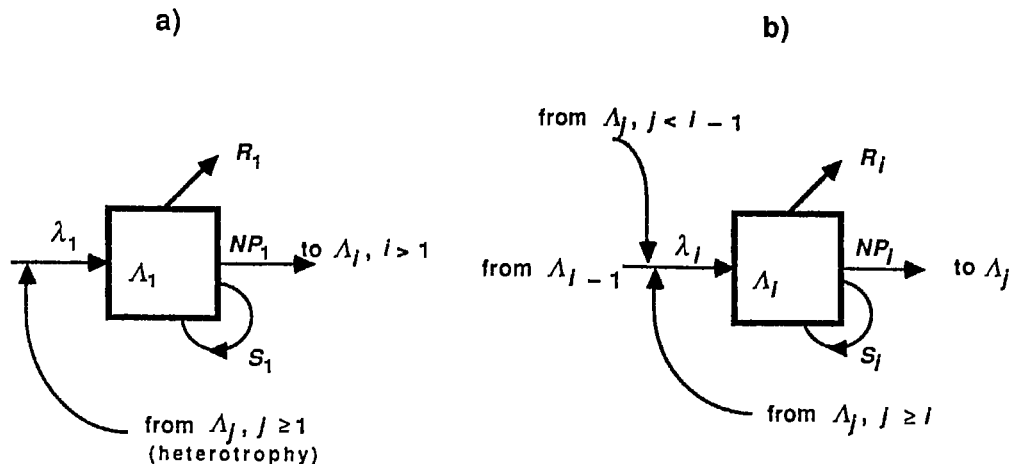


FIG. 4. Representation of heuristic concept of trophic level: (a) generic primary producer, (b) generic consumer. R , is respiration, NP , net production, S , storage, λ , energy input and Λ , energy content of trophic level i .

source in common and which is contained in no other such set. The proposed definition of trophic guild is independent of cliques, but graph theory may provide an unambiguous compartmentation of ecosystems into trophic guilds.

Ecology now has two distinct and complementary concepts for the components of trophic structure (Fig. 5). Trophic guilds are defined as fuzzy sets (e.g., Klir and Folger 1988) of species populations having similar trophic resources. They correspond to the traditional concept of trophic level, a heuristic and generally imprecise classification of organisms as autotrophs, herbivores, carnivores, decomposers, etc. (Fig. 5b). Trophic levels, in accordance with Hutchinson's original intent, are now strictly defined as the sum, over all species populations or components in the ecosystem, of the portions of their energy contents that had been previously assimilated an equal number of times (Fig. 5c). Trophic levels defined in this way are crisp (unfuzzy) sets, quantifiable using network models of energy flows. As such, they may not be identifiable with specific discrete species populations, but they do unambiguously describe the trophic (and dissipative) structure of ecosystems.

SUMMARY AND CONCLUSIONS

G. E. Hutchinson's (*unpublished manuscript*) trophic chain model was inconsistent with Lindeman's (1942) network model of Cedar Bog Lake and the method he used to determine the productivity of his trophic levels. By measuring standing stocks over time, Lindeman accounted for all the inputs to the populations he aggregated to form each trophic level. These inputs could have come, however, from several trophic levels, as well as the trophically unclassified decomposers. When, in accordance with Hutchinson's formalization, Lindeman connected his trophic levels into a simple chain,

his observations of decreasing respiration and increasing progressive efficiencies necessarily appeared contradictory.

Alternative concepts of trophic level are useful in the trophic-dynamic aspect of ecology. Traditional trophic levels (e.g., autotrophs, herbivores, carnivores) have heuristic value when they are not connected in simple chains, but they are defined subjectively and ambiguously, and they have little to no analytical value today. A better term for them is trophic guilds, groups of species populations with similar trophic resources. Trophic levels corresponding to Odum's (1968) abstract energy levels, aggregations of parts of many ecosystem compartments, can now be accurately operationalized (Higashi et al., *in press*) and should be adopted as the working definition of trophic level.

