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Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community

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Abstract

Ecological researchers have long borrowed concepts from the theory of chemical kinetics to describe nutrient dynamics in ecosystems. Contemporary ecology, however, is in the process of creating its own suite of ideas to quantify how whole ecosystems develop. In particular, the theory of ecosystem ascendency can be applied to data on the simultaneous flows of various chemical constituents to determine which element is limiting to each species via which individual input. That is, Liebig's law of the minimum appears a corollary to the broader description of whole-system development. Application of the method to networks of carbon, nitrogen and phosphorous flowing through the 36 major compartments of the Chesapeake Bay ecosystem reveals that, although nitrogen limits the production by most of the planktonic and benthic compartments, the nekton appear to be using phosphorus in limiting proportions. If one links together the ecosystem components via the controlling flows into each node, a new and sometimes dramatic picture of nutrient kinetics emerges. Not surprisingly, during the summer the root nutrient control on the system appears to be the recycle of nitrogen between particulate organic materials in the sediments and their attached bacteria. No coherent pattern of control is evident during the autumn turnover, whereas during winter and spring the ultimate control appears to be exerted by a feedback in the 'microbial loop' that involves both N and P. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

It is commonly recognized that a dearth of any chemical element can affect the dynamics of an organism or population. The basis for quantifying which particular nutrient most impacts organism growth traces back to Liebig (1840), who noted that the "growth of a plant is dependent on the amount of food stuff which is presented to it in minimum quantity". Liebig's notion in turn derives from the earlier observation in chemistry that reactions consume compounds in fixed proportions, and that reactant initially present in least proportion will be the one that eventually limits the course of the reaction.

Little progress has been made during the last century and a half to elaborate Liebig's 'Law of the Minimum'. One modification has been the corollary notion of 'factor interaction' (Odum and Odum, 1959). That is, some factor other than the limiting element may modify the rate of utilization of the

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latter. For the most part, however, ecologists have been inclined to search for the 'silver bullet' that controls the dynamics of a population, and have even tried to extrapolate this notion to the entire ecosystem. For example, phosphorous is regarded to limit primary production in freshwater aquatic ecosystems. Because primary production sets the rate of community metabolism, one speaks of these systems as P-limited (Edmondson, 1970). Similarly, marine ecosystems are considered to be nitrogen-limited (Rhyther and Dunstan, 1971).

Most ecologists are aware that extrapolating the concept of limiting element from the level of the population to that of the whole ecosystem is a major oversimplification. Ecosystems are simply too diverse in terms of their species composition, spatial and temporal patterns to adhere to such a simple scheme. Thus, D'Elia (1988) notes how estuarine ecosystems appear to be sensitive either to nitrogen or to phosphorous, depending upon the time of year and the location along the salinity gradient. More to the point, however, is the possibility that various components of a given ecosystem at any given time and place might be sensitive to the availabilities of different elements or environmental factors (Marsh and Tenore, 1990). For example, while an algal community is limited by the supply of nitrogen, the fish, who feed several trophic levels above the algae, could be starved for phosphorous.

In order to describe the response of whole ecosystems to nutrient availabilities, it is first necessary to quantify the status of the entire system in terms of one or a very few cogent indices. Traditional indices of system status, such as aggregate system biomass or total primary productivity, are likely to prove inadequate representations of system dynamics. As a rule, they quantify *either* system structure *or* function, but do not incorporate the relationship of structure to function, which is the very essence of system dynamics.

Over the past decade we have been promoting the concept of network ascendency as an encapsulation of the diverse and sometimes disparate facets of ecosystem function (Ulanowicz, 1980, 1986, 1989; Baird and Ulanowicz, 1989). Briefly, ascendency measures the extent of activity and degree of organization inherent in a weighted network of ecosystem trophic transfers. Heretofore, the ascendency has been defined entirely in terms of system kinetics, i.e., upon the flows or transfers of materials and energy. Failing the inclusion of structural elements, such as stocks of biomass or chemical elements, the ascendency, like the conventional indices just mentioned, remained inadequate to the task of quantifying nutrient dynamics. There appeared no way to introduce stocks into the definition of ascendency that was both dimensionally consistent and followed naturally from the basic definitions in information theory (with which the ascendency concept was constructed).