Given the recent advance in untangling trophic networks in the ocean (Pomeroy 1985), freshwater systems (Kerfoot and DeMott 1984), and in soils (Coleman 1985, Miles 1985, Hunt et al. 1987), now is the time to use analyses that are capable of capturing the full knowledge of energy-flow structure in ecosystems (e.g., Finn 1976, Matis and Patten 1981, Hannon 1985, Higashi 1986, Patten et al., *in press*). The latter paper, for example, contrasts the results of a Lindeman-type analysis with an input-output flow analysis capable of dealing with multiple inputs to compartments, and thus determining accurately the amount of energy flowing to compartments (Hannon 1973). When all possible pathways, especially cycles, are accounted for properly, the compartments at what would traditionally be considered upper trophic levels experience more energy per unit input to the system than is predicted by the progressive efficiencies along the simple trophic chain (Patten et al., *in press*). Network analyses and the analytical concept of trophic level obviate information-reducing simplifications, such as those Lindeman was

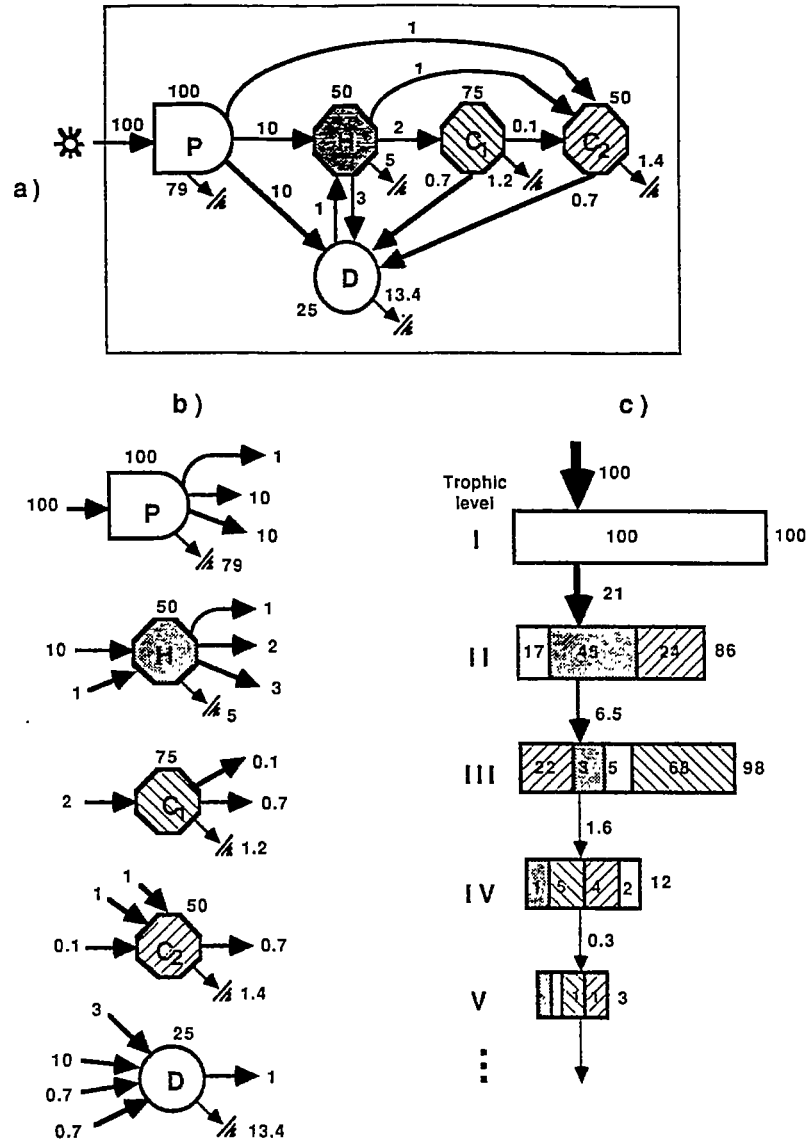


FIG. 5. Illustrations of the analytical and heuristic concepts of trophic units. Numbers associated with compartments are standing stocks and those with arrows are flows: (a) a hypothetical aggregated energy-flow network (P is primary producers, H herbivores, C₁ carnivores, C₂ top carnivores and D decomposers); (b) the five trophic guilds of the network depicted in (a); and (c) composition, standing stock, and productivity of the first five trophic levels of the network depicted in (a). The sizes of boxes as drawn are not proportional to standing stock values.

forced to make, and moves ecology closer to a dynamic aspect of ecosystems that perceives equally the complementary dissipative and productive functions inherent in trophic structure.

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