Fortunately, a coherent way to employ information theory to quantify both the structural and functional aspects of ecosystems (i.e., portray the ecodynamics) was recently discovered (Ulanowicz and Abarca, 1997). The key to elaborating the ascendency was to recognize that the 'average mutual information' of the flow structure was but one component of a more comprehensive measure of information in the system. Specifically, the Kullback– Leibler information measure replaced the narrower mutual information as a measure of the information inherent in passing from the relatively indeterminant possibilities for transfer among a distribution of community stocks toward a specific network of the flows that actually link those stocks.

The main objective of this exercise is methodological: to demonstrate that ecology, like most of the hard sciences, can be carried out in theoretic-deductive manner. In fluid mechanics, or physical oceanography for example, one begins with the Navier–Stokes form of Newton's second law, fits those equations to the particular system being studied, and proceeds to deduce the details of fluid flow. Here we will attempt to invoke the principle of increasing ascendency as a general expression of ecosystem dynamics and apply that principle to a limited set of data on nutrient flows in a specific ecosystem (mesohaline Chesapeake Bay). The process leads to the identification of specific exchanges as 'bottle necks' or rate-limiting transfers.

One difficulty in working with whole-system principles is that such analysis demands large amounts of data. To address the overall question of nutrient limitations in a marine ecosystem would require estimates of all exchanges of all chemical elements flowing through and circulating within the community. It has taken us several years to accumulate estimates of all transfers of carbon, nitrogen and phosphorous among the major taxa of the Chesapeake ecosystem. This seems the minimum diversity of elements necessary to demonstrate how the process works. Of course, this triad of nutrients is not exhaustive of what can control processes in marine ecosystems, so that, absent estimated networks on elements such as iron, manganese, silicon, etc., our analysis will fail to pinpoint where these elements may control system dynamics. Our exercise should, however, make clear how these other media could be factored into the analysis. What will remain beyond the scope of this methodology will be the workings of intensive variables, such as light and temperature.

We begin our exposition of the methodology with a brief summary of the derivation of the biomass-inclusive ascendency, followed by its application to the question of which nutrient transfers control various aspects of system trophic dynamics.

2. Quantitative ecodynamics

The goal in defining the ascendency index is to quantify the organization possessed by the members of a living ecosystem above and beyond that exhibited by a similarly proportioned, but nonadaptable collection of nonliving physical entities. Let B_i represent the amount of biomass (usually measured in terms of a particular chemical element) in population *i*, and *B* be the total system biomass (i.e., B = $\sum_{i=1}^{n} B_i$). Now let us pretend for the moment as though these components were nonadaptable chemical species distributed in the proportions B_i/B . Under these assumptions, the probability that a quantum of biomass eaten at any instant issued from compartment i would be estimated by the fraction B_i/B_i Similarly, the probability that it is devoured by compartment j would be B_i/B . In the absence of any interfering (e.g., organizing) influences, the joint probability that the transferred particle both leaves *i* and enters j would be estimated by the product of these independent estimators, i.e., $B_i B_i / B^2$.

Many readers will recognize that this joint probability also follows from the well-known 'law of mass action' in chemical kinetics. That is, it is the relative potential for flow between i and j taking into account *only* the magnitudes of material currently stored in the putative reactants and products. Not every conceivable flow is realized, however, and the routes of actual transformations are characterized by a set of fixed stoichiometric coefficients and kinetic constants. In ecosystems, even further deviation from these mass action potentials can occur owing to the fact that living systems are comprised of adaptable components.

To quantify the ecological transfers that actually occur, we choose T_{ij} to represent the amount of biomass seen to pass from host *i* to predator *j*. The aggregate of all such exchanges is called the 'total system throughput' and is represented simply by *T* (i.e., $T = \sum_i \sum_j T_{ij}$). Hence, the joint probability of flow from *i* to *j* is estimated 'after the fact' as T_{ii}/T .

The Kullback–Leibler index is a non negative measure of the information that appears when passing from an a priori probability distribution among a given set of categories to its corresponding a posteriori configurations (Kay, 1984). In terms of these probabilities it is defined as

$$I = \sum_{k} p_k \log(p_k/p_k *), \qquad (1)$$

where $p_k *$ is the a priori estimate of the probability of state k and p_k is the probability of the same state after observation. The common practice in ecology is to use logarithms base-2, giving the resulting I the units of 'bits' of information. In working with networks, the state k can be taken as the joint combination i, j, so that the information inherent in the network of stocks and flows thereby becomes

$$I = \sum_{i} \sum_{j} \left(T_{ij} / T \right) \log \left(T_{ij} B^2 / B_i B_j T \right)$$
(2)

Network ascendency is defined as the information in a flow network as scaled by the overall activity of that network (i.e., the total system throughput, I). Whence, the ascendency for stocks and flows becomes

$$A = \sum_{i} \sum_{j} T_{ij} \log \left(T_{ij} B^2 / B_i B_j T \right).$$
(3)

The reader may verify that Eq. (3) reduces to the original form of the ascendency (Ulanowicz, 1986) if and only if $B_i/B = \sum_j T_{ij}/T$ and $B_j/B = \sum_i T_{ij}/T$. Whenever there is any difference in the proportions

of biomass and compartmental inputs or outputs, the ascendency (Eq. (3)) will exceed that calculated from the original form based on flows alone.

Some readers already may have noted that not all flows are between components of the system. Exogenous inputs and exports occur in all real systems. What biomass values should one assign to these exogenous sources and sinks as they appear in Eq. (3)? It turns out to be quite feasible to assign hypothetical biomass values to external sources and sinks in such a way that they do not skew the internal distributions of stocks and flows. One simply chooses a biomass conjugate to each external flow such that the turnover time of that hypothetical biomass is identical to that for the system as a whole [see p. 6 of the paper of Ulanowicz and Abarca (1997)].

Eq. (3) is the ascendency for a flow network of only a single medium averaged over time. As we are interested in following the course of several chemical constituents (e.g., C, N and P) over different intervals of time (say, seasonally), it becomes necessary to elaborate on the biomass by defining B_{ikl} as the amount of biomass of medium k in component *i* during interval *l*. Accordingly, T_{ijkl} will represent the flow of medium k from *i* to *j* during timestep *l*. The ascendency in Eq. (3) then generalizes to

$$A = \sum_{i} \sum_{j} \sum_{k} \sum_{l} T_{ijkl} \log \left(T_{ijkl} B^2 / B_{ikl} B_{jkl} T \right), \quad (4)$$

where *B* and *T* are now summed over all the indices of B_{ikl} and T_{iikl} , respectively.

What, if anything, in Eq. (4) relates to conventional notions of nutrient limitation? To answer this question it is necessary to calculate the amount by which the overall index changes in response to infinitesimal perturbations in each of the flows and stocks taken separately. Using the familiar chain rule from differential calculus we have

$$dA = \sum_{i,k,l} \frac{\partial A}{\partial B_{ikl}} dB_{ikls} + \sum_{i,j,k,l} \frac{\partial A}{\partial T_{ijkl}} dT_{ijkl}$$
(5)

Substituting Eq. (4) into Eq. (5) yields, after considerable algebraic simplification,

$$\frac{\partial A}{\partial B_{prs}} = 2 \left\{ \frac{T}{B} - \frac{1}{2} \left[\frac{\frac{\Sigma}{u} T_{purs}}{B_{prs}} + \frac{\frac{\Sigma}{u} T_{uprs}}{B_{prs}} \right] \right\}$$
(6)

and

$$\frac{\partial A}{\partial T_{pqrs}} = \log\left(T_{pqrs}B^2/B_{prs}B_{qrs}T\right) \tag{7}$$

We now focus our attention on the right hand side of Eq. (6). The first term in brackets is the turnover rate of all elements in the entire system for the full duration of observation. The remaining terms represent the average turnover rate of element r in compartment p during interval s. Hence, Eq. (6) says that if the turnover rate of an element in a particular compartment at a given time is *slower* than the overall rate for the whole system, then that particular combination of element, compartment and time contributes *positively* to overall system ascendency. The converse will hold if the particular turnover rate is faster than that for the system as a whole.

Confining our attention for the moment to a particular compartment, p, and time, s, we may compare all the nutrients, r, in Eq. (6) to uncover which element, if increased, would most benefit the system as a whole. It turns out to be the element with the slowest turnover time.

But a comparison of turnover times is reminiscent of Liebig's analysis. For if one assumes that a population assimilates elements in a fixed ratio (a good approximation for most living species), then one can demonstrate that the element being presented to the compartment in the least proportion will be the one with the slowest turnover rate (Appendix A). Hence, Liebig's law of the minimum appears as a corollary to the phenomenological trend towards ever-higher system ascendency!

We could have spared ourselves much labor by ignoring the ascendency and simply calculating and comparing elemental turnover rates. The question would arise, however, which of the various inputs of the limiting element to a given compartment is most important? The conventional response would be that the largest inflow of the limiting nutrient into a compartment constitutes its most important source. We note, however, that an increase in that largest flow may not be of greatest advantage to the whole system! Of all the inflows of limiting nutrient to a given compartment at a specified time, the one most important to overall system development is that which yields the largest sensitivity coefficient as calculated by Eq. (7). Invoking the concept of system ascendency provides a theoretical foundation for extrapolating population-level concepts to the system as a whole: One first determines which element exhibits the slowest turnover rate within each component at every time step. Next, one calculates the inflow of that 'limiting' element for which the system as a whole is most sensitive. These 'system-limiting flows' can be spliced together to form a network picture of control links that characterizes the nutrient dynamics of the system during each interval of time.

3. The Chesapeake mesohaline ecosystem

Few ecosystems anywhere have been quantified to the elaborate extent necessary to complete the analysis just described. In fact, the only such data set known to us pertains to the mesohaline stretch of the Chesapeake Bay estuary. Over the last decade we have been working to estimate trophic exchanges among the major components of this ecosystem. The analysis of the carbon network was accomplished first (see Baird and Ulanowicz (1989) for details and data sources). The magnitude of 122 flows between 36 compartments as well as 55 exogenous flows of carbon were estimated on a seasonal (4/yr) basis. Recycle routes for carbon were rather sparse, as expected, but, surprisingly, the collection of cycles exhibited a bipartite character. That is, there was some recycle of carbon among the planktonic compartments and a separate cluster of cycles among the benthic and nektonic components. These autonomous domains of recycle were bridged mostly by filter feeding organisms, both sessile and nektonic. The vaunted 'microbial loop' was seen to be no loop at all as regards carbon. Rather, these species functioned more as sinks to convey much of the excess carbon production out of the system (or into DIC).

The pathways of nitrogen transfers through the ecosystem were then addressed (Baird et al., 1995). Our strategy was to build the nitrogen network upon the foundations of the preceding carbon schematic. Thus, it was assumed that the net production issuing from any living compartment bore a fixed C:N ratio characteristic of the donor species. The exogenous inputs of nitrogen had to be estimated independently of the corresponding carbon inputs.

The balance of nitrogen around each living species took the form $C_n = P_n + F_n + U_n$, where C_n is the total consumption of nitrogen, P_n is the net corporeal production of nitrogen, and F_n and U_n are the releases of particulate and dissolved nitrogen, respectively. Because we already knew the inputs of carbon from the various prey species, we divided these inputs by the C:N ratio of each donor in its turn to estimate the separate inputs of nitrogen to the predator. The sum of all such sources was C_n . In the same fashion, because we knew the net production of carbon by each compartment, P_n was obtained by dividing that production figure by the C:N ratio of the source. The sum $F_n + U_n$ was the balance of consumption over production, and usually this excess was partitioned between the dissolved and particulate phases using published excretion rates for either form. The remaining term was calculated by difference.

As expected, the fraction of nitrogen activity contributing to recycle within the system was about twice that for carbon. In particular, the number of pathways for recycle of nitrogen far exceeded that for carbon. Although we counted only 61 simple cycles of carbon in the network, almost 53,000 loops for nitrogen recycle were enumerated. (It should be noted as how the number of simple cycles is a much stronger function of how processes are linked with one another than of the number of links present [see Ulanowicz, 1983].) The components of the microbial loop were active in recycle of nitrogen, however only a small fraction of that reused N processed by microbiota was cycled entirely within the water column. The bulk of the recycling activity by the components of the microbial 'loop' was to return some of the N issuing from the benthos back into the sediments (Baird et al., 1995).

The estimation of the magnitudes of phosphorous exchange in the Chesapeake ecosystem closely followed the methods used to estimate their nitrogen counterparts. The network analysis of the phosphorous webs yielded results not very different than those obtained from the nitrogen flows. For these reasons we have elected not to describe the phosphorous results here in any detail. Instead we refer interested readers to the internal report on the work (Baird, 1998) for sources of data and details on the estimation methods. For those readers not familiar



Fig. 1. Annual exchanges of phosphorous among the 36 major components of the mesohaline Chesapeake Bay ecosystem. Open triangular arrowheads indicate returns to suspended particulate phosphorous pool (35); shaded arrowheads, to dissolved phosphorous (34); and black arrowheads, to sediment particulate phosphorous. Double arrowheads indicate exports from the system. Flows are in mg P m⁻² yr⁻¹. Numbers at the inside bottom of the boxes are the standing stocks in mg P m⁻².

with our earlier papers we present the annual trophic transfers of phosphorous in Fig. 1. The entire data set consists of 12 such networks, one for each season for all three elements.

In the remainder of this paper we turn our attention to using the revised ascendency to uncover the nutrient controls that exist among the carbon, nitrogen and phosphorous networks.

4. Compartmental limitations

Eq. (6) implies that the sensitivity of the community ascendency to changes in the stock of an element in a particular compartment varies inversely as the rate of passage of the element through that compartment. It can be shown that the element being presented to a predator in the least stoichiometric amount is the one with the slowest rate of passage through the compartment (Appendix A). It follows that the element 'limiting' a given component will be the one with the largest value of the sensitivity as calculated by Eq. (6).

Table 1 contains the values of $(\partial A/\partial B_{pr})$ (i.e., sensitivities calculated on the basis of the annual flow matrix). Reading across any row, the largest entry (indicated by an asterisk in the table) reveals which of the three elements is in shortest supply to that particular ecosystem component. It is commonly

Table 1

Deviations of the annual throughput rates for three major nutrient elements from their respective system-wide throughputs (in yr^{-1}) for the major living components of the Chesapeake mesohaline ecosystem (similar to Eq. (6))

	Carbon	Nitrogen	Phosphorous
(1) Phytoplankton	0.411E + 02	0.988E + 02 *	0.879E + 02
(2) Bacteria on suspended POC	-0.483E + 03	-0.186E + 03	-0.813E + 02*
(3) Bacteria on benthic POC	-0.174E + 04	-0.761E + 03*	-0.268E + 04
(4) Benthic diatoms	-0.536E + 03	-0.222E + 03*	-0.223E + 03
(5) Free bacteria	-0.591E + 03	-0.266E + 03	-0.191E + 03*
(6) Heterotrophic microflagellates	-0.433E + 04	-0.207E + 04*	-0.265E + 04
(7) Ciliates	-0.862E + 03	-0.350E + 03*	-0.381E + 03
(8) Mesozooplankton	-0.596E + 03	-0.133E + 03*	-0.259E + 03
(9) Ctenophores	-0.114E + 04	-0.472E + 03*	-0.133E + 04
(10) Sea nettle	-0.169E + 04	-0.198E + 03*	-0.743E + 03
(11) Lumped benthic suspended feeders	0.300E + 03	0.319E + 03 *	0.301E + 03
(12) Mya arenaria (clam)	0.267E + 03	0.306E + 03 *	0.273E + 03
(13) Oysters	0.327E + 03	0.330E + 03 *	0.327E + 03
(14) Lumped polychaete worms	0.114E + 03	0.285E + 03*	0.985E + 02
(15) Nereis sp.	-0.298E + 02	0.235E + 03 *	-0.179E + 03
(16) Macoma spp.	0.291E + 03	0.315E + 03 *	0.269E + 03
(17) Meiofauna	0.555E + 02	0.943E + 01	0.852E + 02*
(18) Crustacean deposit feeders	0.238E + 03	0.256E + 03	0.263E + 03*
(19) Blue crab	0.288E + 03*	0.262E + 03	0.265E + 03
(20) Fish larvae	0.239E + 03	0.260E + 03	0.315E + 03*
(21) Alewife and Herring	0.295E + 03	0.309E + 03	0.330E + 03*
(22) Bay anchovy	0.280E + 03	0.309E + 03	0.329E + 03*
(23) Menhaden	0.316E + 03	0.323E + 03	0.338E + 03*
(24) Shad	0.317E + 03	0.323E + 03	0.335E + 03*
(25) Croaker	0.325E + 03	0.326E + 03	0.335E + 03*
(26) Hogchoker	0.323E + 03	0.327E + 03	0.335E + 03*
(27) Spot	0.318E + 03	0.323E + 03	0.334E + 03*
(28) White perch	0.331E + 03	0.323E + 03	0.335E + 03 *
(29) Catfish	0.325E + 03	0.329E + 03	0.336E + 03*
(30) Bluefish	0.329E + 03	0.318E + 03	0.337E + 03 *
(31) Weakfish	0.311E + 03	0.288E + 03	0.332E + 03*
(32) Summer flounder	0.330E + 03	0.318E + 03	0.337E + 03 *
(33) Striped bass	0.327E + 03	0.321E + 03	0.338E + 03*

Slowest throughput, or limiting element for each compartment, is followed by an asterisk.

held that the mesohaline Chesapeake ecosystem behaves during most of the year (and especially during summer) as a nitrogen-limited system. Indeed, we see in Table 1 that the phytoplankton (component 1) and the benthic algae (#4) both are nitrogen limited over the course of a year. One might expect, then, that all heterotrophic components of the system would likewise be controlled by nitrogen. Obviously, this is not the case!

Perhaps the most noticeable pattern in Table 1 is that *all* the nekton compartments appear to be limited by phosphorous. The possibility that this result is due to a systematic error in our method of estimating the flows cannot be discounted; however, there could also be a physiological reason behind these limitations. The nekton are all vertebrate species and thus demand considerable P for the growth of bones. Most of the P assimilated into skeletal tissue is not recycled until the animal dies. (The reader should not be misled by the apparent uniformity in the magnitudes of the nekton sensitivity coefficients. This is only because the throughput rates for all elements are quite small with respect to the overall system throughput [ca. 170.7 yr⁻¹]. Among themselves the nektonic throughput rates vary significantly.)

The two planktonic bacterial components (#'s 2 and 5) are also P-limited. Possibly this is because the demand for P by these microorganisms is great, given the proportionately large stocks of ATP and DNA found in most bacteria. In contrast, the bacteria



Fig. 2. Control-linkage schematic of nutrient controls in the Chesapeake mesohaline ecosystem during summer. Compartments and flows controlled by nitrogen are indicated by solid lines; those controlled by phosphorous by short dotted line $(\cdots \cdot)$; those by carbon by long dotted lines (----).

in the sediments (#3) are in close proximity to copious phosphorous, where reduced N seems in short supply to most benthic organisms. Why the meiofauna (#17) and crustacean deposit feeders (#18) should be P-limited remains unknown. Likewise, it is not apparent why the blue crab seems to be limited by carbon (or equivalently, energy).

This overall pattern of limitations prevails throughout all seasons with very few exceptions: During the autumn the phytoplankton (#1), ctenophores (#9) and oysters (#13) suddenly become carbon limited. This is reasonable, because falling temperatures during autumn limit primary productivity, causing carbon and energy to become short in supply. Benthic algae (#4) switch from N to P limitation during summer and oysters (#13) do the same in winter, but in both cases control by either element is marginal during all seasons. Finally, the crustacean deposit feeders (#18) join most of the other benthic species in becoming N-limited during the summer.

5. Kinetic considerations

Given the relative stability in the pattern of compartmental nutrient limitations, one might expect the network of 'system limiting flows' (Eq. (7)) would likewise be the same throughout the seasons. Such is not the case. For the purpose of this analysis we define the 'controlling link' into each compartment to be that flow of the limiting element into the node for which the system organization as a whole is most sensitive. For example, nitrogen is the limiting ele-



Fig. 3. Control-linkage schematic of nutrient controls in the Chesapeake mesohaline ecosystem during fall. Compartments and flows controlled by nitrogen are indicated by solid lines; those controlled by phosphorous by short dotted line $(\cdots \cdots)$; those by carbon by long dotted lines (----).

ment for the zooplankton (#8). According to Eq. (7), of all the flows of nitrogen into 8, the ascendency is most sensitive to the flow from the microzooplankton (#7). Now it happens that (#7) is not the source of the most nitrogen to the zooplankton! That distinction belongs to the phytoplankton (#1). If we were concerned only with the dynamics of zooplankton, we would give most attention to the phytoplankton. But our focus here is on the status and behavior of the system as a whole, so in that regard the nitrogen flowing from the microzooplankton (#7) to the mesozooplankton (#8) weighs more importantly on overall system dynamics than does the grazing of phytoplankton by the mesozooplankton.

Having thus defined the controlling transfer into each compartment, we now link the nodes together using the controlling flows. The topology of the resulting network should be most helpful in tracing down the primary nutrient controls for the system. The 'control linkage' diagrams for each season are portrayed in Figs. 2–5. One sees these networks are mostly tree-like in nature. That is, beginning at any of the higher trophic level components on the termini of the branches, one may trace back in linear fashion through controls at successively lower levels. It is surprising, therefore, that in only one season (autumn, Fig. 3) do these control sequences culminate in exogenous inputs. Rather, the 'origin' or 'root' of the control linkages during the other three seasons is a loop of transfers feeding back upon itself.

The picture is probably simplest during the summer, when nitrogen is regarded to be short in supply. During that season all the control sequences funnel back to a feedback loop between particulate nitrogen in the sediments (#36) and the attached bacteria (#3). That is, during summer the recycle of nitrogen



Fig. 4. Control-linkage schematic of nutrient controls in the Chesapeake mesohaline ecosystem during winter. Compartments and flows controlled by nitrogen are indicated by solid lines; those controlled by phosphorous by short dotted line (\cdots) ; those by carbon by long dotted lines (----).



Fig. 5. Control-linkage schematic of nutrient controls in the Chesapeake mesohaline ecosystem during spring. Compartments and flows controlled by nitrogen are indicated by solid lines; those controlled by phosphorous by short dotted line $(\cdots \cdots)$; those by carbon by long dotted lines (----).

by sediment bacteria appears to play the central role in structuring the community. (Although NH_4 may be plentiful in the sediments, organisms there may still be limited by the availability of reduced nitrogen.)

Accompanying the declining temperatures of autumn is a decrease in almost all metabolic demands. The control linkage diagram during this season becomes tripartite, with each 'tree' originating from an exogenous source. Two of the trees are rudimentary. That the input of carbon appears to control the phytoplankton is simply another way of saying that primary production by this compartment has fallen. Benthic primary production becomes sensitive to the external supply of allochthonous nitrogen. At the root of by far the largest tree is the input of dissolved phosphorous. Whereas the community during the summer appears to be structured around the reuse of nitrogen in the sediments, we conclude that the kinetics of the fall ecosystem are driven more by external agencies—declining energy from primary production and the disappearance of phosphorous as more oxygen pervades the water column.

Internal nutrient controls reappear during the winter time, and the new pattern seems to persist into the spring season. The focus of control now becomes the populations of the 'microbial loop'. As mentioned above, the microbial loop does not participate in the recycle of carbon. Furthermore, its role in the recycle of nitrogen and phosphorous is more as a conduit for these elements along cycles that are completed by benthic and nektonic components. It is not until we have expanded the scope of our observation to include the simultaneous transfers of N and P that the intrinsic feedback nature of the microbial loop 'emerges' in an epistemic sense (Ulanowicz, 1990).

At the root of the winter and spring control linkage diagrams sits the three-membered cycle, dissolved organic phosphorous (#34)—free bacteria (#5)—heterotrophic microflagellates (#6). Control in two of the three linkages and components is exerted by phosphorous. The dissolved phosphorous pool is most sensitive to excretion of P by the microflagellates. The free bacteria in their turn are limited by phosphorous, all of which they obtain from the dissolved phase. The third participant in the feedback scenario (#6) is not limited by P. Rather, nitrogen is presented to the microflagellates in least relative measure, and they receive all their N from the free bacteria. The phosphorous that the flagellates ingest along with their bacterial prev is somewhat in excess of what they incorporate. The remainder is released to fertilize the growth of their prev. The result is a mutualistic co-dependency that involves two elements. The pelagic microbial community in the ecosystem of (shallow) Chesapeake Bay does not function to retain either N or P alone. Rather, the microbiota link together in intricate fashion to maintain adequate proportions of both essential elements in circulation

6. Summary and concluding remarks

The concepts heretofore used in ecology to address nutrient kinetics were fashioned around single populations. It is presumptuous to think that these tools can be extrapolated to entire ecosystems, heterogeneous as these larger entities are in both composition and behavior. In order to assess the role of chemical nutrients in complex ecosystems, it becomes necessary first to quantify adequately the status of the system as a whole.

The notion of system ascendency, which derives from information theory applied to trophic transfers, appears to provide a system measure that is both useful as well as theoretically illuminating. In studying how this whole-system attribute responds to changes in its component species and chemical constituents, we retrieve certain facets of single population nutrient dynamics, such as Liebig's law of the minimum, as deductive corollaries. But perhaps more importantly, ascendency, a concept of wide and diverse application, provides us with new insights into nutrient dynamics, that would have remained obscure had we confined our analysis to single populations in their turn.

When the ascendency of the Chesapeake ecosystem was analyzed, some results were as expected, whereas others offered new insights into how the community is functioning. As regards the former, it is commonly held that nitrogen limits system production during summertime. Baird et al. (1995) had intimated that the most crucial process during this season might be the remineralization of N by sediment bacteria when they pointed out how release of N from sediment accounts for almost half of all nitrogen provided at that time (secondary sources being water column regeneration and exogenous inputs). The largest amount of sediment remineralization is accomplished by the resident bacteria (#3).

During the other three seasons exogenous inputs of dissolved nutrients are relatively much greater. One expects, therefore, that such inputs would be at the apex of the control trees. Indeed, during autumn they are (all three of them!), but fall is an anomalous season when the ecosystem itself is more in collapse than in control. Internal control returns during the winter and spring seasons, but in a very interesting form.

To the best of our knowledge, feedback loops with dual nutrient controls do not appear in the ecological literature. Although unexpected, such a scenario makes sense in hindsight. Balanced growth has always been an indication of health in organisms. Although ecosystems are *not* organisms, they do exhibit some degree of internal control. A feedback control loop that enmeshes both essential macronutrients could be the vehicle by which balanced metabolism is maintained by the system as a whole.

Heretofore, data on several nutrients as they appear in a full compliment of ecosystem components have been exceedingly scarce. Such information is now available for the Chesapeake ecosystem, however, making it possible to regard nutrient dynamics from a new, broader perspective. Some of the phenomena we have inferred are bound to seem unfamiliar when viewed from the conventional frame of reference. We submit them, nevertheless, in the hope of stimulating (or provoking!) others to test these ideas and methods on their ecosystem of choice. It is our opinion that ecology can only be enriched by the

continuing dialogue on research at the level of the whole ecosystem.

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Appendix A

We wish to demonstrate that the element in foodstuff that is presented in least proportion is always the one with the slowest compartmental turnover rate. This will allow one to ascertain the Liebig (1840) limiting element from information comparing nutrient turnover rates.

As in the body of the paper, we let T_{ijk} be the amount of element k flowing from component i to component j. A dot in place of one of the subscripts indicates that it has been summed. Hence, $T_{.jk}$ (= $\sum_i T_{ijk}$) is the sum of all inputs of element k into species j.

We begin by considering the hypothetical situation of ideally balanced growth (production). We assumed that the proportions of chemical elements in the biomass of a living population are constant. In perfectly balanced growth, the elements are presented to the population in exactly the proportions that are assimilated into the biomass. This can be stated in quantitative fashion: For any arbitrary combination of foodstuff elements, p and q, used by compartment j,

$$\frac{T_{:jp}*}{T_{:jq}*} = \frac{B_{jp}}{B_{jq}},$$
(A.1)

where an asterisk is used to indicate a flow associated with balanced growth.

Now we suppose that one and only one element, say p without loss of generality, enters j in excess

of the proportion needed. That is, $T_{.jp} = T_{.jp} * + e_p$, where e_p represents the excess amount of p presented to j. Under these conditions we have the inequality

$$\frac{T_{.jp} * + e_p}{T_{.jq} *} > \frac{B_{jp}}{B_{jq}}.$$
 (A.2)

Multiplying both sides of inequality (A.2) by the ratio $(T_{ia} * / B_{ip})$ yields

$$\frac{T_{\cdot jp} * + e_p}{B_{jp}} > \frac{T_{\cdot jq} *}{B_{jq}}$$
(A.3)

In words, inequality (A.3) says that the input rate of p into j is greater (faster) than that of any other element by the 'stoichiometric' amount e_p/B_{jp} . Over a long enough interval, inputs and outputs must balance, and so we can speak about the input rate and throughput rate as being one and the same. (This does not weaken our argument, as there is an implied steady-state assumption in the Liebig statement as well.)

Now we suppose that only two of the elements flowing into *j* are supplied in excess. Again, without loss of generality, we call the second element *q*. It is immediately apparent that if $e_p/B_{jp} > e_q/B_{jq}$, then the throughput rate of *p* exceeds that of *q*, and vice-versa. That is, a slower throughput rate indicates that one is closer to stoichiometric proportions.

This last result can be generalized by mathematical induction to conclude that the element having the slowest throughput rate is being presented in the least stoichiometric proportion, i.e., it is limiting in the sense of Liebig.

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